NEST-SITE SELECTION AND TEMPORAL PATTERNS IN HABITAT USE OF ROSEATE AND COMMON TERNS

JOANNA BURGER[1] AND MICHAEL GOCHFELD[2]

[1]*Department of Biological Sciences, Rutgers University, Piscataway, New Jersey 08855 USA, and*
[2]*Environmental and Community Medicine, UMDNJ–Robert Wood Johnson Medical School, Piscataway, New Jersey 08854 USA*

ABSTRACT.—Roseate Terns (*Sterna dougallii*) nest in a wide variety of habitats. We examined nest-site selection in a mixed-species colony of Roseate and Common (*S. hirundo*) terns on the interdune area of a barrier beach to determine species differences, to identify which characteristics at nest sites differed from the available habitat, and to compare nest-site preferences of early- and late-nesting Roseate Terns. Both species nested in the same area, but Roseate Terns nested under dense vegetation and Common Terns nested in more open sites. For Roseate Terns, cover within 0.5 m of the nest was greater than that within 1 m; the opposite was true for Common Terns. Cover within 5 m was similar for both species. Roseate and Common terns select different habitat features. Site characteristics of early- and late-nesting Roseate Tern nests differed. Late-nesting terns used sites with greater cover within 0.5 m, less cover within 5 m, taller vegetation, and with less visibility compared with early-nesting terns. Late-nesting Roseate Terns were still able to find sites in dense cover. At this colony, competition between the two species may not be limiting, and abundant sites remain available. *Received 23 October 1987, accepted 30 January 1988.*

HABITAT selection affects reproductive fitness and survival during all phases of the life cycle of animals. For birds, habitat selection during the breeding season is important because species are confined to the nest site during incubation and the chick period, except for species with precocial young (reviewed by Burger 1980, 1985). Thus, nest-site selection is a decision a pair must live with for several weeks or months if their breeding attempt is to be successful. Variations in available habitat make selection possible (Partridge 1978) and allow partitioning among species (Cody 1985). Competition for nest sites might be intense in mixed-species colonies where species nest in close proximity, leading to a clear separation of site preferences. Often the species in such colonies vary markedly in size, and in direct competition for space the larger species usually wins (Schoener 1974). Temporal differences affect nest-site choices; early-nesting species may have clearly established sites before the second species arrives (Burger 1983).

We previously described the nest-site characteristics of Common and Roseate terns (*Sterna hirundo* and *S. dougallii*) in a New York sand beach colony, but did not compare nest sites with available habitat or examine temporal differences in nest-site choices (Gochfeld and Burger 1988). In this study we compared nests of Roseate and Common terns intermixed in the same parts of a large colony, compared nest sites with available habitat, and examined differences in nest-site choices of early- and late-nesting Roseate Terns. The colony provided an opportunity to study nest-site selection and resource partitioning because the two tern species are similar in size, arrive at the colony at about the same time, have similar breeding phenologies, and have similar-size eggs, nests, and young.

The Roseate Tern breeds on all continents except Antarctica, but populations are disjunct. Its center of abundance is in tropical latitudes (Nisbet 1980, Gochfeld 1983). It has declined dramatically in North America (Buckley and Buckley 1981) and Europe, and was listed in 1987 as an endangered species in the United States. Understanding its nest-site requirements is thus important, not only for information about nest-site selection, resource allocation, and spatial competition, but for an endangered species, which in the northeastern United States is restricted to very few colonies (Nisbet *in* Kress et al. 1983).

METHODS

We studied Roseate and Common terns at Cedar Beach, 65 km east of New York City, Suffolk Co., New

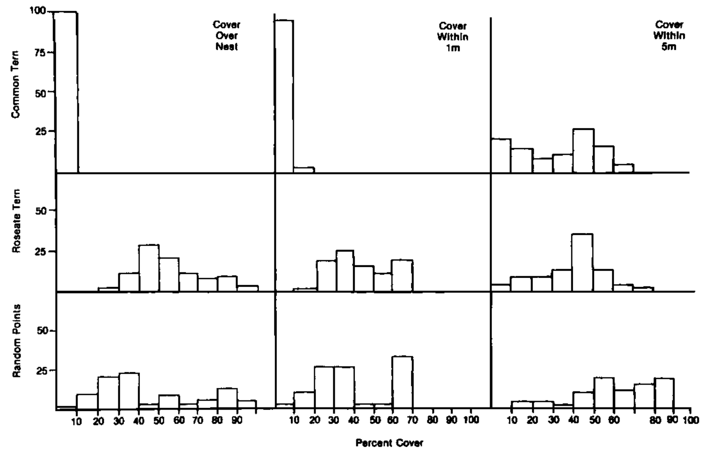

Fig. 1. Comparison of cover above the nest and within 1- and 5-m radii of nests for early-nesting Roseate and Common terns and for random points.

York. The colony is located on a barrier beach in the interdune area between artificially stabilized dunes (Gochfeld 1976). The colony ranges from 30 to 180 m wide and is about 1,000 m in length. In 1987 there were more than 7,000 breeding pairs of Common Terns, 125 pairs of Roseate Terns, and 200 pairs of Black Skimmers (*Rynchops niger*). Most of the Roseate Terns nested in four discrete groups of 7-40 nests. The quadrats containing Roseate Tern nests also contained Common Tern nests. The great majority of both species nest in May to mid-June, with a smaller late wave in late June to early July. The late wave includes birds that renest after failures and young birds that nest for the first time (Austin 1933, Gochfeld 1976, DiCostanzo 1980).

We collected data in 1987 on all early (before 10 June) and late (3-17 July) Roseate Tern nests. During the early wave we studied Common Tern nests that were located within the Roseate Tern nesting area. Site characteristics were measured for 51 nests each of Common and Roseate terns in June, for 33 late-nesting Roseate Terns in July, and for 51 random points in early June and 33 in early July. The early and late samples of Roseate Terns included all nests in natural settings found during that time period. Random points were selected by a table of random numbers to locate points along a transect, the distance from the transect, and the direction from the transect. Random points were located in the area where we sampled tern nests. We used an additional 51 random points and selected the closest Common Tern nest for examination.

Characteristics recorded at nest sites and random points included: percentage cover (of any type) within a 0.5-, 1-, and 5-m radius of the site, percentage grass and nongrass vegetation (usually Seaside Goldenrod, *Solidago sempervirens*) cover within a 0.5-m radius of the nest, distance to the closest vegetation, height of the closest vegetation, visibility (from above the nest, from 1 m, and from 5 m), distance to the nearest neighboring nest, and species of nearest neighbor. Visibility was measured by walking the required distance in a direction determined from a table of random numbers, and estimating the percentage of the nest that was visible.

We compared nests with random points for both Roseate and Common terns, nests of Common Terns with nests of Roseate Terns, and nests of early- with nests of late-nesting Roseate Terns. We used Kruskal-Wallis tests to compare distributions. Values are presented as means ± 1 SE in the text and tables.

RESULTS

Early-nesting Roseate Terns.—In 1987 early-nesting Roseate Terns initiated egg laying in early June, about 5 days later than Common Terns. Roseate Terns nested mainly on the low dunes or raised areas within the interdune area, and these sections had more and larger goldenrod bushes than other sections. Roseate Tern nests averaged 33 ± 3 m from the edge of the colony.

Nest-site characteristics of the early-nesting Roseate Terns differed from those of the random points. They generally had a higher percentage of cover within 0.5 m, but lower cover within 5 m, were closer to taller vegetation, had less grass cover and more goldenrod, and were less visible from above and from 1 and 2 m (Tables 1 and 2). From the available habitat Roseate Terns selected more sites that were under goldenrod, and sites with greater cover and low visibility (Fig. 1). Early-nesting Roseate Terns had other Roseates for nearest neighbors 50%

TABLE 1. Characteristics of Roseate and Common tern nests and of random points at Cedar Beach, New York.

	Early sample[a]			Late sample[b]	
	Common tern	Roseate tern	Random	Roseate tern	Random
Number	51	51	51	33	33
Percentage cover					
Within 0.5 m	2 ± 0.3	60 ± 2	48 ± 5	71 ± 3	19 ± 7
Within 1 m	5 ± 0.6	48 ± 2	46 ± 4	56 ± 3	18 ± 4
Within 5 m	36 ± 3	42 ± 2	63 ± 3	33 ± 3	17 ± 3
Distance to vegetation (cm)	29 ± 3	0.1 ± 0.1	6 ± 2	0 ± 0	6 ± 2
Vegetation height (cm)	28 ± 2	43 ± 2	40 ± 4	50 ± 2	39 ± 4
Percentage grass cover	1.0 ± 0.2	3 ± 1	24 ± 4	0 ± 0	19 ± 6
Percentage nongrass cover	1.0 ± 0.3	59 ± 2	25 ± 5	71 ± 3	29 ± 7
Visibility					
From above	99 ± 0.02	20 ± 4	82 ± 6	10 ± 4	62 ± 11
From 1 m	99 ± 0.0	61 ± 5	85 ± 5	33 ± 8	69 ± 10
From 2 m	99 ± 0.0	63 ± 5	87 ± 4	22 ± 6	61 ± 9
Nearest-neighbor distance (cm)	123 ± 7	143 ± 9	223 ± 35	167 ± 24	239 ± 39

[a] Early June 1987.
[b] Early July 1987.

of the time, similar to the random points within the Roseate Tern nesting area.

Common Terns.—Common Terns generally nested in the lower and more open sections surrounding the places where Roseates nested. Nest-site characteristics of the early-nesting Common Terns differed from the random points. They had less cover above the nest and within 1 and 5 m, were farther from shorter vegetation, had less grass cover, and had greater visibility from above and from 1 and 2 m (Tables 1 and 2). Given the available habitat in these sections, they nested in the sparsest available spots (Fig. 1). Common Terns had Roseate Terns for nearest neighbors 33% of the time and Common Terns 67% of the time, similar to the random points (32% Roseate Terns, 68% Common Terns).

Comparison of early-nesting Roseate and Common terns.—The nest-site characteristics of Roseate and Common terns differed significantly with respect to all characteristics except percentage cover within 5 m of the nest (Table 2). The latter exception is not surprising because they nested in the same parts of the colony. Overall, Roseate Terns nested closer to taller vegetation that provided more cover and less visibility (Table 1, Fig. 1). Common Terns had significantly closer nearest neighbors than Roseate Terns (Tables 1 and 2).

Late-nesting Roseate Terns.—Late-nesting Roseate Terns nested in the same type of habitat as early-nesting Roseates. Nest site characteristics differed from the late random points. They had more cover within 0.5, 1 and 5 m around the nest, were closer to taller vegetation, with more goldenrod and no grass, and had less visibility from above and from 1 and 2 m (Tables 1 and 2). The late birds also selected sites with a high percentage of cover (and low visibility; Fig. 1). Late-nesting Roseate Terns had other Roseate Terns for nearest neighbors 80% of the time, which differed significantly from the random points ($\chi^2 = 5.2$, df = 1, $P < 0.05$) and from early-nesting Roseate Terns ($\chi^2 = 4.9$, df = 1, $P < 0.05$).

Comparison of early and late Roseate Terns.—Nest sites of late-nesting Roseate Terns had significantly more cover above and less cover within 5 m, taller nearest vegetation, and less visibility from 1 and 2 m (but similar visibility from above; Tables 1 and 2) than early-nesting Roseate Tern nests. Thus, both groups nested under goldenrod with low visibility from above, but late-nesting Roseate Tern nests and eggs were less visible from 1 and 2 m. Nearest-neighbor distances did not differ.

These differences might reflect changing preferences, decreases in availability of optimal sites, or changes in vegetation. To address this question we compared the early and late random points (Tables 1 and 2). The available habitat, as illustrated by the random points, differed significantly with respect to percentage cover and visibility, but not with respect to percentage of grass compared with goldenrod, vegetation height, and distance to vegetation. This

TABLE 2. Comparison of site characteristics of early nests of Roseate and Common terns, early vs. late nests of Roseate Terns, and nests vs. random points for nests of Common and Roseate terns. Given are Kruskal-Wallis χ^2 values and levels of significance (P-values in parentheses; NS = not significant).

Characteristic	Nests vs. random points			Nest sites		
	Common Tern	Early Roseate Tern	Late Roseate Tern	Common vs. Roseate tern	Early vs. late Roseate Tern	Early vs. late random points
Percentage cover						
Above nest	55.7 (0.0001)	7.88 (0.005)	20.33 (0.0001)	76.88 (0.0001)	11.61 (0.002)	14.01 (0.0002)
Within 1 m	54.38 (0.0001)	0.76 (NS)	25.01 (0.0001)	76.28 (0.0001)	2.35 (NS)	18.05 (0.0001)
Within 5 m	24.52 (0.0001)	19.57 (0.0001)	12.33 (0.0004)	1.88 (NS)	10.23 (0.002)	32.28 (0.0001)
Percentage grass cover	45.59 (0.0001)	32.22 (0.0001)	10.82 (0.001)	5.22 (0.02)	1.32 (NS)	0.41 (NS)
Percentage nongrass cover	48.21 (0.0001)	11.02 (0.01)	56.2 (0.0001)	77.65 (0.0001)	62.21 (0.0001)	0.68 (NS)
Distance to vegetation	32.08 (0.0001)	31.25 (0.0001)	44.96 (0.0001)	85.94 (0.0001)	0.65 (NS)	17.31 (0.0001)
Vegetation height	5.79 (0.02)	0.39 (NS)	4.62 (0.03)	25.52 (0.0001)	7.27 (0.01)	0.01 (NS)
Visibility						
From above	26.40 (0.0001)	37.83 (0.0001)	14.84 (0.0001)	81.97 (0.0001)	0.61 (NS)	0.30 (NS)
From 1 m	22.00 (0.0001)	14.07 (0.0002)	6.74 (0.009)	66.97 (0.0001)	5.43 (0.02)	0.23 (NS)
From 2 m	22.0 (0.0001)	11.45 (0.0007)	5.01 (0.05)	55.96 (0.0001)	15.50 (0.001)	37.44 (0.0001)
Nearest-neighbor distance (cm)	5.67 (0.02)	1.77 (NS)	3.04 (0.08)	4.95 (0.02)	0.06 (NS)	0.19 (NS)

indicates that the individual plants were becoming broader and bushier, rather than growing taller, and that increased cover was not due to new plants.

DISCUSSION

Nest-site selection in Roseate Terns.—In northeastern North America, Roseate Terns nest on moderately to heavily vegetated sites, and Nisbet (1981) estimated that 80% vegetation cover is optimum. We estimated cover in the Roseate Tern sections of Cedar Beach at 20–45%. Early- and late-nesting Roseate Terns chose nest sites that differed from the available habitat (Tables 1 and 2), and they selected sites that provided cover and low visibility. Cover could be advantageous because it provides protection from inclement weather or heat stress (Austin 1933), as well as protection from predators (Veen 1977, Richards and Morris 1984) and reduced aggression from Common Terns. Low visibility from above reduces the probability of aerial predation, and low visibility from 1 and 2 m to the side reduces the probability of ground predation. At Cedar Beach in 1987 approximately 3 Herring Gulls (*Larus argentatus*) patrolled the interdune area and were observed to take tern eggs or chicks daily. Further, we have observed Northern Harriers (*Circus cyaneus*) taking chicks. Although terns mob both species, the relatively large size of the predators results in their continuing to search the colony.

We previously reported that Roseate Terns nested under goldenrod, but we did not examine quantitatively the available habitat, nor compare early and late nests (Gochfeld and Burger 1988). In the three years of data discussed, visibility from above was greater (19–50% of nests with visibilities greater than 30%) for Roseate Terns than reported here. This difference may be due to the late phenology of 1987, the low level of goldenrod defoliation by the chrysomelid beetle *Trirhabda canadensis* in 1987, or varying preferences. Roseate Terns nested 1–2 weeks later in 1987 than in other years, but goldenrod growth and defoliation phenology were similar. Predation rates by both Herring Gulls and Northern Harriers have increased steadily over the years, however. In 1987 a Herring Gull pair that nested at the edge of the colony specialized on Common Tern eggs and chicks, bringing them back to feed their chicks. Because the Herring Gull had eggs when the terns arrived to nest, terns might have chosen less visible nests in response to this predation threat. In 1987 all Roseate Terns nested within 10 cm of vegetation or under other cover, whereas in the other years as many as 8% did not (Gochfeld and Burger 1988).

Early- and late-nesting Roseate Terns.—Nest-site characteristics of early- and late-nesting birds might be expected to differ if (1) all optimal sites are taken and late-nesting birds are forced to use suboptimal sites, (2) the habitat changes in the interim, or (3) changes in the environment (such as increased temperatures) result in shifts in preferences.

We reject the possibility that optimal sites are unavailable because late-nesting Roseate Terns nested under goldenrod, and sufficient goldenrod was available so they could select larger ones that provided more cover. Also, both groups exhibited similar nearest-neighbor distances, certainly not indicative of increased crowding.

We found that early and late nest sites differed significantly with respect to cover above the nest and within 5 m, vegetation height, and visibility from 1 and 2 m (but not from above). During this time the available habitat, as measured by random points, also differed in all measures of percentage cover and of visibility. Thus, the habitat changed during the observation period. The later random points had less ground cover, while late-nesting Roseate Terns nested on spots with more cover than early-nesting Roseate Terns. On the contrary, the later random points had lower visibility, and the late-nesting Roseate Terns also had lower visibility than early-nesting terns. Although the vegetation available to late-nesting terns was not taller, the late terns selected taller vegetation than early-nesting terns. These results suggest that although the vegetation was less dense (lower cover), the Roseate Terns placed their nests farther under the vegetation, making their eggs less visible from all angles. We believe that the vegetation was filling in, and the terns were selecting sites with greater cover. Because they could have placed their nests farther from the stem of goldenrod, they could have achieved cover values similar to early-nesting terns.

In other northeastern United States colonies, Roseate Terns nest in the open (Spendelow pers. comm.), under rocks (Great Gull Island; H. Hays pers. comm.), or in sparse vegetation (Nisbet 1981, Spendelow 1982, Gochfeld 1983). Indeed, at Falkner Island they nest in all these types (Spendelow pers. comm.). They may nest in the open where they are exposed to fewer predators or aggressive competitors, but this idea requires testing in other colonies.

Nest-site comparisons of Roseate and Common terns.—The phenologies of the two tern species are similar; Roseate Terns nest about 5 days later than Common Terns (see also Nisbet and Drury 1972). The difference is not sufficient to expect significant changes in the vegetation of a colony. We found that Roseate and Common tern nest-site characteristics differed significantly with respect to percentage cover, vegetation height, distance to nearest vegetation, visibility, and nearest-neighbor distance. Common Terns arrive and nest earlier than Roseate Terns (and so have first access to sites), and Common Terns are slightly larger than Roseates (and so presumably would win interspecific encounters; Schoener 1974). Further, earlier-nesting Common Terns did not nest under goldenrod. If Common Terns preferred sites with low visibility, they could have used them. Interspecific competition for concealed sites does not seem to occur. Conversely, there are abundant open spaces at Cedar Beach with space remaining to accommodate the 125 pairs of Roseate Terns at open sites. If there were competition for limited nest sites, late-nesting Roseate Terns should be forced into suboptimal sites, but both early- and late-nesting Roseates nest under dense goldenrod that provides concealment.

The species difference in nest-site selection may relate to nest defense strategies. In North America and Europe Roseate Terns nest in Common Tern colonies (Marples and Marples 1934, Cramp et al. 1974, Nisbet 1981). In the Cedar Beach colony Roseate Terns are far less aggressive in defense of their nests than are Common Terns (unpubl. data). Common Terns at Cedar Beach engage in frequent dive bombing and aerial attacks, sometimes hitting humans and other predators, which effectively deters some predators; Roseate Terns are far less aggressive, dive fewer times, and never hit intruders. Further, Common Terns give alarm calls when predators enter the colony, providing early warnings to Roseate Terns nesting under dense vegetation (Burger and Gochfeld unpubl. data). The Roseate Terns may derive antipredator benefits from the Common Terns (Nuechterlein 1981, Burger 1984), but, with their lower levels of defense, they may rely more on having concealed nests than do Common Terns.

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