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NEST-SITE SELECTION BY ROSEATE TERNS AND COMMON TERNS IN THE AZORES

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ABSTRACT.—Nest-site characteristics of Roseate Terns (*Sterna dougallii*) and Common Terns (*S. hirundo*) in mixed and unmixed colonies were examined at a number of sites in the Azores archipelago using discriminant analysis. Colonies were stratified and points located in a systematic way. Physical parameters, nearest-neighbor distance, vegetation cover, and density of nests were measured. Measured nest-site parameters were compared between species and with habitat points selected in the colony. Significant interspecific differences in nesting sites were found. Roseate Terns nested in areas with high relief and/or tall vegetation and with higher nesting densities. Common Terns selected more-open areas. There was considerable variability in nest-site selection of both tern species among colonies. Roseate Terns were more specialized as their nest sites differed more significantly than those of Common Terns from the available habitats. In contrast to findings of studies in North America, nest concealment by Roseate Terns did not influence hatching success. Competition may be important in nest resource partitioning in individual mixed colonies depending on colony size and habitat structure. The need to maintain/create optimal nesting areas for Roseate Terns is stressed. As habitat descriminators varied greatly between colonies, management should be planned on a colony-by-colony basis. *Received 15 March 1994, accepted 15 May 1994.*

A GIVEN SPECIES will occur in a variety of habitats or ecological conditions. The choice of the breeding site or habitat is likely to be adaptive as it may have a pronounced influence upon reproductive success and survival (Birkhead et al. 1985). Habitat preferences exist as a consequence of variation in quality of available habitat and have been demonstrated in many species (Partridge 1978).

Avian habitat relationships can be addressed by several different approaches (see Rice et al. 1983). Two approaches are used in our work: (1) discrimination between used and available habitat characteristics; and (2) between-species discriminant analysis of the habitat characteristics of two species. This latter approach contributes to investigate resource partitioning in mixed colonies of Roseate Terns (*Sterna dougallii*) and Common Terns (*S. hirundo*), the main subjects of our study. Previous studies showed that Common Terns prefer relatively open areas while Roseate Terns prefer sheltered areas (Langham 1974, Richards and Morris 1984). Common Terns are slightly larger and more agressive than Roseate Terns (Cramp 1985, Burger and Gochfeld 1988b), and interspecific competition may occur in mixed colonies. In smaller colony sites, Roseate Terns may nest in areas with substantial open ground and compete with Common Terns for available nest sites (Spendelow 1982).

The aim of our work was to elucidate the nest-site preferences of Roseate and Common terns in the Azores archipelago. Discriminant analysis was used to differentiate between nest sites and available habitat both within and between species. The Roseate Tern has a patchily tropical and temperate breeding distribution. The Atlantic race, *S. d. dougallii,* has declined dramatically on both sides of the Atlantic and is now considered threatened or endangered (Gochfeld 1983). The total European population is currently estimated at about 1,600 pairs (del Nevo et al. 1994) of which about 1,050 pairs (66%) breed in the Azores. An understanding of nest-site characteristics for both Roseate and Common terns may form the basis of future conservation measures, allowing the protection of some "preferred" habitats and the artificial construction of others.

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TABLE 1. Site variables recorded for nest sites and habitat points.

Site variable	Description
1 Walls	Number of walls around nest (0–4).
2 Overhang	(0) None; (0.5) partial; (1) complete.
3 Substrate	(0) Soft (soil, vegetation or mixed); (1) hard (bare rock).
4 Slope	Maximum slope within 2-m section around nest: (1) <5°; (2) 6-20°; (3) 21-60°; (4) 61-89°; (5) cliff.
5 Vegetation type	(0) Not grass; (1) grass.
6 Vegetation distance	Distance to nearest vegetation (cm).
7 Vegetation height	Height of nearest vegetation (cm).
8 Cover within 0.5 m	Vegetation cover within 0.5 m of nest (%).
9 Cover within 3 m	Vegetation cover within 3 m of nest (%).
10 Visibility from above	Nest site visible from above (%).
11 Neighbor distance	Distance to nearest neighbor (cm).
12 Neighbor number	Number of neighbors within 2 m.
13 Position	Position in colony: (0) edge; (1) center.

STUDY AREA AND METHODS

The Azores archipelago (36°55'N–39°43'N, 25–31°30'W), which is 1,400 km from the Portugese mainland, consists of nine main islands and has a temperate oceanic climate. One hundred and seven tern colonies were found in the Azores (del Nevo et al. 1994); 20 were mixed (Roseate and Common terns) and 87 were unmixed (Common Terns). Detailed nest-site characteristics were measured in a variety of habitat types: (1)100% bare rock islets (TER4); (2) moderately vegetated rocky islets (FLW55, FLW60, PIX4, PIX11, GRW5, SMA13); (3) heavily vegetated rochy islets with soil (FLW54, FLW56, FLW57); (4) loose lava with gravel and soil (GRW1); (5) mainland boulder beaches (GRW8); and (6) bare rock-slope areas (HOR1). Mixed colonies were FLW55, FLW56, FLW60, PIX4, TER4, GRW1, and SMA13. The locations and detailed descriptions of colony sites were given by del Nevo et al. (1990, 1994). In 1990, colonies held from 2 to 216 Roseate Tern breeding pairs and 2 to 326 Common Tern breeding pairs. Most terns laid eggs between early May and mid-June. Late-nesting birds were recorded on colony SMA13 in mid-July; other colonies were not visited at this time.

Fieldwork was conducted from 15 May until 15 July 1990. At each colony, we knew the number of breeding pairs and the seasonal status of individual nesting sites. Shortly after peak egg laying, a sample of nest sites was selected in each colony for detailed measurements. For small colonies (<20 pairs), data were obtained from all nest sites. Larger colonies were sampled using a stratified procedure; colony sites were approximately rectangular and were divided in two, three, or four areas according to their size. Two transects were made along the diagonals of each area; 12 to 35 points were distributed along each transect at regular intervals—240 or 120 cm, depending on the size of the colony. Site characteristics were recorded for these habitat points within the Roseate and Common tern nesting areas. Generally, Common Terns nested around a Roseate Tern subcolony. Habitat points were located in larger colony sites: FLW55, FLW60, FLW57, PIX4, TER4, GRW1, and SMA13. At colony-site FLW60 habitat points were located within the Roseate Tern nesting area only. Nest-site characteristics were recorded for the closest tern nest to these habitat points within the main nesting areas of both tern species. Data were collected from 181 habitat points, 182 Roseate Tern nests, 145 Common Tern nests in mixed colonies and 123 nests in unmixed colonies, and 15 nests of late-nesting Roseate Terns at colony SMA13.

For each nest-site and habitat point, 13 variables were recorded (Table 1). Linear discriminant analysis (DA) was used to differentiate between nest sites of Roseate and Common terns, and to contrast nest sites from habitat points of the area where we sampled tern nests. This technique compares the between-group to the within-group variation and establishes optimal separation of groups based on linear transformation of the independent variables (Green 1971, Gauch 1982). The Fortran programs DISCRIM and CANVAR (courtesy of B. Huntley) were used for these two procedures.

Discriminant analyses using site characteristics were performed on individual colony data and, for an investigation of overall habitat differentiation, on pooled colony data. Analyses were performed using transformed data. Arcsine transformation was employed on percentage variables, a logarithmic transformation on other continuous variables, and a square-root transformation on counts (Sokal and Rolhf 1969) so as to bring skewed distributions to normality. The percentage of scores classified correctly into their respective group was used to indicate the effectiveness of the DA (Clark et al. 1983, Rice et al. 1983). Used in this way, DA is a data exploratory tool for which statistical assumptions (see Green 1971 and Williams 1983) are less restrictive. Overall statistical significance between DA paired groups was based on an ANOVA using the discriminant scores as the dependent variable and the two group variables as the independent variables (Norusis 1988).

Three main hyphotheses were examined with DA: (1) Do Roseate and Common terns exhibit nest-site selection? The comparison of characteristics of Roseate Tern and Common Tern nest sites against those of habitat points tested the null hypothesis that sites chosen for nesting did not differ from available potential "nest sites." (2) Do Roseate Terns differ from Common Terns in the features they select when choosing a nest site? By examining overlap of nests of the two species along the discriminant function and the contribution of each important variable to that discriminant function, we determined which species showed a higher degree of habitat selectivity. (3) Do nest-site characteristics of Common Terns in mixed colonies differ from those in unmixed colonies?

Hatching success was calculated from every marked nest with a known outcome for both tern species in mixed colonies. Overhanging rocks, holes, and burrows provide cover and may result in higher hatching success for Roseate Terns, thus explaining the reason for nest concealment in this species (Burger and Gochfeld 1988a, Spendelow 1982). To investigate such patterns, every nest site with a partial and total overhang was recorded and, at colony SMA13, nest sites were divided into four categories: total overhang, partial overhang, closer to rocks but with no overhang, and closer to vegetation. Hatching success was compared among these categories of nest sites using a chi-square analysis.

RESULTS

Roseate Tern nest sites and habitat points.—Nest-site characteristics differed from those of habitat points for each individual colony (Fig. 1) and for pooled colony data (ANOVA of DA, $F = 21.1$, df = 13 and 265, $P < 0.001$). The percentage of Roseate Tern nests classified correctly was 88.5% (Fig. 2). From the available habitat, Roseate Terns selected more sites than expected by chance that were surrounded by walls, had more neighbors within 2 m, and were less visible from above (Table 2). Overall, these variables were consistently of greater importance to discriminate between nest sites and habitat points; however, considerable variation existed among individual colonies (Fig. 1). By integrating the action of several variables (e.g. walls, cover and overhang), visibility from above appears to be of considerable importance to characterize Roseate Tern nest-site selection.

In pooled colony data, cover within 0.5 m was highly correlated with cover within 3 m ($r = 0.91$, $P < 0.001$), indicating that the effect of cover on nesting Roseate Terns can be evaluated using the variable cover up to 0.5 m. In colony FLW60, Roseate Terns selected to nest in places where grass was the nearest vegetation (Fig. 1). In that colony, this grass was taller than other plant types.

Common Tern nest sites and habitat points.—Overall, the discriminant analysis differentiated significantly between Common Tern nest sites and habitat points (ANOVA of DA, $F = 4.31$, df = 13 and 231, $P < 0.001$), although discriminant scores overlapped quite extensively (Fig. 2). Eight variables contributed to the discriminant equation (Table 2).

Common Terns nested on soft substrates within open areas, avoiding overhangs and tall vegetation. Their nests were closer to vegetation and were situated in less-steep slopes than habitat points. Also, nests had greater cover within 0.5 m, but the DA indicated that cover within 3 m is a better discriminator (correlation between two variables, $r = 0.89$, $P < 0.01$). As with the Roseate Terns, the most important discriminators differed among colonies (Fig. 1).

Roseate and Common tern nest sites.—Site characteristics of Roseate Terns differed significantly from those of Common Terns (ANOVA of DA, $F = 29.71$, df = 13 and 260, $P < 0.001$). Walls, visibility, number of neighbors, cover within 0.5 m, and position were the variables that, in combination, best distinguished the two tern species nest sites (Table 2). The scores for Roseate Terns had little overlap with those for Common Terns (Fig. 2)

Overall, Roseate Terns had more walls around their nests and greater cover within 0.5 m of their nests, which provided less visibility from above. Roseate Terns nested closer to other terns and had more neighbors within 2 m, but the discriminant function showed that the number of neighbors within 2 m is a better social character in distinguishing between Roseate and Common tern nest sites. Therefore, although the maximum nest density is related to the substrate structure of the colonies, Roseate Terns seemed to tolerate closer neighbors than did Common Terns.

The discriminant function to contrast the characteristics of Roseate Tern nest sites and habitat points included only four variables that

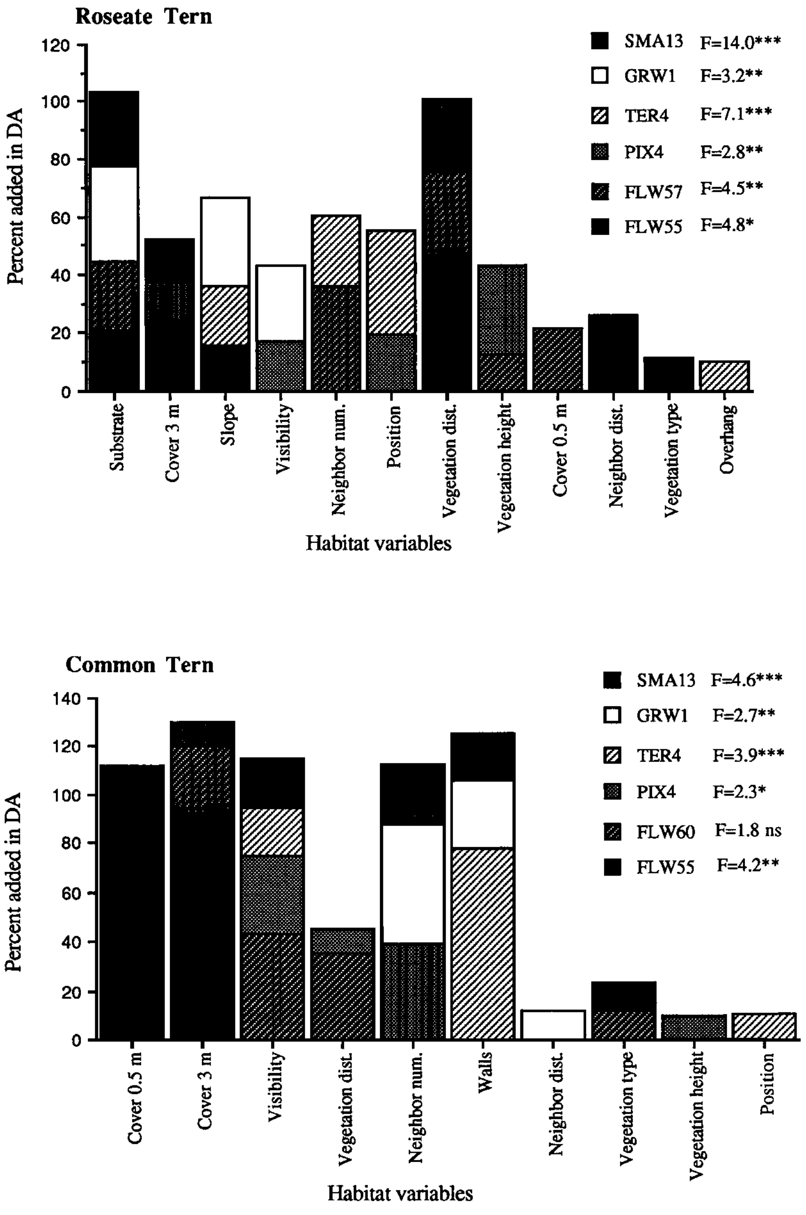

Fig. 1. Importance of each habitat variable (expressed in terms of percent added in DA) in distinguishing Roseate Tern nest sites and Common Tern nest sites from habitat points at different individual colonies (only variables explaining more than 10% of DA shown). *F*-values of the ANOVA on DA scores indicated: ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. All colonies are mixed except FLW57.

explain at least 10% of the variation, whereas for Common Terns seven variables were selected (Table 2). Among colonies, important discriminators consistently accounted for more of the variability for Roseate Terns than for Common Terns (Fig. 1). The differences in rates of correct classification of the pooled colony data between Roseate Tern nest sites and habitat points on the one hand, and Common Tern nest sites and habitat points on the other was highly significant ($G = 21.34$, df = 1 with Yates correction, $P < 0.001$). These results show that nest

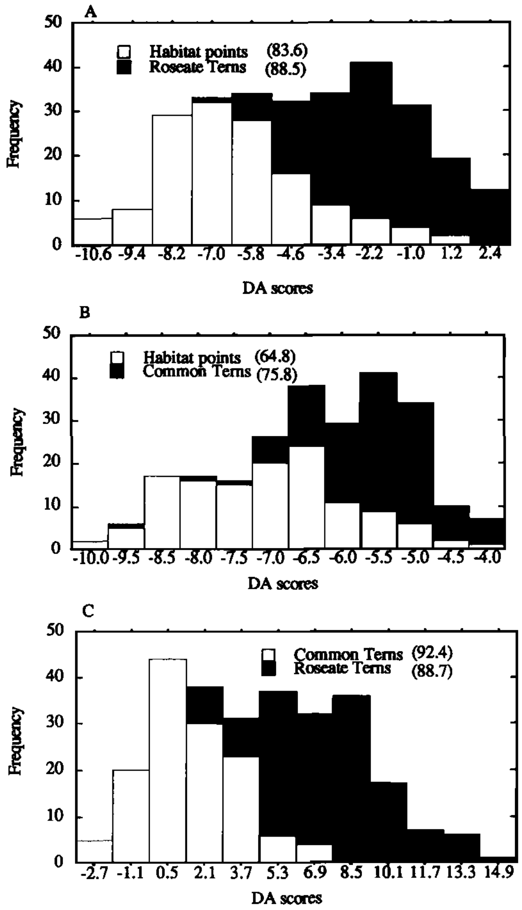

Fig. 2. Frequency distribution discriminant-function scores from analysis of: (A) Roseate Tern nest sites and habitat points; (B) Common Tern nest sites and habitat points; and (C) nests sites of Roseate and Common terns. Percent scores classified correctly into respective group given in parentheses.

sites where Roseate Terns chose to nest differed more from the available habitat than nest sites where Common Terns nested, suggesting Roseate Terns are more selective in their choice of nest sites than Common Terns.

Early and late Roseate Tern nest sites.—The characteristics of nest sites of late-nesting Roseate Terns differed from those of early-nesting birds at colony SMA13 (ANOVA of DA, $F = 5.65$, df $= 13$ and 33, $P < 0.001$). The DA scores of the two groups of nests overlapped very little (Fig. 3). Late nests had fewer neighbors within 2 m, had more cover within 3 m and 0.5 m, and were closer to higher vegetation (Table 2). The characters differentiating between nests of early-nesting Roseate Terns and available habitat were of minor importance in separating early from late Roseate Tern nest sites. The differences between early and late Roseate Tern nests are better explained by seasonal changes in the vegetation rather than a decrease in the availability of optimal sites; new plants were growing and older plants were becoming broader and taller. The reduced number of neighbors within 2 m of late-nesting Roseate Terns reflects the scattered nesting of these birds (Nisbet and Drury 1972).

Mixed and unmixed Common Tern colonies.—The overall degree of discrimination between nest sites of Common Terns in mixed and unmixed colonies showed a significant difference (ANOVA of DA, $F = 7.12$, df $= 13$ and 139, $P < 0.001$), largely explained by four variables (Table 2). The DA scores of the two groups overlapped moderately (Fig. 4). In mixed colonies, Common Terns had more neighbors within 2 m of the nest (nested closer to Roseate Terns), had grass as the nearest vegetation type, and nested further from vegetation and on steeper slopes. Nest-site attributes of birds in mixed and unmixed colonies are expected to differ if: (1) the structure of the habitat differs between the two colony types; and/or (2) if colony organization changes between colonies. The latter could arise if intraspecific and interspecific interactions assumed greater importance in mixed colonies. Point 1 is important because the mixed colonies that were entered in this discriminant analysis (FLW55, FLW56, PIX4 and SMA13) had more grass than the unmixed Common Tern colonies (FLW54, FLW57 and PIX11).

Although Roseate Terns started to nest about 5 to 10 days earlier than Common Terns, it seems unlikely that this explains the open-ground nesting of Common Terns. Common Terns avoid tall vegetation (Table 2) and, thus, their nesting closer to vegetation in unmixed colonies is partly due to the presence of shorter vegetation in those colonies. In colony FLW55, nests initiated in early May were closer to vegetation ($\bar{x} = 58.6$ cm, $n = 16$) than nests initiated in early June ($\bar{x} = 409.2$ cm, $n = 12$; $t = 5.1$, $P < 0.001$, log-transformed data); Common Terns avoid placing their nests in tall vegetation. One of the reasons why Common Terns do not nest closer to vegetation is because such sites are occupied by the early-nesting Roseate Terns. Denser nesting in mixed colonies means that, for Com-

TABLE 2. Discriminant-function scores from analysis of site variables, with percent added in DA in parentheses.

Variable	Habitat points and nests of Roseate Terns	Habitat points and nests of Common Terns	Roseate Tern and Common Tern nests	Early and late Roseate Tern nests	Common Tern nests in mixed and unmixed colonies
Walls	1.29 (35.6)	−0.04 (2.9)	1.73 (31.2)	−0.22 (−0.6)	−0.27 (1.9)
Overhang	−0.17 (−5.5)	−0.15 (19.9)	2.59 (3.9)	0.32 (1.4)	−0.06 (0.8)
Substrate	−1.26 (0.7)	−0.39 (12.1)	1.36 (−0.2)	−0.01 (0)	−0.22 (0.2)
Slope	0.59 (1.6)	−0.33 (15.7)	−2.88 (0.4)	−0.72 (−1.1)	1.16 (17.7)
Vegetation type	−0.13 (−0.5)	0.11 (−1.8)	0.42 (0)	0.69 (1.2)	−0.44 (29.6)
Vegetation distance	0.42 (10.3)	−0.50 (10.7)	0.08 (4.4)	−2.59 (−0.3)	0.22 (19.3)
Vegetation height	−0.79 (1.6)	0.30 (13.1)	−1.11 (0.2)	−1.03 (13.6)	1.45 (−1.2)
Cover within 0.5 m	−1.20 (4.5)	−0.52 (−12.6)	0.01 (15.3)	−1.25 (11.3)	0.76 (−4.4)
Cover within 3 m	−0.30 (−1.6)	−0.54 (12.4)	0.20 (−5.1)	−2.05 (16.3)	1.20 (−0.4)
Visibility from above	−0.41 (26.4)	−0.40 (−1.7)	−0.47 (21.9)	−0.68 (2.19)	−0.73 (2.6)
Neighbor distance	−0.35 (2.7)	0.52 (9.0)	0.68 (−5.9)	1.39 (−13.2)	0.41 (−6.2)
Neighbor number	−0.21 (26.0)	−0.45 (1.3)	0.26 (24.3)	3.41 (69)	0.42 (34.8)
Position	1.14 (−1.5)	−0.41 (18.9)	−0.93 (9.6)	−0.04 (0.3)	−0.85 (5.2)

mon Terns nesting in these colonies, intraspecific and interspecific interactions become increasingly important.

Roseate Tern hatching success and habitat.—Hatching success was tabulated to see if there was a relationship between nest-site selection and reproductive success in Roseate Terns. Hatching success did not differ significantly between mixed colonies for both Roseate (X^2 = 1.36, ns) and Common Terns (X^2 = 0.28, ns; Table 3). This was not true for unmixed colonies, such differences being explained by predation. In colony HOR1 (a mainland site with 15 nests), every nest was destroyed by predators, presumably by a mammal. In colony FLW57, a Grey Heron (*Ardea cinerea*) was observed preying on eggs and chicks (of 131 eggs studied, 58% hatched).

The presence of overhanging rock, albeit being of some importance in nonvegetated colonies, did not have any significant effect on Roseate Tern hatching success in colonies PIX4 (X^2 = 0.18, ns), TER4 (X^2 = 0.17, ns), and SMA13 (X^2 = 0.24, ns; Table 4). Furthermore, in colony SMA13, no difference was found between the hatching success of nests with a total overhang (n = 21 eggs, 81% hatched), partial overhang (n = 26, 69% hatched), closer to rocks but with no overhang (n = 28, 89% hatched), and closer to vegetation (n = 15, 93% hatched; X^2 = 0.52, ns). Of the 18 eggs laid by late-nesting Roseate terns in colony SMA13, only 40% hatched. It is likely that the parents were mainly young and/or inexperienced birds. Therefore, in 1990, nest concealment by Roseate Terns in the Azores did not contribute to higher hatching levels.

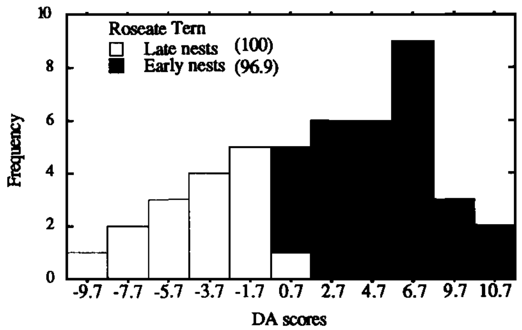

Fig. 3. Frequency distribution discriminant-function scores from analysis of early and late Roseate Tern nest sites in colony SMA13. Percent scores classified correctly given in parentheses.

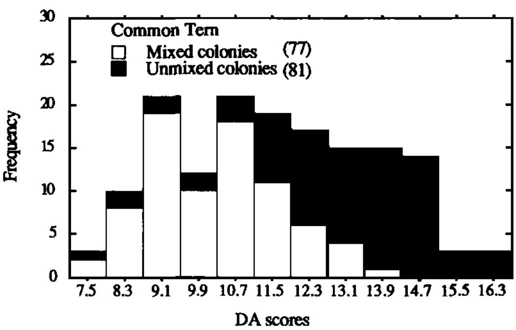

Fig. 4. Frequency distribution of discriminant-function scores from analysis of Common Tern nest sites in mixed and unmixed colonies. Percent scores classified correctly given in parentheses.

TABLE 3. Number of eggs in mixed colonies of Roseate and Common terns (from marked nests with a known outcome), with percent hatched in parentheses.

Colony	Roseate Tern	Common Tern
FLW 55	12 (83)	43 (70)
FLW 56	49 (94)	31 (77)
FLW 60	34 (97)	5 (80)
PIX 4	46 (85)	31 (81)
TER 4	39 (85)	—
GRW 1	113 (75)	56 (70)
SMA 13	121 (79)	—

TABLE 4. Number of Roseate Tern eggs from nest sites with total, partial and no overhang (percent hatched in parentheses).

Colony	Overhang		
	Total	Partial	None
PIX 4	7 (100)	8 (75)	38 (84)
TER 4	8 (88)	7 (100)	33 (79)
SMA 13	21 (79)	26 (69)	99 (82)

DISCUSSION

Nest-site selection of Roseate and Common terns.—Both tern species exhibited nest-site selection. Roseate Terns preferred sites surrounded by walls and/or within vegetation; these types of cover result in nests not being easily visible from above. Common Terns avoided walls, overhangs, and tall vegetation; they selected open areas with soft substrates when available.

The results of our DA analyses reaffirm much of what has been suggested for Roseate and Common tern nest-site selection based upon univariate methods (Langham 1974, Blokpoll et al. 1978, Burger and Lesser 1978, Burger and Gochfeld 1988a, 1988c, Gochfeld and Burger 1988). However, our study also highlights the fact that there is considerable variability in nest-site selection of Roseate and Common terns among colonies. Previous studies have been carried out in only one or two colonies, thus failing to reveal this factor. Also, our study indicates more clearly the combination of variables that contribute the most to Roseate and Common tern nest-site selection. Important discriminators between the nest sites of both species and the available habitat varied greatly among colonies, which suggests that scale factors affect habitat selection, as indicated by Burger and Gochfeld (1988c). Our findings suggest that researchers should consider different colonies independently in studies of habitat selection; this is especially the case for Roseate Terns.

Nest-site differences between Roseate and Common terns in mixed colonies.—In our study, invoking interspecific competition between Roseate and Common terns is not necessary to account for the observed patterns of nest-site selection. The species showed markedly different nest-site preferences. If Roseate Terns had preferred less-concealed sites they could have found and used them, especially in colony FLW60, where only two Common Terns nested. Also, in colony SMA13, late-nesting Roseate Terns managed to find concealed sites. Common Terns in unmixed colonies did not select concealed sites and, in mixed colonies, they could have nested in the remaining areas, with uneven surface, not used by Roseate Terns. Roseate Tern populations in North America and Europe, which are in sympatry with Common Terns, nest in cover and/or in virtual contact with an elevated object (Langham 1974, Gochfeld and Burger 1988). Tropical populations in Puerto Rico, which are allopatric with Common Terns, nest more in the open than do temperate populations, although a tendency to place nests close to tall vegetation (that provides cover over the nest) was found (Burger and Gochfeld 1988c). The more-open nesting habits of this population must be examined in relation to habitat availability in that area. Habitat points were significantly less visible than nest sites in only one of four subcolonies studied (Burger and Gochfeld 1988c), reflecting the more-open habitat in Puerto Rico. Moreover, any comparison of disjunct populations presents limitations, in particular the potential existence of different selection pressures.

Although the discussion above suggests that at present there is no competition for nest sites, an observational approach will not reveal the importance of competition. Therefore, our study does not invalidate the hypothesis that competition, under some circumstances, may be relevant. An evaluation of this hypothesis provides some insight into the organization of Roseate and Common tern mixed colonies. Several studies indicate that the quality of habitat acquired by colonial seabirds is related to the age and experience of the individuals. This is reflected in their breeding performance (e.g. Coulson 1968, Potts et al. 1980). This occurs through segregation of birds at the time of their recruitment; older birds arrive early in the breeding grounds, occupy the optimal areas, lay first, and have higher productivity than younger birds (Coulson and White 1958, 1960, Wooler and Coulson 1977, Hays 1978, Potts et al. 1980).

In our study, the density of neighbors was one of the most important factors in statistically explaining Roseate Tern nest-site selection. Temporal variation in the onset of laying and in productivity occurred in colony SMA13 (and presumably in other colonies), where at least 18 breeding pairs laid about two to three weeks after the first breeders. These were probably younger birds or failed breeders from another colony, as similar temporal variations seem to occur in Roseate Terns in Connecticut (Spendelow 1982) and have been demonstrated for both Common Terns (Hays 1978) and Arctic Terns (*Sterna paradisaea*; Cramp 1985). Generally, it seems that Roseate Tern subcolonies present a social structure similar to that of other colonial seabirds. Thus, although good nesting areas are probably available outside the colony, younger Roseate Terns are likely to nest in the less-optimal areas on the edge of the subcolony.

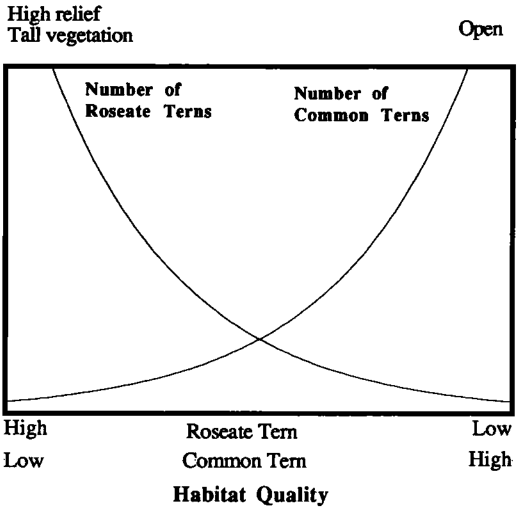

Fig. 5. Diagram showing number of Roseate and Common terns of a colony site as reflection of habitat quality.

The larger and more aggressive Common Terns have greater competitive ability (Schoener 1974), thus should have higher probabilities of acquiring a nest site. The more specialized nesting preferences of Roseate Terns and their more restricted nesting locations suggest that they might face a shortage of optimal nest sites. In the Azores, Roseate Terns significantly outnumbered Common Terns in most of the mixed colonies; the reverse is true for most colonies in northeastern North America (Burger and Gochfeld 1988b) and in Britain (Langham 1974). In Cedar Beach, New York, 50% of Roseate Terns had Common Terns as their nearest neighbors, and they nested in four discrete groups, whereas in the Azores they always had other Roseate Terns for nearest neighbors and nested in one dense group. Differences in the spatial distribution of Roseate Tern optimal nesting areas between the Azores and Cedar Beach might be the origin of these differences. As a result, Roseate Terns at Cedar Beach could be exposed more often to the more aggressive Common Terns, which are more likely to win interspecific encounters. Spendelow (1982) suggested that the most-sheltered sites are the first ones to become occupied. These will be defended by older, more-competitive Roseate Terns, forcing younger Roseate Terns into more-open areas, where they might have to face aggressive Common Terns. On Falker Island, Connecticut (a colony with higher nesting density than Cedar Beach), when nesting on open ground, Roseate Terns compete with Common Terns for available nest sites (Spendelow 1982).

In northeastern colonies in North America, predation has been invoked as an important factor to explain concealment by Roseate Terns at Cedar Beach (Burger and Gochfeld 1988b). In the Azores, at least in 1990, the role of predation was thought to be insignificant. Roseate Terns lay smaller clutches, are less synchronous breeders (Nisbet 1975), and are more specialized in their foraging substrate (Safina 1990) than Common Terns. Interspecific competition could have played a more important role than predation in driving the nesting differentiation of the two species. This may be expected when terns nest in isolated places where predators are absent.

The number of Roseate and Common terns of a particular colony may be perceived as a function of habitat quality (Fig. 5). Presumably, the optimal colony sites are those to which all Roseate Terns and most Common Terns move, leaving the unmixed colonies both less preferred and less dense. If early-nesting birds stimulate breeding, Common Terns in mixed colonies should begin to lay before Common Terns in unmixed colonies. This needs further study. Experiments can be devised to evaluate the idea presented on Figure 5 (e.g. removing or providing areas with highly uneven surface in mixed colonies where Roseate Terns used to nest; see also Richards and Morris 1984). Population-dynamic studies of terns at various individual colonies also are important to evaluate this idea.

In summary, our study indicates that Roseate Terns on the Azores prefer nesting habitat characterized by: areas with high relief; pitted ground with cracks, crevices and fissures; and/or tall vegetation. Therefore, management actions should be taken to maintain these conditions, especially because nesting in open areas might be disrupted by competition with Common Terns. Selected habitat variables differed from colony to colony; thus, management should be considered and planned on a colony-to-colony basis.

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