

## HABITAT USE AND FORAGING SUCCESS OF ROSEATE AND COMMON TERNS FEEDING IN FLOCKS IN THE AZORES

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**SUMMARY.**—*Habitat use and foraging success of roseate and common terns feeding in flocks in the Azores.*

**Aims:** To study the foraging ecology of roseate terns and common terns in the Azores sub-tropical waters where the former species is relatively abundant compared to congeners. In particular, we asked whether foraging behaviour differed between both species, which factors determined individual success at foraging-flocks, and how did our findings compare with previous studies of Atlantic populations in North America (temperate), and Caribbean (tropical).

**Location:** Ponta das Contendas (38°39'N, 27°05'W), Terceira Island, Azores.

**Methods:** Foraging-flocks were characterized and compared in terms of species (single- or mixed-species), size (no. of individuals), type of habitat (inshore, exposed coast, deep blue water), and presence-absence of biotic effects. We used a generalized linear model (GLM) approach to study the effect of selected factors (species, habitat, biotic effect, cloud cover, wind speed, and their interactions) on individual foraging parameters at these flocks (number of dives min<sup>-1</sup>, number of aborted dives min<sup>-1</sup>, number of prey caught min<sup>-1</sup>).

**Results:** Both tern species were most often observed in mixed-flocks in the exposed coast habitat, but roseate terns were also prone to feed in mono-specific flocks over blue water. Only one quarter of the total number of flocks recorded was in the presence of biotic effects, a situation where common terns, but not roseate terns, were twice more numerous. The GLM results suggested that species and habitat alone were good predictors of prey caught min<sup>-1</sup>: common terns achieved the highest success in inshore bays (1.2 fish min<sup>-1</sup>) while roseate terns maximized their success on exposed coasts (0.8 fish min<sup>-1</sup>). In the presence of biotic effects, both species dove at a higher frequency, and aborted fewer dives per min, but there was no marked effect on capture rates. Increasing wind speed negatively affected the rate at which both species aborted dives, but again, there was no effect on capture success.

**Conclusions:** Foraging success did not increase in the presence of biotic associations that should normally facilitate prey capture. This suggests that interspecies competition may arise at mixed-flocks, as found in North American studies. Overall, our results paralleled previous findings that the common tern is adapted to feed in calm, inshore bays. Because this latter habitat was scarce in the study area, we hypothesized that this contributes towards explaining why common terns do not breed in high numbers at this colony site (ten percent of the Azores population). Conversely, the large area occupied by the marine coastal (exposed coast) and oceanic (blue water) environments in the study area may, at least in part, justify the large number of roseate terns found there (one quarter of the Azores population) in 2001.

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RESUMEN.—*Uso del hábitat y éxito en la búsqueda de alimento en bandos del charrán rosado y charrán común en Azores.*

**Objetivos:** Estudiar la ecología de la búsqueda de alimento del charrán rosado y común en las aguas subtropicales de Azores donde el primero es relativamente más abundante que su congénere. En particular, nos preguntamos si el comportamiento en la búsqueda de alimento difiere entre ambas especies, que factores son los que determinan el éxito individual en la búsqueda de alimento en bandos, y como nuestros resultados son comparables con previos estudios en poblaciones atlánticas en Norteamérica (zona templada) y el Caribe (zona tropical).

**Localidad:** Ponta das Contendas (38°39'N, 27°05'W), isla Terceira, Azores.

**Metodos:** Bandos de aves buscando alimento se caracterizaron y compararon en términos de número de especies (una o varias), el tamaño (número de individuos), tipo de hábitat (cerca de la orilla, costa expuesta, mar abierto), y la presencia-ausencia de efectos bióticos. Usamos modelos generalizables lineales (GLM) para estudiar el efecto de los factores seleccionados (especie, hábitat, efectos bióticos, cobertura de nubes, velocidad del viento, y sus interacciones) en los parámetros individuales de búsqueda de alimento en estos bandos de charranes (nº de inmersiones por minuto, número de inmersiones abortadas por minuto, número de capturas por minuto).

**Resultados:** Ambas especies fueron más frecuentemente observadas en bandos mixtos y en hábitats costeros expuestos, pero el charrán rosado tuvo una mayor tendencia a alimentarse en bandos mono-específicos en aguas abiertas que el charrán común. Los resultados de los análisis nos muestran que el tipo de especie y de hábitat son unos buenos predictores de las capturas por minuto realizadas: el charrán común obtuvo el mayor éxito en las orillas de las bahías (1,2 peces/min) mientras que el charrán rosado maximizó su éxito en costas expuestas (0,8 peces/min). En presencia de efectos bióticos, ambas especies realizan inmersiones a altas frecuencias y tienen un menor número de inmersiones abortadas por minuto, pero no presentaban marcadas diferencias en las tasas de capturas. Un aumento de la velocidad del viento afecta a la tasa de inmersiones abortadas en ambas especies, pero de nuevo, no existía un efecto en el éxito de captura.

**Conclusiones:** El éxito en la búsqueda de alimento no aumentó en la presencia de asociaciones bióticas que deberían normalmente facilitar la captura de presas. Esto sugiere que la competencia interespecífica debe aumentar en bandos mixtos, como ha sido descrito en estudios norteamericanos. Nuestros resultados confirman anteriores estudios que indican que el charrán común está adaptado a buscar el alimento en las orillas de las bahías con aguas calmas. Debido a que este tipo de hábitat es escaso en nuestra área de estudio, podemos hipotetizar que esto contribuiría a explicar porque el charrán común no se reproduce de forma frecuente en esta colonia (10 % de la población en Azores). En nuestra área de estudio, la gran superficie ocupada por las costas expuestas al oleaje y por las aguas abiertas, podría en parte justificar el gran número de charranes rosados encontrados en el año 2001 (un cuarto de la población de las Azores).

*Palabras clave:* charrán rosado, charrán común, éxito de alimentación, depredadores de peces, competencia en la alimentación, conservación de aves marinas, Azores, *Sterna dougallii*, *Sterna hirundo*.

## INTRODUCTION

Solitary feeding is rarely found among tern species that instead gather in flocks where prey is locally abundant (Shealer, 2001). Foraging success at flocks depends on a vast array of fac-

tors that may affect food provisioning rate of tern chicks, and thus overall productivity of colonies (Monaghan 1989; Frank, 1992; Anderson, 2005). This includes (1) environmental factors such as weather conditions (e.g., wind speed; Dunn, 1973; Stienen *et al.*, 2000),

habitat use (e.g., inshore, offshore; Frank, 1992), association with biotic effects (e.g., subsurface predators; Safina and Burger, 1985), (2) intrinsic factors (age, experience; Shealer, 2001), and (3) social factors such as flock size, type (single, or mixed-species; Shealer and Burger, 1993) and intra- or inter-specific competition (Safina, 1990a). The understanding of how these factors affect foraging decisions and foraging success is particularly important in threatened or endangered seabird populations for which improved knowledge of their marine habitat requirements may help conservation efforts.

The roseate tern *Sterna dougallii* is primarily a tropical species with a highly scattered distribution (Gochfeld 1983) extending to temperate areas in the Atlantic Ocean (Ratcliffe *et al.*, 2004), where it is largely outnumbered by the common tern *S. hirundo* (Europe, North America). In American populations, the role of environmental and social factors affecting roseate tern foraging success has been studied. There, the species is considered as a specialist forager attracted to physical oceanographic features (shoals and tide rips; Safina, 1990a) or biotic effects such as brown pelicans *Pelecanus occidentalis* and subsurface predators that drive prey close to the surface (Shealer, 1996). Roseate terns are, however, prone to avoid large, multispecies flocks, where they are an inferior competitor often outnumbered by other species (e.g., common tern), being forced to peripheral areas of the flock where prey is more dispersed and foraging success depressed (Duffy, 1986; Shealer and Burger, 1993). As a result, these specialized foraging requirements, as well as the competitive disadvantage of roseate terns at multispecies flocks, have been invoked to explain the relative low population levels of this species in the North Atlantic Ocean compared to more abundant sympatric congeners that forage over a wider range of conditions (Safina 1990a, Shealer, 1996).

In Europe, the roseate tern is classified as endangered (Tucker and Heath, 1994) and

the Azores holds the largest numbers (del Nevo *et al.*, 1993). Roseate and common terns breed sympatrically throughout the archipelago in single and mixed colonies (Ramos, 1995). Nesting habitat characteristics (Ramos and Del Nevo, 1995) and diets (Ramos *et al.*, 1998a, 1998b; Monteiro *et al.*, 1996) have been studied in both species. To date, however, information on their foraging ecology was lacking. Although roseate terns are less numerous than common terns in the Azores, the ratio is more balanced than at other temperate (North America) breeding quarters (1/3 vs. 1/20, respectively; Safina 1990a; Heath *et al.*, 2000). Moreover, at some Azorean colonies the number of roseate tern pairs exceeds that of common tern pairs, providing an opportunity to investigate a situation where roseate terns were expected to be, on average, numerically dominant at mixed flocks.

In 2001, we studied foraging habitat use and individual foraging success of roseate and common terns in the vicinity of a mixed colony on Terceira Island, Azores. We asked (1) whether foraging habitat use differed between species, (2) which factors were likely to determine foraging success at flocks, and (3) whether these results differ from other Atlantic populations. In particular, we predicted that foraging conditions in the study area should include some of roseate terns' preferred features, which could justify the large breeding population found in the Azores. We also predicted that due to their numerical superiority in the study area, roseate terns may not be at a competitive disadvantage with common terns at mixed flocks, as found in American studies.

## MATERIAL AND METHODS

### *Study area*

In 2001, the roseate tern stronghold in the Azores archipelago (36–39°N, 25–31°W) was on an islet off Ponta das Contendas (38°39'N,

27°05'W; Ratcliffe, 2001), south-eastern coast of Terceira Island, where a mixed roseate and common tern colony with 350 and 220 breeding pairs, respectively, was located. This was the only breeding area throughout the archipelago where the former species outnumbered the latter. Roseate terns nested in tall vegetation and did so at high densities, while common terns nested in the periphery of the roseate tern subcolony, in more open areas and at lower densities (Ramos and Del Nevo, 1995).

### *Location of flocks*

During the breeding season, from late May to mid July, we searched for foraging flocks in the area surrounding the colony by scanning the ocean with 10 x 50 binoculars and a telescope. Three onshore vantage points overlooking the colony were chosen. The first vantage point was located in front of the colony whilst the other two were located *ca.* 500 m apart, one on each side of the colony. Since the terns' feeding activity is higher in the morning and in the late afternoon (Ramos *et al.*, 1998a; Stienen *et al.*, 2000), vantage-point attendance was defined as either early morning (07:00 - 08:30), late morning (11:30 - 13:00) or evening (17:00 - 18:30) for a total daily observation-period of 4.5 hours. At least two hours per day were spent covering the shore around Terceira Island to find flocks opportunistically, and time was devoted to search for foraging terns during several boat cruises with a local fisherman.

### *Foraging habitat definition*

Each flock encountered was assigned to one of three foraging habitats classified in relation to water colour (Shealer, 1996) and distance from the shore estimated visually. Since the coastal habitats on Terceira Island mostly consist of rocky cliffs that fall steeply to great

depths (Ospar, 2000), we were often able to make a distinction between areas of (1) open, blue water (deep blue oceanic water > 50 - 100 m from the shore and characterized by sea swells), (2) exposed coast (waters < 50 m, close to the rocky shore, often with emerging stacks, rocks and water colour with more white than over blue water) and (3) inshore, shallow-water habitat (calm, clear blue-green waters less than 3 - 4 m deep), encompassing sheltered bays found along the irregular coastline of the island.

### *Flock characterization*

Flock composition (with a minimum of two birds) was recorded as either monospecific, with roseate or common terns only, or comprising both species (mixed species flock), and the number of individuals of each species was counted. In small flocks, birds were counted individually while for larger groups, we assessed the flock size by counting terns as blocks (e.g., 5, 10, 20; Bibby *et al.*, 1992). Flock-density was evaluated by visually estimating the nearest distance between foraging neighbors (NND) as dense (NND < 5m), moderate ( $5 \leq \text{NND} \leq 15\text{m}$ ), or loose (NND > 15m).

### *Weather conditions and association with biotic features*

Cloud cover was estimated as < 1/3; 1/3 - 2/3; and or 2/3, and we obtained wind speed values ( $\text{km hour}^{-1}$ ) from the nearest meteorological station on Terceira Island (Instituto Nacional de Meteorologia e Geofisica; 38°39'05''N; 27°13'04''W).

The presence of predatory fish (Delphinidae, Scombridae) under a foraging flock was determined by relying on sightings at the water surface (e.g., dorsal fin obvious) and behaviour of the birds (Safina and Burger, 1985). However, since the presence of that biotic effect was

sometimes hard to detect, especially for observations at long range or in agitated waters, we assumed that Cory's shearwaters *Calonectris diomedea* actively feeding around a tern flock indicated the presence of subsurface predators (Martin, 1986). We refer to both situations in the results as "association with biotic effects".

### *Foraging behaviour*

At flocks located within reasonable observation distance (< 200m), a foraging individual of each species was randomly selected with binoculars or telescope, and followed during its complete feeding bout or until lost from sight (Shealer, 1996; Ramos, 2000). Both species are skilful air-to-water plunge-divers that can also feed by dipping-to-surface (Cramp 1985), but we did not differentiate between these two strategies when recording (1) the number of diving attempts, (2) the number of aborted diving attempts, defined as the number of trials where the tern began a dive but did not touch the surface (Safina, 1990a), and (3) the number of prey caught during the whole bird's feeding bout. Individuals merely followed for a single trial were systematically discarded and a new bird was selected (Ramos, 2000). During data analysis, our observations were standardized (i.e., no. of observations  $\text{min}^{-1}$ ) as: (1) diving rate, (2) aborted rate, and (3) capture rate. In the latter case, the number of prey caught per min corresponded to the number of successful dives per min, even though some individuals were seldom observed catching more than one prey in a single successful attempt. We excluded from capture rate analysis individuals for which the outcome of each feeding trial was uncertain.

### *Data treatment*

Data on flock counts were analysed with chi-square or Fisher Exact test (discrete variables),

and data on species counts were compared by using non parametric Mann-Whitney *U*-test (2 groups), or Kruskal-Wallis ANOVA *H*-test since the assumptions of normality were often not met, or because unequal variances between samples were found (Zar, 1999). We used Generalized Linear Models (GLM; StatSoft, 2003) to assess the effect of the following explanatory terms and interactions on each of three response variables: diving rate, aborted rate and capture rate. For example, for diving rate the model was Diving rate = species + habitat + wind speed + biotic association + cloud cover + species \* habitat + species \* biotic association. Species, habitat, biotic association, and cloud cover had 2, 3, 2, and 3 levels, respectively. The significant effect of each explanatory variable was assessed with Generalized Linear Modelling using a  $\chi^2$  statistic on likelihood ratios that compares the likelihood for the model including all effects (variables) except the current effect (explanatory variable tested) with the likelihood of an overall model including all effects (StatSoft, 2003). Each response variable was log (x+1) transformed and treated as normally distributed with an identity link function. We used sigma-restricted parameterization and looked at Type III analysis. Values are given as mean  $\pm$  SE.

## RESULTS

### *Foraging habitat use and flock type*

The majority of the flocks encountered were mixed species flocks (55 %,  $n = 119$ ), especially on exposed coasts (31 %; Table 1). A significant association between flock type and foraging habitat was detected because a greater than expected number of roseate tern monospecific flocks was found over blue water ( $\chi^2 = 11.3$ ,  $df = 4$ ,  $P < 0.03$ ; Table 1). Overall, 24 % ( $n = 119$ ) of the total number of flocks were recorded in the presence of predatory fish ( $n = 12$ ) and Cory's shearwaters ( $n = 17$ ). No for-

TABLE 1

Roseate tern, common tern and mixed-species flocks recorded in different foraging habitats during the 2001 breeding season on Terceira Island, Azores.

[*Bandos monoespecíficos de charranes rosados o comunes y bandos mixtos registrados en los distintos hábitats de alimentación (costas expuestas al oleaje, costas no expuestas a oleaje y aguas abiertas) en la temporada reproductiva del año 2001 en la isla de Terceira, Azores.*]

Foraging habitat	Nº. of roseate tern flocks	Nº of common tern flocks	Nº of mixed species flocks
Inshore shallow	6	2	15
Exposed coast	15	11	37
Blue water	18	2	13

aging association was found between a particular type of flock (i.e., mono-specific 11/54 = 20 % or mixed species 18/65 = 28 %) and the presence of predatory fish and Cory's shearwaters (Fisher Exact test,  $P = 0.239$ ). Terns feeding with biotic effects did so in moderate or dense flocks (17/39 = 44 %) more often than in loose flocks (12/80 = 15 %, Fisher Exact,  $P < 0.001$ ).

#### Flock size

The number of common tern individuals per flock did not differ significantly between exposed coast ( $5.5 \pm 1.2$ ), blue water ( $4.1 \pm 0.7$ ) and inshore shallow ( $5.4 \pm 1.4$ ) foraging habitats (Kruskal-Wallis ANOVA:  $H_2 = 0.6$ ,  $n = 80$ ,  $P = 0.741$ ). In some cases, mixed species flocks were recorded comprising only a single common tern individual, but the number of flocks at which such a situation arose did not differ between habitat types (27 % in shallowwaters, 27 % on exposed coasts and 15 % over blue-water;  $\chi^2 = 0.7$ ,  $df = 2$ ,  $P > 0.05$ ). In roseate terns, no statistical difference in the number of birds per flock recorded in the three foraging habitats was detected ( $15.7 \pm 1.8$ ,  $16.6 \pm 3.9$ , and  $9.8 \pm 1.7$  for exposed coasts, blue water and inshore shallows, respectively; Kruskal-Wallis ANOVA:  $H_2 = 4.2$ ,  $n = 104$ ,  $P = 0.123$ )

but when all habitats were pooled, the mean number of roseate terns differed significantly between mono-specific and mixed flocks (Mann-Whitney test:  $U = 93$ ,  $n = 104$ ,  $P < 0.02$ ), whilst no difference was found for common terns ( $U = 451$ ,  $n = 80$ ,  $P = 0.65$ ; Fig. 1). At mixed flocks, common tern individuals were significantly more numerous when foraging in association ( $9.6 \pm 2.7$ ) than in absence ( $4.5 \pm 0.9$ ) of predatory fish ( $U = 113.5$ ,  $n = 65$ ,  $P < 0.01$ ), whereas there was no significant difference between the number of roseate tern individuals foraging with ( $17.5 \pm 2.4$ ) and without ( $14.9 \pm 4.7$ ) predatory fish ( $U = 241.5$ ,  $n = 65$ ,  $P = 0.54$ ).

#### Diving rate

For both species, the mean number of plunge-diving attempts increased significantly with increasing flock density (one-way ANOVA:  $F_{2,96} = 13.84$ ,  $P < 0.001$  and  $F_{2,65} = 7.16$ ,  $P < 0.01$  for roseate and common terns, respectively; Fig. 2). There was a significant species effect on the number of dives per min (GLM:  $P = 0.047$ ; Table 2). Roseate terns dove at a higher rate ( $2.29 \pm 0.13$ ,  $n = 99$ ) than did common terns ( $1.75 \pm 0.24$ ,  $n = 67$ ). The presence-absence of association with biotic effects was also a significant explanatory

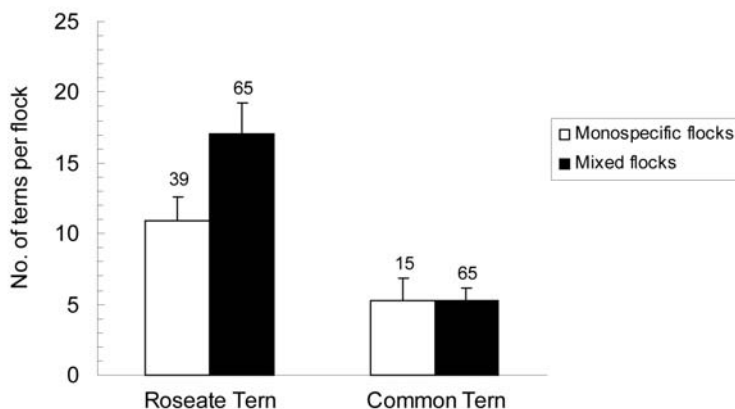


FIG. 1.—Number of roseate and common tern individuals recorded in mono-specific and mixed species flocks during the 2001 breeding season on Terceira Island, Azores (mean  $\pm$  SE,  $n$  at top of bars).

[Número de individuos de charranes rosados y comunes registrados en bandos mono-específicos y mixtos en la temporada reproductiva del año 2001 en la isla de Terceira, Azores (media  $\pm$  SE,  $n$  sobre las barras).]

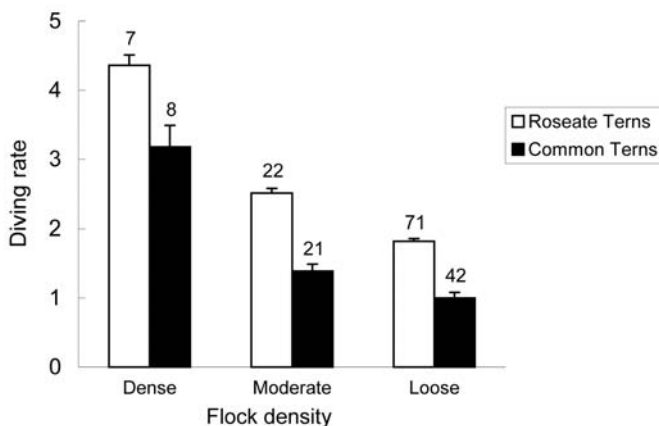


FIG. 2.—Comparison of diving rate (no. of diving-attempts per min) between roseate and common terns in relation to flock density during the 2001 breeding season on Terceira Island, Azores (mean  $\pm$  SE;  $n$  at top of bars).

[Tasa de inmersiones por minuto de los charranes rosado y común en relación a la densidad de bandos (densa, moderada y laxa) en la temporada reproductiva del año 2001 en la isla de Terceira, Azores (media  $\pm$  SE,  $n$  sobre las barras).]

TABLE 2

Results of a generalized linear model analysis (Type III) testing the effect of five explanatory terms and two interactions (species, foraging habitat, biotic association, wind speed, cloud cover, species x foraging habitat, species x biotic association) on 3 response variables (diving rate, aborted rate, and capture rate). Only significant terms and parameters are shown.

[Resultados del GLM (Tipo III) comprobando el efecto de 5 variables dependientes y sus interacciones (especie, hábitat de alimentación, asociación biótica, velocidad del viento, cobertura de nubes, especie x hábitat de alimentación, especie x asociación biótica) sobre tres variables: tasa de inmersiones, tasa de inmersiones abortadas y tasa de captura. Únicamente se muestran los términos significativos.]

Variable / Predictor <sup>1</sup>	$\chi^2$ (Type III)	df	P	Parameter	Level of effect <sup>2</sup>
<b>Diving rate</b> (n° of dives per min, $n = 166$ ) <sup>2</sup>					
Species	3.94	1	0.047	-0.038	Common Tern
Biotic association	4.04	1	0.04	-0.035	No association
<b>Aborted rate</b> (n° of aborted dives per min, $n = 166$ )					
Foraging habitat	13.98	2	< 0.001	-0.085	Inshore
Biotic association	5.78	1	0.016	+0.038	No association
Wind speed	8.29	1	0.003	-0.004	
<b>Capture rate</b> (n° of prey captured per min, $n = 166$ )					
Foraging habitat	14.76	2	< 0.001	+0.062	Inshore
				-0.085	Blue water
Species x foraging habitat	13.70	2	0.001	+0.088	C.T. x Inshore
				-0.052	C.T. x Blue water

<sup>1</sup> Levels of categorical predictors: species: Roseate Tern (RT), Common Tern (CT); Foraging habitat: exposed coast, inshore-shallow, blue water; Biotic association: presence, absence.

<sup>2</sup> Level of effect indicates for each significant categorical predictor the reference level used for relative comparison to the other levels: e.g., fewer dives were aborted in Inshore (-0.085) compared to the two other groups (exposed coast **and** blue water).

[<sup>1</sup> Los niveles categóricos de las variables predictoras son para la especie: charrán rosado (RT) y charrán común (CT), para el hábitat de alimentación: costas expuestas al oleaje, costas no expuestas a oleaje y aguas abiertas, y para las asociaciones bióticas: presencia y ausencia.

<sup>2</sup> Los niveles de los efectos indican para cada variable categórica predictorora el nivel referencia utilizado para compararse con el resto, así por ejemplo, menos inmersiones son abortadas en las costas no expuestas a oleaje (-0.085) que en los otros dos niveles (costas expuestas a oleaje y aguas abiertas).]

variable in the model ( $P = 0.04$ ; Table 2), with both species diving at a higher rate when associated with biotic features (Fig. 3).

#### Aborted rate

There was a significant influence of foraging habitat on the number of aborted dives in the

model ( $P < 0.001$ ; Table 2). Fewer dives were aborted in inshore shallow ( $0.59 \pm 0.09$ ,  $n = 32$ ) compared to exposed coast ( $1.06 \pm 0.10$ ,  $n = 90$ ) and blue water ( $1.08 \pm 0.12$ ,  $n = 44$ ). We also detected a significant effect of both biotic association ( $P = 0.016$ ) and wind speed ( $P = 0.003$ ; Table 2). Foraging terns had a tendency to abort less dives per min in the presence of biotic effects ( $0.83 \pm 0.13$ ,  $n = 41$ ) than in their absence



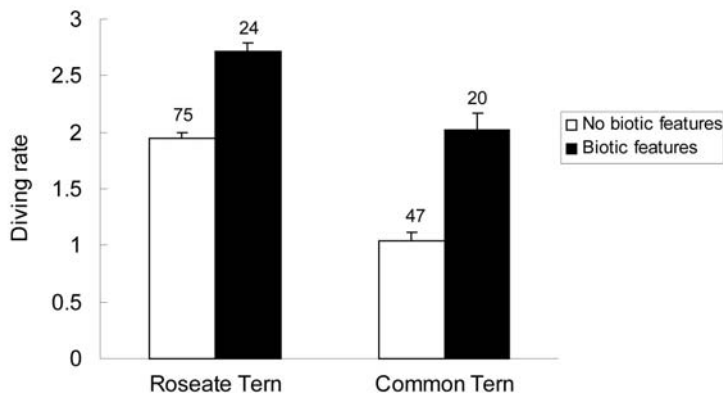


FIG. 3.—Diving rate (no. of dives  $\text{min}^{-1}$ ) of roseate and common tern individuals recorded in presence - absence of a biotic association with predatory fish/shearwaters, in 2001, Terceira Island, Azores (mean  $\pm$  SE,  $n$  at top of bars).

[Tasa de inmersión por minuto de los charranes rosados y comunes registradas en presencia o ausencia de asociaciones bióticas con depredadores de peces en la temporada reproductiva del año 2001 en la isla de Terceira, Azores (media  $\pm$  SE,  $n$  sobre las barras).]

( $1.03 \pm 0.08$ ,  $n = 125$ ). The sign of wind speed included in the model was negative, which suggests that the aborted rate of diving for both species decreased as wind speed increased.

#### Capture rate

The GLM identified a significant effect of foraging habitat on the number of prey captured per min ( $P < 0.001$ ; Table 2). This was mainly attributable to an overall lower success over blue water ( $0.24 \pm 0.05$ ,  $n = 44$ ) compared to inshore shallow ( $0.70 \pm 0.16$ ,  $n = 32$ ) and exposed coast ( $0.72 \pm 0.12$ ,  $n = 90$ ). Moreover, there was a significant interaction between foraging habitat and species ( $P = 0.001$ ; Table 2). Roseate terns achieved a higher capture success in exposed coast ( $0.78 \pm 0.14$ ) than in inshore shallow ( $0.35 \pm 0.12$ ) and over blue water ( $0.32 \pm 0.06$ ; Fig. 4). On the contrary, common terns showed a higher capture rate in inshore shallow ( $1.19 \pm 0.30$ ), intermediate in exposed coast ( $0.65 \pm 0.21$ ), and almost zero over blue water ( $0.07 \pm 0.04$ ; Fig. 4).

#### DISCUSSION

##### *Foraging habitat use and success*

Both species were often associated in mixed foraging-flocks along exposed coasts. On average, foraging common terns were less numerous (c. 4 - 6 birds per flock) than roseate terns (c. 9 - 17 birds per flock), which roughly corresponded to the ratio of 2/3 breeding pairs found at the colony. Overall, roseate terns were often feeding in small-sized, loose flocks rather than large, dense flocks, a foraging preference previously found in both tropical (Shealer and Burger, 1993) and temperate roseate tern populations (Duffy, 1986). The largest flocks recorded along the study were over blue water and exposed coast habitats, and comprised 95 roseate tern and 44 common tern individuals, respectively.

Roseate terns were prone to forage in single-species flocks over deep, oceanic blue water (Table 1) as previously reported around colonies in Puerto Rico (Shealer, 1996). Nonetheless, capture rate was higher in the

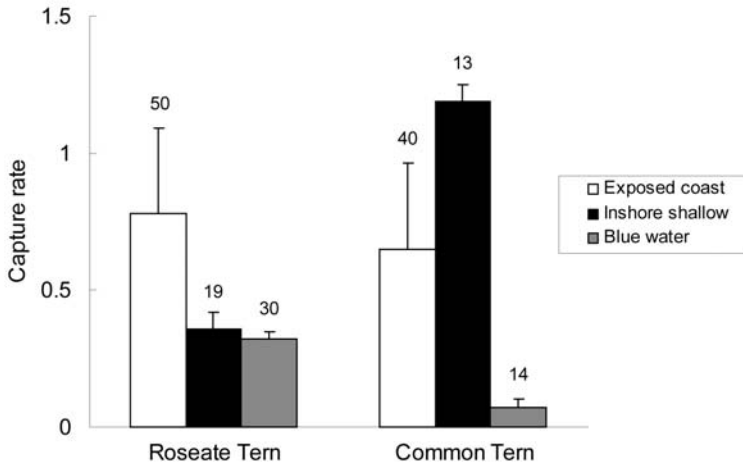


FIG. 4.—Capture rate (no. of fish caught  $\text{min}^{-1}$ ) of roseate and common terns recorded in different foraging habitats during the 2001 breeding season on Terceira Island, Azores (mean  $\pm$  SE;  $n$  at top of bars). [*Tasa de captura de peces por minuto de los charranes rosados y comunes registradas en distintos hábitats (costas expuestas al oleaje, costas no expuestas a oleaje y aguas abiertas) en la temporada reproductiva del año 2001 en la isla de Terceira, Azores (media  $\pm$  SE, n sobre las barras).*]

most frequented habitat, namely exposed coast, which is consistent with theory of optimal food intake rate (Krebs and Kacelnik, 1991). In contrast, common tern foraging success was high in shallow-waters (bays), although we recorded few common tern flocks in that habitat. Elsewhere common terns have been found to exhibit a preference for calm, inshore shallow-waters (e.g., Langham, 1968; Burger and Gochfeld, 1991). However this foraging habitat was relatively scarce in the study area, and common terns were often recorded in exposed coast and, to a lesser extent, over blue water. In these latter habitats, they aborted more dives (as roseate terns did) probably due to more agitated waters, and achieved a low success rate reflecting their lower ability to forage under oceanic conditions compared to roseate terns.

#### *Association with biotic effects*

The mean foraging rates obtained for roseate terns (diving rate, capture rate) in this study

fall within the range of those found at other temperate and tropical colonies in the Atlantic Ocean (Table 3). The highest values are recorded around tropical colonies when birds forage in association with biotic effects (Shealer, 1996; Table 3). In tropical seabirds in general (Ballance and Pitman, 1999), and roseate terns in particular (Shealer, 1996; Ramos, 2000), the interaction with subsurface predators is an important feeding strategy, presumably as a direct consequence of the more patchy distribution of prey relatively to non-tropical areas. Dense flocks associated to biotic effects (predatory fishes / Cory's shearwater) were less frequently observed in this study (24 % of flocks) than at other tropical locations (e.g., 84 % of flocks in Puerto Rico; Shealer, 1996), therefore this association should be less important for roseate terns in the Azores than in the tropics.

Unlike roseate terns, common terns were twice more numerous at mixed flocks in association with biotic effects, which suggests that their foraging decisions were related to the

TABLE 3

Comparison of diving rate (no. of diving attempts  $\text{min}^{-1}$ ) and capture rate (number of fish caught  $\text{min}^{-1}$ ) of roseate terns from two locations in the North Atlantic. Given are minimum, maximum and mean values. [*Comparación de las tasas de inmersiones y capturas por minuto del charrán rosado en dos localidades del océano Atlántico norte. Se dan los valores mínimos, máximos y la media.*]

Location [Localidad]	n	Diving rate	Capture rate	Type of association	Reference
Tropical Atlantic (Puerto Rico, Caribbean)	52	1.5 – 2.5	0.3 – 0.5	None	Shealer, 1996
Tropical Atlantic (Puerto Rico, Caribbean)	25	1.5 – 9.6	0.7 – 2.3	Biotic effects	Shealer, 1996
Temperate Atlantic (Long Island, US)	235	1.0 – 1.7	0.3 – 0.5	None/Biotic effects <sup>1</sup>	Safina, 1990a

<sup>1</sup> No difference made between the two situations in the study.

association with predatory fishes (biotic features). Over blue waters and exposed coasts, the water column is deeper with fish presumably less accessible for terns than in shallow-waters where prey movement is limited downwards. Since roseate terns are able to dive deeper (Nisbet, 1981), it might be assumed that the passive role of subsurface predators that force prey close to the water surface is more important for common terns (Safina, 1990a, 1990b). Common terns have been previously found to benefit from the association with predatory fishes in North America (Safina and Burger, 1985; Safina, 1990a).

#### *Interspecies competition*

Our GLM results suggest that, while the number of dives increased for both species in the presence of predatory fish (and aborted rate decreased), there was no subsequent increase in capture rates. Thus, at these flocks, interspecific competition may have adversely affected foraging success of roseate and common terns. In North America, the success rate of the roseate tern at mixed flocks associated with predatory fish is depressed by the com-

mon tern (Safina, 1990b), because roseate tern individuals are less able to maintain central positions in the flock where prey is concentrated. This competitive inferiority is related to different factors acting together such as a numerical inferiority, a lower ability to hover for long periods (Nisbet, 1981), and a slightly smaller size compared to common terns (Safina, 1990b). In this study, however, the association with biotic effects had no effect on the capture rate of roseate terns. Therefore, although morphological differences with common terns could, at least in part, have put the species at a competitive disadvantage in the presence of predatory fish, this effect may have been counterbalanced by their numerical dominance at most flocks (prediction 2).

#### *Effect of weather*

Weather conditions such as wind speed and cloud cover influence the foraging ability of terns (Dunn, 1973). Strong cloud cover may affect visibility of prey at distance by foraging terns, but this variable had no significant effect on foraging success in this study, presumably owing to the mild and consistent condi-

tions encountered. Stormy conditions may depress capture success of common terns (Frank, 1992), but moderate winds facilitate prey capture compared to absence of wind (Dunn, 1973). Wind speed requirements are seemingly higher for roseate terns (Safina, 1990a) but strong evidence of an optimum is still lacking (Ramos *et al.*, 2002). In this study, wind speed ranged from 0 - 58 km h<sup>-1</sup>, and no effect on diving and capture rates was detected in the analyses. However, both species had a tendency to abort fewer dives as wind increased. In Forster's terns *S. forsteri*, diving rate, but not success rate, decreased significantly as wind conditions changed from no wind to moderate wind (Reed and Ha, 1983). This was suspected to result from an improvement of aerodynamic stability (i.e., ability to hover for longer periods; Reed and Ha, 1983), which may also contribute to explain the decrease in number of aborted dives observed here.

### Conservation implications

Altogether, our results paralleled a recent study at Rockabill (Irish Sea), the major roseate tern breeding site in Europe (Ratcliffe, 2001; Ratcliffe *et al.*, 2004), where most of them were found foraging within 3.5 km of the colony, with a strong preference exhibited for open waters 20 - 30m deep (Newton and Crowe, 2000). Roseate terns in the Azores were foraging primarily within 5 km of the breeding islet (*unpub. data*), along exposed coasts and over blue water, seldom recorded feeding in bays. The large area occupied by the first two habitats in the vicinity of Terceira Island may contribute to explain the large number of roseate terns breeding at this colony site in 2001 (350 pairs; 1/4 of the Azores population). On the other hand, the restricted area covered by shallowwaters (bays), as well as the relative low predatory fish activity detected under foraging flocks, may help to explain why common terns do not breed there in high numbers, relative to their

overall population size in the Azores (220 pairs; 1/10 of the Azores population).

Because feeding activities of terns were concentrated along the coastal areas of Terceira Island, we believe that this ecosystem is of great importance to the conservation of common and roseate terns during the breeding season, and should therefore be protected by the Regional Government. In practical terms, this goal should be partly met by extending the special protection area (*sensu* E.C. Birds Directive), currently virtually restricted to the breeding site only, towards nearby exposed coasts and oceanic waters.

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