FORAGING HABITAT USE AND PROFITABILITY IN TROPICAL ROSEATE TERNS AND SANDWICH TERNS

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ABSTRACT.—I studied the foraging habitat use of Roseate Terns (*Sterna dougallii*) and Sandwich Terns (*S. sandvicensis*) in southwestern Puerto Rico from 1991 to 1994, and determined foraging success of each species in three distinct habitat types: blue water, inshore shallows, and along reefs. The proportion of Roseate Tern foraging flocks differed significantly among the three habitat types, with over one-half of the flocks occurring in blue water. The proportion of Sandwich Tern flocks did not differ significantly among the three habitats. A higher proportion of Roseate Tern (84%) than Sandwich Tern (59%) foraging flocks occurred over schools of predatory fish, and mean flock size of Roseate Terns, but not of Sandwich Terns, was greater in the presence of predatory fish. Capture success (no. successful dives/ no. attempts) of Roseate Terns was highest in shallow-water habitats, when they pirated fish from Brown Pelicans (*Pelecanus occidentalis*) or used diving pelicans to scare fish to the surface. However, both capture rate (no. fish caught/min) and relative profitability (g fish caught/ min) were highest in blue-water flocks over predatory fish. Foraging success of Sandwich Terns was measured only for shallow-water habitats, and did not differ when foraging with or without pelicans. These results suggest that Roseate Terns in Puerto Rico forage primarily in habitats that result in the highest rate of prey capture. Moreover, Roseate Terns may rely heavily on predatory fish or pelicans to increase prey availability to them during the breeding season, whereas Sandwich Terns rely less on these sources to facilitate prey capture. *Received 24 March 1995, accepted 20 June 1995.*

THEORETICALLY, an animal should forage most frequently in a habitat or patch where its capture success or net energy gain is maximized (Krebs and Cowie 1976). Some studies of terrestrial birds have confirmed this prediction (Smith and Dawkins 1971, Wakeley 1978). In recent years, much attention has been devoted to studies of foraging habitat preferences among seabirds (Abraham and Ankney 1984, Haney 1986, Safina 1990a, Ainley et al. 1993, Becker et al. 1993). However, few studies have determined the relationship between foraging success in patches of variable quality and relative patch use (but see Brandt 1984). In marine ecosystems, patches are temporally unstable, as prey usually are mobile. Thus, most investigators studying foraging habitat selection in seabirds have confined themselves to the larger habitat scale rather than to prey patches (but see Safina 1990a).

Previous studies of Roseate Terns (*Sterna dougallii*) indicate that this species is relatively specialized in both its use of foraging habitat and in the diversity of prey adults feed to chicks. For example, both Safina (1990a) and Heinemann (unpubl. 1992 report) found that foraging Roseate Terns are attracted to specific features,

such as tide rips and shoals, that bring prey close to the water surface. At several mixed-species colony sites, prey delivered by Roseate Terns to chicks were less diverse than prey delivered by Common Terns (*S. hirundo*; Richards and Schew 1989, Safina et al. 1990, Shealer and Kress 1994). Thus, the limited diversity of prey taken by Roseate Terns may be a consequence of foraging habitat specialization, rather than diet preference per se.

I studied foraging habitat use and profitability in tropical Roseate Terns and, to a lesser extent, Sandwich Terns (*S. sandvicensis*) in southwestern Puerto Rico. I characterized the habitats in which Roseate and Sandwich terns typically foraged, and determined whether the frequencies at which Roseate Terns occurred in specific habitats were related to foraging success or profitability. Previous studies have indicated that Roseate Terns in Puerto Rico forage over schools of predatory fish (Shealer 1992, Shealer and Burger 1993), but the extent of this association has not been quantified. Roseate and Sandwich terns are the only two plunge-diving terns that breed in the study region. This situation provided an opportunity to compare
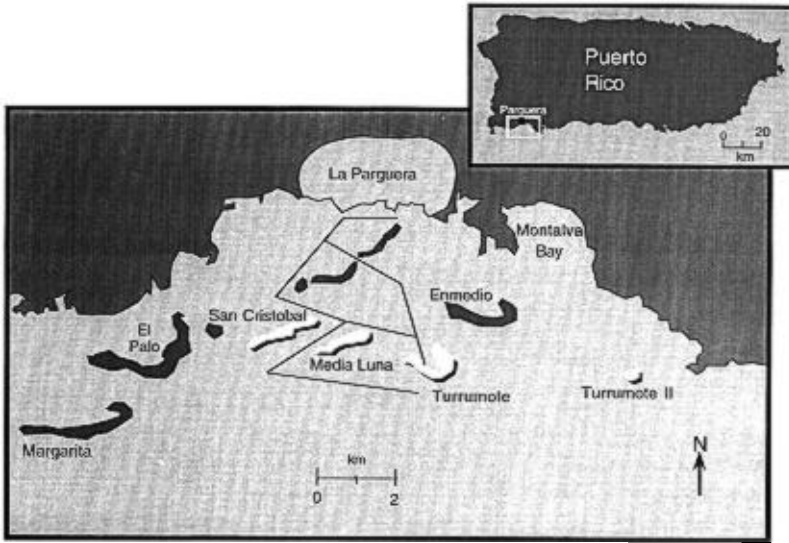
Fig. 1. Map of study area in southwestern Puerto Rico, showing cayos of La Parguera (with tern colonies in white). Routes of boat surveys conducted in 1993 indicated by lines.

habitat use and foraging success of these species, and to examine potential negative interactions between them.

Roseate Terns breed in both temperate and tropical areas (Cramp 1985). However, the worldwide breeding range of this species is fragmented (Gochfeld 1983), with small, isolated breeding populations that fluctuate drastically in number and colony-site selection among years (Britton and Brown 1974, Hulsman 1977, Avery 1991, Shealer 1995). Temperate Zone Roseate Tern populations in northwestern Europe have declined to critical levels (Avery 1991), in South Africa have been reduced to just two breeding sites (Randall and Randall 1981), and in northeastern North America recently have been listed as endangered (U.S. Fish and Wildlife Service 1987). The stronghold of this species is in tropical areas, particularly in the Indian Ocean (Gochfeld 1983), but little is known about its breeding biology or foraging ecology in the tropics.

STUDY AREA AND METHODS

I studied Roseate and Sandwich terns near several colony sites (Fig. 1) in southwestern Puerto Rico (17°56'N, 67°05'W) from mid-May to mid-July in 1991 through 1993, and from mid-May to mid-June 1994. Roseate and Sandwich terns nested together on two cays each year, but birds shifted colony sites among

years. The two species arrived in the area in early May and foraged in the surrounding waters. Colony selection and the onset of egg laying usually occurred by the third week of May. The breeding season was short, with most adults and fledglings departing the area by early August.

In 1993, I conducted boat surveys through all potential foraging habitats for Roseate and Sandwich terns near breeding colony sites (Fig. 1). Each survey consisted of one to five linear transects run through discrete habitats: mangrove channels ($n = 28$ transects); inshore shallows ($n = 28$); inshore ($n = 28$) and offshore ($n = 33$) reef zones; and blue water ($n = 19$). Mangrove channels were defined as shallow (<3 m), turbid waters adjacent to shore that were lined with red mangroves (*Rhizopora mangle*). Inshore, shallow-water areas were defined as calm, clear water less than 10 m deep. Reef zones encompassed shallow water surrounding inner and outer reefs, extending to a distance of approximately 20 m from the reef and to a 10-m depth. Blue water was defined as deeper oceanic water, more than 10 m deep, and characterized by sea swells and strong currents. Inshore, reef, and blue water habitats were easy to distinguish because of sharp contrasts in water color.

At five-day intervals during the breeding season, two surveys were made each day at a constant boat speed of 5 km/h, one in the morning (0700–0800 AST), and the other in the afternoon (1600–1700), at times when terns were feeding actively. Transect length was approximately 1 km for each habitat, and transect width was approximately 100 m on either side of the boat. During a given survey period, only one transect was run through a particular habitat, but routes were

such that not all habitats were sampled during each survey. However, transect lengths and durations were similar among all habitats; thus, the number of transects provided a comparable index of total time and area coverage for each habitat. During each transect, location, species composition and flock size of foraging terns were plotted on a nautical chart. The presence or absence of predatory fish also was noted. When present, predatory fish were conspicuous at the water surface, feeding on smaller prey fish. Due to the mobility of feeding flocks, a single flock potentially could have been included in two adjacent transects (e.g. inshore shallows and reef); when this situation arose, I recorded flock characteristics and location only during the first time the flock was encountered. In 1991, 1992, and 1994, I also observed foraging flocks from an offshore cay where, during a 360° scan, I could sample all habitats except mangrove channels. Data collected in 1993 initially were analyzed separately from the other years.

In addition to surveys, foraging success of individual Roseate and Sandwich terns was recorded in different habitats on an opportunistic basis. I conducted these observations (=trials) by selecting a single individual from the flock and watching it through binoculars for the duration of its feeding bout or until I lost sight of it. I timed each trial with a stopwatch, recording success and failure of all foraging attempts. Roseate and Sandwich terns plunge dive for fish from variable heights and emerge from the water with the fish held crosswise in the bill before swallowing; thus, foraging success was easy to quantify. Capture success was defined as the number of captures divided by the number of attempts. I excluded from analyses any trial in which I could not determine the outcome for all observed attempts of a single individual. In addition, each trial was standardized such that attempts and captures were expressed as a rate. Attempt and capture rates were defined as the number of attempts and captures per minute. This procedure weighted the foraging performance of each individual equally, regardless of the length of time I followed it or the number of attempts it made. However, only terns that made five or more attempts were included in the analyses. This minimum criterion was used to reduce the contribution of a single attempt to an individual's overall performance, and should not have biased the results toward less successful birds, because the mean number of fish caught per foraging trip for Roseate Terns was 11.8 and for Sandwich Terns was 4.1 (Shealer 1995).

In 1993, I sampled prey fish of the terns in two ways. In shallow-water areas, I observed with binoculars the species and sizes of prey caught by foraging terns. The length of each fish was estimated by comparing it to the length of the tern's bill (ca. 35 mm). Following these observations, I used a cast net (2.5 m diameter, 0.6 cm mesh) to catch fish under foraging terns. Prey samples were stored temporarily
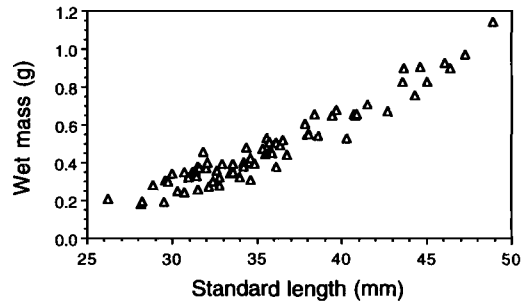

Fig. 2.   Regression of wet mass on standard length of dwarf herring caught by cast net in Turrumote lagoon in 1993. Best-fit curve is second-order polynomial ($F_{2,68} = 506.8$, $P < 0.001$, $R^2 = 0.937$). Equation is $y = 0.307 - 0.028x + 0.00089x^2$, where y is wet mass in grams and x is standard length in millimeters.

in ethanol and transported to the laboratory. I sorted the fish by species, weighed each fish (to nearest 0.01 g) using an electronic balance, and measured with calipers the standard length (to nearest 0.05 mm) from the tip of the snout to the posterior end of the caudal peduncle. I then regressed wet mass on standard length for each species to estimate the mass of each fish caught by terns in shallow-water areas. Figure 2 shows the mass/length relationship for dwarf herrings (*Jenkinsia lamprotaenia*). I sampled fish from blue-water habitats by concealing myself in a blind in the middle of a ternery, locating individual terns returning from blue-water feeding flocks that were visible from the colony, and then capturing the terns on the nest using a wire-mesh treadle trap placed over the eggs. This procedure often caused terns to regurgitate. Regurgitated boluses were collected and analyzed as above.

Dwarf herrings were the primary prey items taken by Roseate Terns, comprising over 85% of all catches in all habitats (Shealer 1995). For this reason, I estimated profitability (g of fish ingested/min) to Roseate Terns foraging in different habitats, using data only on dwarf herrings. This analysis was not conducted for Sandwich Terns because this species fed on a greater diversity of prey, both within and among habitats, than did Roseate Terns (Shealer 1995).

Data on habitat use were analyzed using chi-square values computed from contingency tables. Data on flock size differences among habitats often had disparate sample sizes and were resistent to normalizing transformation, necessary to meet the assumptions of analysis of variance. Thus, I opted to analyze these data using the nonparametric Kruskal-Wallis test (Sokal and Rohlf 1981:429). When variances between two-sample analyses were heteroscedastic, I used an unequal-variances *t*-test, which calculates an approximate *t*-value and compares it to a critical value of *t*, determined from the weighted average of the critical values of *t* based on the degrees of freedom from the

TABLE 1. Number of transects conducted and locations of Roseate and Sandwich tern foraging flocks encountered during boat surveys in southwestern Puerto Rico, 1993.

| Location | No. transects | No. flocks (%) with | |
		Roseate Terns	Sandwich Terns
Mangrove channel	28	0 (0.0)	0 (0.0)
Inshore shallows	28	6 (21.4)	5 (17.9)
Inshore reef	28	2 (7.1)	9 (32.1)
Outer reef	33	2 (6.1)	1 (3.0)
Blue water	19	11 (57.9)	6 (31.6)

two samples (Sokal and Rohlf 1981:408). I used regression analysis to explain variation in mean flock size of the two tern species throughout the nine weeks of the breeding season.

RESULTS

Foraging habitat use and flock size.—During 48 boat surveys (136 transects) in 1993, I encountered 31 tern flocks: 10 flocks containing only Roseate Terns, 10 flocks containing only Sandwich Terns, and 11 flocks containing both species. Both Roseate and Sandwich terns were observed foraging in all habitats except mangrove channels. Habitat use by Roseate Terns differed among inshore shallows, reefs, and blue water ($X^2 = 24.5$, df = 2, $P < 0.001$; Table 1). One-half of Roseate Tern flocks occurred in blue water. In contrast, the frequency of Sandwich Tern flocks did not differ among the three habitats ($X^2 = 2.78$, df = 2, $P > 0.20$; Table 1).

Association of Roseate and Sandwich tern flocks with different habitats in 1993 did not differ from all other years combined (Roseate Tern, $X^2 = 0.30$, df = 2, $P > 0.80$; Sandwich Tern, $X^2 = 4.11$, df = 2, $P > 0.10$; Table 2). I pooled all flock data (1991 to 1994) to increase sample size in subsequent analyses. Blue-water and reef flocks of Roseate Terns were, on av-

erage, twice as large as inshore flocks (Fig. 3), but because of one inshore flock of over 100 Roseate Terns, no statistical difference was evident (Kruskal-Wallis test, $H = 4.43$, df = 2, $P = 0.11$). Flock size of Sandwich Terns also did not differ significantly among habitats ($H = 0.71$, df = 2, $P = 0.70$).

A greater proportion of Roseate Tern foraging flocks was associated with predatory fish (66/79 flocks, 83.5%) than were Sandwich Tern flocks (38/65 flocks, 58.5%; $X^2 = 9.9$, df = 1, $P < 0.001$). For all habitats combined, the mean flock size of Roseate Terns was greater in association with predatory fish (23.9 ± SE of 2.8) than when not (13.4 ± 4.5; unequal variances, $t = 2.22$, df = 44, $P = 0.032$). Flock size of Sandwich Terns did not differ significantly in the presence (6.8 ± 1.4) or the absence (4.0 ± 1.1) of predatory fish ($t = 1.57$, df = 58, $P = 0.121$).

Over the nine weeks of the breeding season (all years pooled; week one = 14 to 20 May), flock size of Roseate Terns increased (linear regression, $F_{1,55} = 6.05$, $P = 0.017$, Fig. 4A). Flock size in Sandwich Terns reached a peak between weeks 5 and 7 (11 to 30 June), coinciding with the chick-rearing period in most years, and then decreased after this period (Fig. 4B). However, the linear relationship was not significant ($F_{1,45} = 3.26$, $P = 0.078$). The second-order polynomial regression increased the R^2-value (from 0.07 to 0.09), but decreased the significance level ($P = 0.124$).

Foraging success and profitability.—The success of prey capture by Roseate Terns differed significantly among the four situations in which it was measured (Kruskal-Wallis test, $H = 13.7$, df = 3, $P = 0.003$). Roseate Terns achieved the highest capture success in inshore shallow water when associated with Brown Pelicans (*Pelecanus occidentalis*; Table 3). Diving pelicans served as beaters, churning fish to the surface where terns could capture them. Success was significantly lower in the absence of pelicans

TABLE 2. Locations of Roseate and Sandwich tern foraging flocks in three general habitats in 1993, compared to all other years (1991, 1992, 1994).

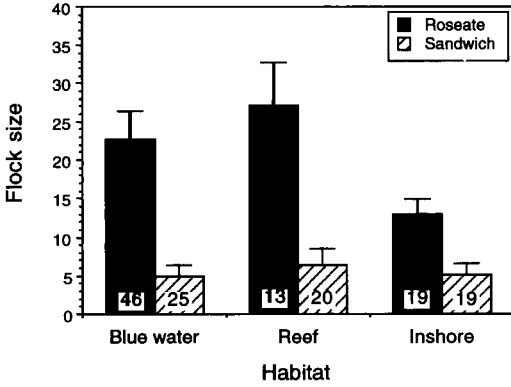| Location | No. flocks (%) with | | | |
| | Roseate Terns | | Sandwich Terns | |
	1993	All other	1993	All other
Inshore shallows	6 (28.6)	14 (24.1)	5 (23.8)	15 (34.1)
Reef	4 (19.0)	9 (15.5)	10 (47.6)	10 (22.7)
Blue water	11 (52.4)	35 (60.3)	6 (28.6)	19 (43.2)

Fig. 3. Sizes ($\bar{x}$ with whisker indicating SE and n given at base of each bar) of Roseate and Sandwich tern foraging flocks in three habitats in southwestern Puerto Rico, 1991–1994.

and in blue-water flocks both with and without predatory fish. I was unable to measure capture success of Roseate Terns foraging over reefs. However, as most of the reef flocks occurred over predatory fish, I assumed that capture success did not differ appreciably from blue-water situations over predatory fish. Both attempt rate ($H = 30.7, P < 0.001$) and capture rate ($H = 20.4$, $P < 0.001$) also differed among the four situations. Attempt and capture rates were significantly higher for Roseate Terns in blue-water flocks when over predatory fish compared to when predatory fish were absent (Table 3). Foraging in association with pelicans improved capture rate significantly for Roseate Terns, but not attempt rate.

Foraging success of Sandwich Terns was determined only in shallow-water areas where they foraged either with or without pelicans. No significant differences for any measure of foraging performance were evident for Sandwich Terns in these two situations (Table 3), perhaps due to the small sample size of this species foraging with pelicans.

Dwarf herring caught by Roseate Terns differed in body size between shallow- and deep-water areas. Estimated mean mass of individual prey fish caught by terns in inshore shallows was 0.59 ± 0.06 g ($n = 122$), whereas regurgitations of adult Roseate Terns that had been foraging in blue water averaged 0.20 ± 0.06 g/fish ($n = 84$). This size differences of prey fish between habitats resulted from the larger adult clupeids (dwarf herrings, sardines [*Harengula* spp.]) moving to inshore waters to spawn,
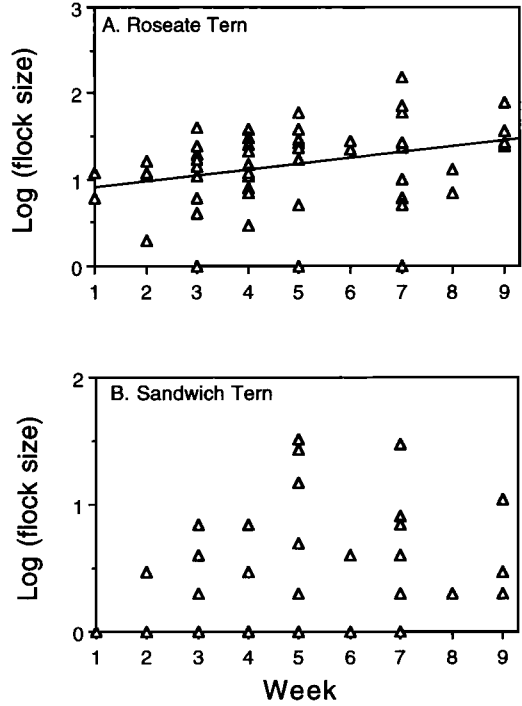

Fig. 4. Sizes of individual foraging flocks for (A) Roseate and (B) Sandwich terns during the nine weeks of the breeding season, with week 1 beginning 14 May and week 9 beginning 8 July. Data pooled for all years (1991–1993). Regression equations where y is size of foraging flock and x is week of breeding season, were: for Roseate Tern, $y = 1.73 + 4.25x$ ($R^2 = 0.140$); and Sandwich Tern, $y = -4.05 + 3.32x - 0.26x^2$ ($R^2 = 0.067$).

whereas juveniles were strictly pelagic (Shealer 1995). Profitability to Roseate Terns feeding in each situation was calculated by multiplying mean capture rate by the mean mass of an individual dwarf herring (0.59 g in shallow water, 0.20 g in blue water), expressed as grams of fish ingested per minute.

The mean profitability for Roseate Terns differed among the four situations (Kruskal-Wallis test, $H = 21.1$, df $= 3$, $P < 0.001$). In inshore shallows, profitability was greater when terns fed with (0.42 ± 0.11 g/min) than without (0.18 ± 0.04) Brown Pelicans (Mann-Whitney $U = 103.5, P = 0.036$). Profitability in blue water also differed markedly, when terns fed with (0.45 ± 0.07 g/min) or without (0.09 ± 0.03) predatory fish ($U = 33.5$, $P < 0.001$). Thus, in both blue- and shallow-water foraging situations, profitability to Roseate Terns was increased by foraging over predatory fish and in association with

TABLE 3. Summary of Roseate and Sandwich tern foraging success ($\bar{x} \pm$ SE) in different habitats, 1991–1994. Mann-Whitney U-statistics are presented with associated probabilities for comparisons within habitats (inshore shallows, blue water).

Habitat	No. indi-viduals	Capture success (%)	Obser-vation time (min)	Attempts/min	Captures/min
Roseate Tern					
Inshore shallows					
Without pelicans	23	26.2 ± 6.2	66.8	1.48 ± 0.27	0.31 ± 0.07
With pelicans	15	63.7 ± 10.7	29.7	1.52 ± 0.25	0.72 ± 0.19
Mann-Whitney U		85.5**		154.5	104.1*
Blue water					
Without predatory fish	29	18.0 ± 4.8	39.4	2.46 ± 0.31	0.46 ± 0.13
With predatory fish	10	28.5 ± 4.7	11.3	9.58 ± 1.38	2.27 ± 0.35
Mann-Whitney U		80.5		5.0***	33.5***
Sandwich Tern					
Inshore shallows					
Without pelicans	18	41.5 ± 6.7	65.2	1.57 ± 0.24	0.61 ± 0.11
With pelicans	7	52.4 ± 13.1	33.8	1.23 ± 0.32	0.52 ± 0.12
Mann-Whitney U		55.5		79.0	67.5

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

pelicans, respectively. I was unable to make comparisons of profitability for Sandwich Terns.

DISCUSSION

Roseate Terns in southwestern Puerto Rico showed distinct preferences for foraging in blue water compared to all other habitats, whereas Sandwich Terns used all foraging habitats, except mangrove channels, in approximately equivalent proportions. Most Roseate Tern foraging flocks, but a smaller proportion of Sandwich Tern flocks, occurred in association with predatory fish. Foraging habitat had no significant effect on mean flock size of either Roseate or Sandwich terns. However, Roseate Tern flocks over predatory fish were significantly larger than those feeding in the absence of predatory fish. Mean flock size of Sandwich Terns was not affected by the presence of predatory fish. These results indicate that: (1) Roseate Terns are more strongly attracted to the activities of predatory fish than are Sandwich Terns; and (2) Roseate Terns in southwestern Puerto Rico did not exhibit the same preferences for physical features of the ocean, as found by Safina (1990a) and Heinemann (unpubl. 1992 report), for this species in northeastern North America. Although a majority of Roseate Tern flocks occurred in blue water, there was no predictable daily pattern to the specific location of Roseate Tern for-

aging flocks in this habitat, except that terns usually were located over predatory fish, which were highly mobile. If the blue-water habitat surrounding the tern colonies had some inherent physical attributes attractive to foraging terns, I would have expected to find flocks in the same locations on different days. The evidence from this study indicates that Roseate Terns specialized on a biotic factor, namely the presence of predatory fish, to make prey available to them.

Despite the high capture success in inshore shallows, Roseate Terns foraged primarily in blue-water flocks. Clearly, this was because mean capture rate for Roseate Terns in blue-water flocks over predatory fish was four times as high as in any other situation. Even though capture success was low and the fish were smaller in blue-water habitats, profitability (mean mass of fish ingested per unit time) to Roseate Terns was high. Sandwich Terns showed less of a propensity than Roseate Terns to forage in blue-water flocks over predatory fish. I attribute this difference to the small size of individual prey in these situations. Sandwich Terns select larger prey than Roseate Terns, both for themselves and for their chicks (Shealer 1995). The mean bolus mass regurgitated by adult Sandwich Terns was 8.3 g. Assuming that the capture rate for Sandwich Terns is at least as high as that of Roseate Terns in blue-water flocks over pred-

atory fish, Sandwich Terns would have to catch 41.5 fish to obtain 8.3 g of fish. This would require 18 min of continuous foraging, assuming that prey are constantly available during the entire period. The mean bolus mass regurgitated by adult Roseate Terns was 3.2 g, indicating that they would have to catch 16 fish, requiring only 7 min of continuous foraging. However, observations of blue-water flocks in 1991 indicated that prey actually were available only about 33% of the time that flocks were cohesive. That is, there would be a period of fierce activity, during which terns would repeatedly plunge to the surface, followed by a period of no plunging while terns tracked fish schools below the surface. Thus, Sandwich Terns would need to associate in these flocks for nearly an hour at a time to catch 8.3 g of fish, while Roseate Terns could catch 3.2 g of fish in about 20 min.

Although data on foraging habitat selection in Roseate Terns are scant, three previous studies are relevant to this one. Hulsman (1989) found that Roseate Terns in Australia fed primarily in the open sea and at greater distances from the colony, on average, than did other sympatric species of inshore terns. This information suggests to me that Roseate Terns were tracking schools of predatory fish offshore, but Hulsman did not mention this in his paper. Heinemann (unpubl. 1992 report) noted that Roseate Terns in Massachusetts traveled up to 30 km from the breeding colony to forage and were attracted both to biotic (predatory fish), as well as physical (shoals and tide rips) features. Safina (1990a) found that most Roseate Tern flocks he observed occurred in association with physical, rather than biotic, features of the ocean. Thus, the important common factor is some extrinsic mechanism that forces fish to the surface. In Puerto Rico, this factor was the activities of predatory fishes.

The association of foraging seabirds with other marine animals has been well documented in both temperate and tropical seas (see chapters in Burger 1988), and seabird feeding flocks are recognized by fishermen as cues to locating larger game fishes (Erdman 1967). Presumably, these relationships either facilitate prey location for, or enhance the foraging success of, seabirds that engage in them. Until recently it was thought that these associations were incidental, or facultative at best (Evans 1982). However, new evidence suggests that some species of seabirds rely heavily on foraging associations with subsurface animals, and that these relationships may be obligatory during certain periods of the year, particularly in the tropical seas (Au and Pitman 1986, Pitman and Ballance 1992). Since tropical oceans are more resource-depauperate than temperate seas, these associations may be critical for foraging seabirds to find enough food to survive or to rear chicks. However, the actual benefit to seabirds engaged in these associations, relative to foraging on their own, has not been documented conclusively until my study.

Foraging Roseate Terns may rely heavily on predatory fish in the Caribbean. First, as I have reported, Roseate Terns experience a much higher prey-capture rate when foraging over predatory fish than all other situations. Second, although the breeding season for Roseate Terns in the Caribbean is seasonal (May to July), prey fish are present in coastal waters throughout the year, with the best catches by humans reported in autumn (Wagner and Wolfe 1974, Kimmel 1991). However, nearshore abundance of larger predatory fishes may coincide with the terns' breeding season. In the Dry Tortugas, juvenile scombrids (mackerels, tunas) were absent from the diet of Sooty Terns (*Sterna fuscata*) in April, but became more common in June and July, suggesting that spawning occurs in that area in the spring (Potthoff and Richards 1970). Major sport-fishing tournaments are held in Puerto Rico every year in June and July, when scombrids and other predatory fishes are landed close to shore. Since 1991, the first predatory fish activity around the tern colonies has been between 15 and 25 May (pers. obs.), in close parallel to laying of first eggs of the season for Roseate Terns. Thus, there may be a causal relationship between the inshore arrival of predatory fishes and the onset of egg laying in terns. However, additional years of data are needed to confirm such a relationship.

One problem that Roseate Terns encounter in some parts of their breeding range is foraging-flock competition with other species. Physical or biotic situations that cause prey to be brought to the surface attract not only Roseate Terns, but other species as well. In areas where they have been studied, Roseate Terns do not appear to be good competitors in dense foraging flocks. Duffy (1986) showed that Common Terns (*Sterna hirundo*) in New York force Roseate Terns to peripheral areas of the flock,

where prey are less dense. As a result, foraging success of Roseate Terns is depressed in flocks containing Common Terns over predatory fish (Safina 1990b). Shealer and Burger (1993) found that Roseate Terns in Puerto Rico have lower attempt rates in flocks with Brown Noddies (*Anous stolidus*) relative to monospecific flocks and, thus, tend to avoid large noddy flocks. Noddies in Puerto Rico appear to form large flocks only when predatory fish are active, and the mutual attraction to this situation is detrimental to Roseate Terns (Shealer and Burger 1993). Thus, interference by other species in foraging flocks can depress foraging success of Roseate Terns and may be one reason why breeding populations are small and fragmented throughout most of the species' range (Gochfeld 1983).

Brown Noddies do not breed in southwestern Puerto Rico and, except for occasional transients, they are absent from the area during the Roseate Tern's breeding season. As Roseate Terns are the only species in the area that forms large flocks over predatory fish, they are not affected drastically by interspecific competition, and there are apparently no negative intraspecific effects in foraging flocks (Shealer and Burger 1993). Mean flock size of Roseate Terns foraging over predatory fish was nearly twice as great than that of flocks in the absence of predatory fish. Moreover, capture success and capture rate were both higher in blue-water flocks over predatory fish relative to flocks in the absence of predatory fish. The disparity between my results and those of Safina (1990b) is most likely due to the effects of interspecific foraging competition in New York, a factor not found in southwestern Puerto Rico.

LITERATURE CITED

ABRAHAM, D. M., AND C. D. ANKNEY. 1984. Partitioning of foraging habitat by breeding Sabine's Gulls and Arctic Terns. Wilson Bull. 96:161–172.

AINLEY, D. G., C. A. RIBIC, AND L. B. SPEAR. 1993. Species-habitat relationships among Antarctic seabirds: A function of physical or biological factors? Condor 95:806–816.

AU, D. W., AND R. L. PITMAN. 1986. Seabird interactions with dolphins and tuna in the Eastern Tropical Pacific. Condor 88:304–317.

AVERY, M. 1991. Roseate Tern *Sterna dougallii*. Pages 204–215 *in* The status of seabirds in Britain and Ireland (C. Lloyd, M. L. Tasker, and K. Partridge, Eds.). T. and A. D. Poyser, London.

BECKER, P. H., D. FRANK, AND S. R. SUDMANN. 1993. Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. Oecologia 93:389–393.

BRANDT, C. A. 1984. Age and hunting success in the Brown Pelican: Influences of skill and patch choice on foraging efficiency. Oecologia 62:132–137.

BRITTON, P. L., AND L. H. BROWN. 1974. The status and breeding behaviour of East African Lari. Ostrich 45:63–82.

BURGER, J. (ED.). 1988. Seabirds and other marine vertebrates: Competition, predation and other interactions. Columbia Univ. Press, New York.

CRAMP, S. (ED.). 1985. The birds of the western Palearctic, vol. 4. Oxford Univ. Press, Oxford.

DUFFY, D. C. 1986. Foraging at patches: Interactions between Common and Roseate terns. Ornis Scand. 17:47–52.

ERDMAN, D. 1967. Sea birds in relation to game fish schools off Puerto Rico and the Virgin Islands. Carib. J. Sci. 7:79–85.

EVANS, P. G. H. 1982. Associations between seabirds and cetaceans: A review. Mammal. Rev. 12:186–206.

GOCHFELD, M. 1983. The Roseate Tern: World distribution and status of a threatened species. Biol. Conserv. 25:103–125.

HANEY, J. C. 1986. Seabird patchiness in tropical oceanic waters: The influence of Sargassum "reefs." Auk 103:141–151.

HULSMAN, K. 1977. Breeding success and mortality of terns at One Tree Island, Great Barrier Reef. Emu 77:49–60.

HULSMAN, K. 1989. The structure of seabird communities: An example from Australian waters. Pages 59–91 *in* Seabirds and other marine vertebrates: Competition, predation and other interactions (J. Burger, Ed.). Columbia Univ. Press, New York.

KIMMEL, J. J. 1991. A fisheries dependent survey of baitfishes in Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 40:64–81.

KREBS, J. R., AND R. J. COWIE. 1976. Foraging strategies in birds. Ardea 64:98–116.

PITMAN, R. L., AND L. T. BALLANCE. 1992. Parkinson's Petrel distribution and foraging ecology in the eastern Pacific: Aspects of an exclusive feeding relationship with dolphins. Condor 94:825–835.

POTTHOFF, T., AND W. J. RICHARDS. 1970. Juvenile bluefin tuna, *Thunnus thynnus* (Linnaeus), and other scombrids taken by terns in the Dry Tortugas, Florida. Bull. Mar. Sci. 27:788–801.

RANDALL, R. M., AND B. M. RANDALL. 1981. Roseate Tern breeding biology and factors responsible for low chick production in Algoa Bay, South Africa. Ostrich 52:17–24.

RICHARDS, S. W., AND W. A. SCHEW. 1989. Species composition of food brought to Roseate Tern chicks on Falkner Island, Connecticut in summer 1984. Conn. Warbler 9:1–5.

SAFINA, C. 1990a. Foraging habitat partitioning in Roseate and Common terns. Auk 107:351–358.

SAFINA, C. 1990b. Bluefish mediation of foraging competition between Roseate and Common terns. Ecology 71:1804–1809.

SAFINA, C., R. H. WAGNER, D. A. WITTING, AND K. J. SMITH. 1990. Prey delivered to Roseate and Common tern chicks; composition and temporal variability. J. Field Ornithol. 61:331–338.

SHEALER, D. A. 1992. Behavioral and ecological factors affecting reproductive success in a threatened population of tropical Roseate Terns. M.S. thesis, Rutgers Univ., New Brunswick, New Jersey.

SHEALER, D. A. 1995. Comparative foraging ecology of Roseate and Sandwich terns in Puerto Rico and its relation to breeding performance. Ph.D. dissertation, Rutgers Univ., New Brunswick, New Jersey.

SHEALER, D. A., AND J. BURGER. 1993. Effects of interference competition on the foraging activity of tropical Roseate Terns. Condor 95:322–329.

SHEALER, D. A., AND S. W. KRESS. 1994. Post-breeding movements and prey selection of Roseate Terns at Stratton Island, Maine. J. Field Ornithol. 65: 349–362.

SMITH, J. N. M., AND R. DAWKINS. 1971. The hunting behavior of individual Great Tits in relation to spatial variations in their food density. Anim. Behav. 19:695–706.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman, San Francisco.

U.S. FISH AND WILDLIFE SERVICE. 1987. Endangered and threatened wildlife and plants: Determination of endangered and threatened status for two populations of the Roseate Tern. Federal Register 52:42064–42071.

WAGNER, D. P., AND R. S. WOLFE. 1974. Results of troll fishing explorations in the Caribbean. Mar. Fish. Rev. 36:35–43.

WAKELEY, J. S. 1978. Factors affecting the use of hunting sites by Ferruginous Hawks. Condor 80:316–326.