

FORAGING HABITAT PARTITIONING IN ROSEATE AND COMMON TERNS

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ABSTRACT.—I examined foraging by sympatrically breeding Roseate (*Sterna dougallii*) and Common (*S. hirundo*) terns to investigate whether habitat was partitioned, and whether use of foraging habitat was related to disparate population sizes between the species. Foraging Roseate Terns were associated with physical features such as shoals and drift lines more frequently than Common Terns were. Common Terns foraged under a wider range of habitat conditions than Roseate Terns did, and Common Terns were associated with predatory bluefish (*Pomatomus saltatrix*) more often. Flocks in which proportions of Roseate Terns were higher than expected (based on the relative sizes of the breeding populations) were smaller and less dense than other foraging flocks, and they formed at sites which were shallower, closer to shore, and windier. Roseate Terns were more successful in flocks in which proportions of Roseate Terns were higher than expected than when in other flocks. Common Terns' foraging efficiency was lower in flocks in which proportions of Roseate Terns were higher than expected than in other flocks. Roseate Terns have a smaller area of preferred foraging habitat available than do Common Terns, and this may be reflected in their population sizes. Received 11 May 1989, accepted 1 December 1989.

THE QUESTION of how species coexist has long been of interest, because to understand the differing mechanisms that allow coexistence is to comprehend much of the natural control of biological diversity (Schoener 1974a). When two sympatric, closely related species appear to have very similar needs, we may ask whether mechanisms exist that enable them to avoid direct competition. Implicit in this question is the presumption that two species with identical requirements cannot coexist (Gause 1934).

Roseate (*Sterna dougallii*) and Common (*S. hirundo*) terns are partially sympatric, closely related congeners, which occasionally hybridize (Hays 1975). Their North Atlantic range has largely overlapped throughout historical time, yet Roseate Terns appear always to have been far less numerous than Common Terns (Nisbet 1980). To address this question, the factors that limit these species must be identified. The Roseate Tern's northwest Atlantic population has recently been listed as "endangered" (Federal Register 52 FR 42064), which makes identification of limiting factors a matter of practical as well as academic interest. The recovery plan (Andrews et al. 1988) calls for quantitative investigations of their foraging ecology.

It has been observed that Roseate Terns sometimes feed separately from Common Terns (Nisbet 1981), that foraging Roseates are attracted to certain physical features, and that they follow

bluefish (*Pomatomus saltatrix*) less frequently than do Common Terns (Safina 1985, Kirkham and Nisbet 1987). However, Roseate and Common terns are frequently found in mixed flocks (Nisbet 1981, Duffy 1986), and at these times they take the same prey. Competition occurs between the species (Safina in press).

When species compete, the inferior competitor should be either driven to extinction (Gause 1934), forced to coevolve a habitat shift (Schoener 1974b), or limited to a "realized niche" (Hutchinson 1958) by competition. Because Roseate Terns in the northwest North Atlantic have long coexisted with Common Terns in relatively low numbers, it seems unlikely that Roseate Terns are being forced to extinction through competition with Common Terns (it is concern over human predation and colony-site loss that has resulted in this population's "endangered" designation). We might expect, then, to find evidence of partitioning mechanisms. The mechanisms by which species partition their habitat, not merely the presence of differences in habitat use, are of principal interest (Schoener 1974a).

In this study I sought to establish what quantitative differences exist in the physical and biotic characteristics of foraging habitat used by these two species, whether differential foraging efficiencies exist in different situations, and whether differences in foraging habitat use can

help explain the low relative numbers of Roseate Terns as well as their long coexistence with the numerically dominant Common Terns in this region. I made three predictions: first, that foraging-site characteristics would differ between species; second, that each species' foraging efficiency would be greater in their principal foraging situations; and third, that Roseate Terns' use of foraging habitat would be more specialized (they would forage in a smaller range of conditions), resulting in smaller exploitable foraging area.

METHODS

In 1984 and 1985 I worked among tern flocks on Long Island, New York, in the vicinity of Fire Island Inlet (near the Cedar Beach ternery; ca. 5,800 pairs of Common Terns and 80 pairs of Roseate Terns), and in eastern Long Island Sound (around the Falkner Island ternery; ca. 2,800 pairs of Common Terns and 140 pairs of Roseate Terns). In 1987 and 1988 I worked in western Block Island Sound (in an area bounded by Gardiner's Island, Montauk Point, Fisher's Island, and Orient Point; the vicinity of the Great Gull Island ternery; ca. 6,000 pairs of Common Terns and 1,000 pairs of Roseate Terns). Foraging flocks were located opportunistically; I searched with binoculars for flocks or I traveled toward areas where I had previously found foraging terns. Flocks that contained more Roseate Terns than expected by chance (based on the relative sizes of local breeding populations in a given area in a given year) are referred to as *Roseate flocks*. Others are referred to as *Common flocks*. I obtained data at 235 Roseate flocks and 154 Common flocks.

At flock sites I measured water clarity, depth, and temperature, and I noted the *most prominent feature* at the site (defined as that feature on which the birds appeared to have cued while searching for food [e.g., shoal, tide rip, dense prey school, predatory fish]), and whether either prey fish or bottom substrate were visible. I estimated distance to shore, current velocity, wind speed, and flock size. An estimated *flock-density index* was noted (in 1987 and 1988 only) as either 1 (sparse: mean nearest neighbor distance [NND] > 40 m), 2 (loose: NND = 15–40 m), 3 (moderate: NND = 5–15 m), or 4 (dense: NND < 5 m). I obtained a ratio of Roseate to Common terns either by counting all flock members at the time I arrived or, for large flocks, by tallying by species the first 50 birds that I identified. The presence or apparent absence of predatory fish was noted, based on sighting at the surface, the behavior of terns, the behavior of prey fish, marks on the boat's echosounder, and the activities of fishermen.

At each flock, I used binoculars to observe adult terns for 10 min per species. During these observations I recorded the number of successful, unsuccess-

ful, and aborted dives, and agonistic behaviors (vocal threats and chases). Dives in which terns touched or entered the water are referred to as *completed dives*; if a tern began a plunge but did not touch the water, the dive was counted as *aborted*. If a bird we were watching left the flock without carrying a fish, it was noted as having left. Birds leaving with fish were not recorded because they had ceased foraging. If a bird left or was lost from sight, another individual was watched, until the observation period was finished.

Data were analyzed using SAS programs at Rutgers University.

RESULTS

Physical features at Roseate and Common tern flocks.—Because Common Terns greatly outnumber Roseate Terns in the study area, Roseate flocks could be, and often were, numerically dominated by Common Terns. Nonetheless, mean \pm SD ratio of Roseate Terns to Common terns was 1.87 ± 0.67 in Roseate flocks and 0.02 ± 0.04 in Common flocks.

Roseate Tern flocks were found over shallower water than Common Tern flocks (Kruskal-Wallis $\chi^2 = 36.07$, $df = 1$, $P < 0.0001$; Fig. 1). Bottom substrate was visible in 30% of Roseate flocks, but in only 5% of Common flocks (contingency table $\chi^2 = 14.05$, $df = 1$, $P < 0.0001$). Roseate flocks formed much closer to shore on average than Common flocks (Kruskal-Wallis $\chi^2 = 32.01$, $df = 1$, $P < 0.0001$; Fig. 1). Windspeed was higher at Roseate flocks than at Common flocks (Kruskal-Wallis $\chi^2 = 4.32$, $df = 1$, $P < 0.05$; Fig. 1). Mean (\pm SD) water temperature was warmer at Roseate flocks ($17.51 \pm 0.91^\circ\text{C}$) than at Common Flocks ($16.85 \pm 0.82^\circ\text{C}$; Kruskal-Wallis $\chi^2 = 3.74$, $df = 1$, $P < 0.05$). There were no statistically significant differences in mean current rate, water clarity, and sea surface conditions (swell and chop) between Roseate and Common tern flocks, and the range and coefficient of variation of these variables was similar between species.

Proportions of the major physical and biological features differed between Roseate and Common tern flocks (contingency table $\chi^2 = 79.92$, $df = 1$, $P < 0.0001$; Fig. 2). Roseate Terns were oriented to physical features such as shoals and tide rips more than were Common Terns. Approximately 70% of Roseate flocks were found at sites where the most prominent features were physical (goodness of fit $\chi^2 = 33.29$, $df = 1$, $P < 0.0001$), whereas ca. 70% of Common Tern

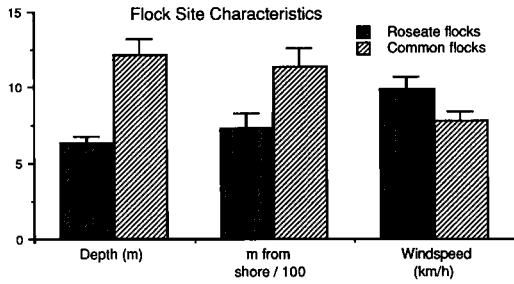


Fig. 1. Some physical characteristics of sites where Roseate and Common tern flocks were observed ($\bar{x} \pm SE$).

flocks were found at locations where the most prominent features were biotic (predatory fish or prey schools, or both) (goodness of fit $\chi^2 = 13.24$, $df = 1$, $P < 0.0001$; Fig. 2).

To explore the relative degree to which flock type (Roseate or Common) depended on physical attributes of sites, I performed a log linear analysis with the independent variables depth, distance to shore and physical feature. Flock type depended most on physical feature ($\chi^2 = 39.67$, $P < 0.0001$), followed by depth ($\chi^2 = 7.57$, $P < 0.01$), and distance to shore ($\chi^2 = 7.04$, $P < 0.01$). Distance to shore and depth were correlated (Pearson $r = 0.34$, $n = 306$, $P < 0.001$).

In the vicinity of Cedar Beach, where a greater variety of macrohabitats (ocean, inlet, and estuary) existed than in the waters surrounding Falkner and Great Gull islands, Roseate Terns exhibited more specialization than Common Terns in choosing among these macrohabitats (Fig. 3). Niche breadth indices (Levins 1968) were consequently higher for Common ($\beta = 2.49$) than for Roseate ($\beta = 1.76$) terns.

Activities of fish.—During this study, predatory fish under tern flocks were virtually always bluefish (*Pomatomus saltatrix*). Occasionally,

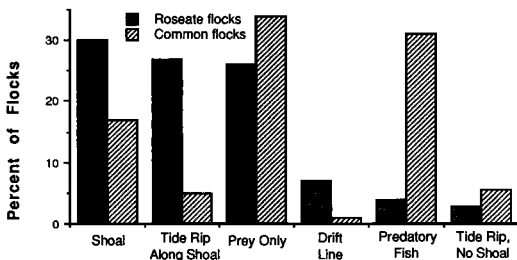


Fig. 2. Prominent physical and biotic features of Roseate and Common tern foraging sites.

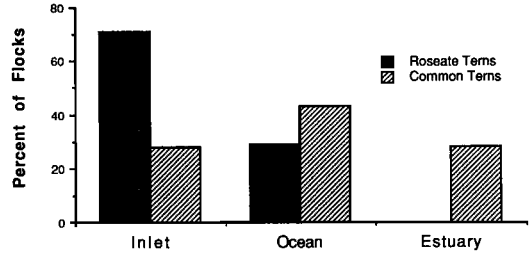


Fig. 3. Macrohabitat distribution of Roseate and Common tern flocks in the vicinity of Fire Island Inlet.

small proportions of weakfish (*Cynoscion regalis*) or striped bass (*Morone saxatilis*) were mixed among them. Predatory fish were present less often under Roseate than under Common flocks (contingency table $\chi^2 = 33.38$, $df = 1$, $P < 0.0001$; 45% of Common flocks vs. 18% of Roseate flocks).

To explore the relative degree to which predatory fish presence depended on physical attributes of sites, a log linear analysis was performed using the independent variables depth, distance to shore, and physical feature. Predatory fish presence depended most on physical feature ($\chi^2 = 76.78$, $P < 0.0001$), followed by distance to shore ($\chi^2 = 5.25$, $P < 0.02$). Predatory fish presence was independent of depth ($\chi^2 = 0.22$, $P > 0.5$). Distance to shore and depth were correlated (Pearson $r = 0.34$, $n = 306$, $P < 0.001$).

Prey fish schools were visible from my boat more frequently at Roseate flocks than at Common flocks (contingency table $\chi^2 = 8.68$, $df = 1$, $P < 0.01$; Fig. 4); this suggested higher densities of fish under Roseate flocks.

Bird foraging at Roseate and Common tern flocks.—Ninety-five percent of Roseate flocks had Common Terns mixed with them during observations, whereas only 30% of Common flocks had

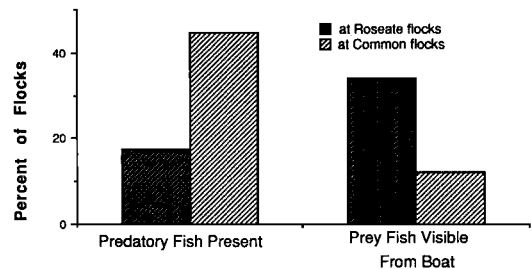


Fig. 4. Presence of predatory bluefish and visibility of prey fish under Roseate and Common tern flocks.

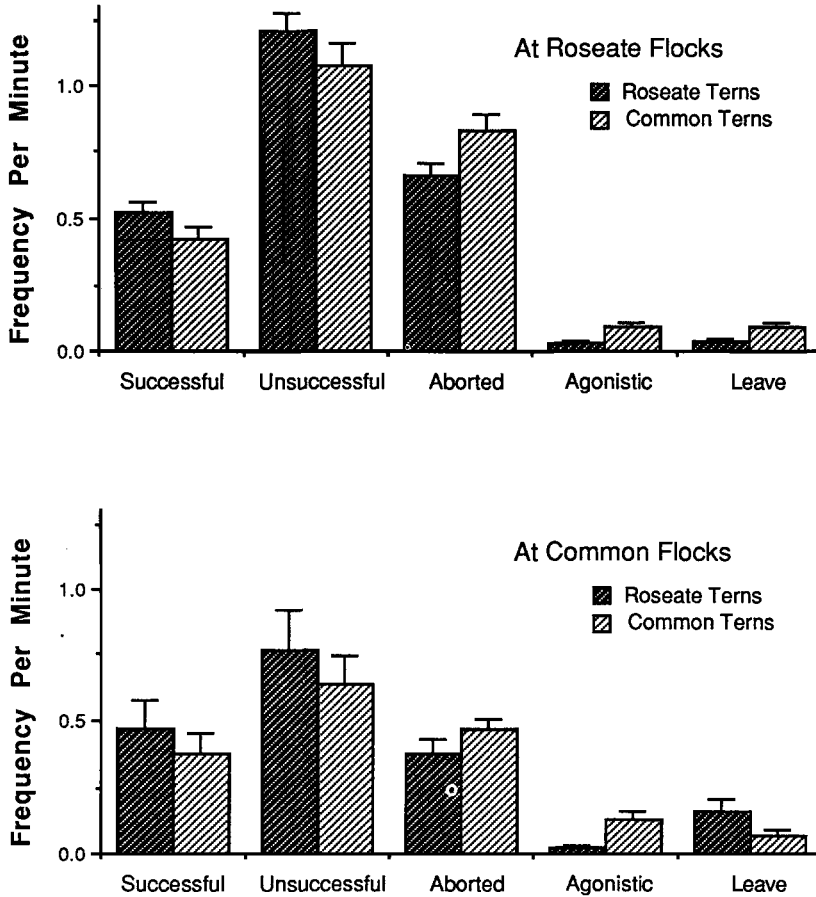


Fig. 5. Interspecies, intraflock comparisons of foraging activities of Roseate and Common terns ($\bar{x} \pm SE$).

Roseate Terns present (2×2 contingency table, $\chi^2 = 227.9$, $df = 1$, $P < 0.0001$). Roseate flocks were less dense than Common flocks (Kruskal-Wallis $\chi^2 = 22.63$, $df = 1$, $P < 0.0001$) and were also smaller ($\chi^2 = 6.13$, $df = 1$, $P < 0.01$).

Interspecies comparisons within flock types.—At Roseate flocks, Roseate Terns dove at more successful rates than Common Terns (Kruskal-Wallis $\chi^2 = 6.79$, $df = 1$, $P < 0.01$; Fig. 5), and Roseate Terns' total completed dive (successful + unsuccessful) rate was higher than Common Terns' rate (Kruskal-Wallis $\chi^2 = 4.59$, $df = 1$, $P < 0.03$). Common Terns foraging in Roseate flocks aborted dives at a higher rate than Roseate Terns (Kruskal-Wallis $\chi^2 = 3.88$, $df = 1$, $P < 0.05$), engaged in more agonistic interactions (Kruskal-Wallis $\chi^2 = 8.61$, $df = 1$, $P < 0.005$), and left flocks more frequently (Kruskal-Wallis $\chi^2 = 3.51$, $df = 1$, $P < 0.06$) than Roseate Terns. In Roseate

flocks there was no statistically significant between-species difference in the rate of unsuccessful dives, or the percentage of completed dives which were successful (31% for Roseate Terns, 28% for Common Terns).

In Common flocks, foraging Roseate Terns left at a higher rate than did Common Terns (Kruskal-Wallis $\chi^2 = 3.87$, $df = 1$, $P < 0.05$), and Common Terns engaged in agonistic interactions more frequently than did Roseate Terns (Kruskal-Wallis $\chi^2 = 15.77$; $df = 1$, $P < 0.0001$). In Common flocks there was no between-species difference in the rate of successful or unsuccessful dives, total aborted dives, or the percentage of completed dives that were successful (35% for Roseate and 39% for Common terns).

Intraspecies comparisons between flock types.—Roseate Terns dove more frequently in Roseate flocks than in Common flocks (Kruskal-Wallis

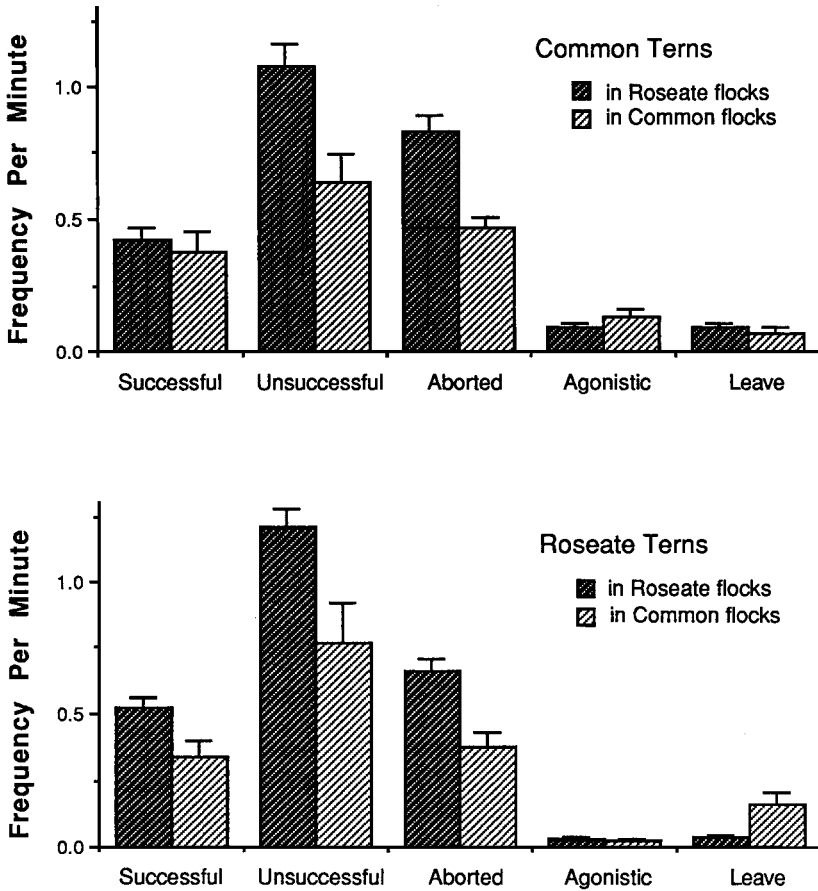


Fig. 6. Interflock, intraspecies comparisons of foraging activities of Roseate and Common terns ($\bar{x} \pm SE$).

$\chi^2 = 13.21$, $df = 1$, $P < 0.0003$). The rate (per minute) of successful dives was higher for Roseate Terns while fishing in Roseate flocks compared with Common flocks (Kruskal-Wallis $\chi^2 = 4.54$, $df = 1$, $P < 0.03$; Fig. 6). Roseate Terns' rate of unsuccessful dives was also higher while foraging in Roseate flocks (Kruskal-Wallis $\chi^2 = 14.85$, $df = 1$, $P < 0.0001$; Fig. 6). Roseate Terns made more aborted dives per minute while fishing in Roseate flocks (Kruskal-Wallis $\chi^2 = 10.14$, $df = 1$, $P < 0.001$; Fig. 6). Foraging Roseate Terns left Common flocks at a higher rate than they left Roseate flocks (Kruskal-Wallis $\chi^2 = 10.13$, $df = 1$, $P < 0.001$; Fig. 6). There was no difference in the mean proportion of dives that were successful, nor in the rate at which foraging birds engaged in agonistic interactions between Roseate Terns fishing in Common flocks compared with those in Roseate flocks.

Common Terns made more dives per minute (successful + unsuccessful dives) in Roseate flocks than in Common flocks (Kruskal-Wallis $\chi^2 = 19.24$, $df = 1$, $P < 0.0001$; Fig. 6). For Common Terns, there was no difference in the rate of successful dives while fishing in Common vs. Roseate flocks. However, Common Terns' rate of unsuccessful dives was higher while foraging in Roseate flocks (Kruskal-Wallis $\chi^2 = 23.53$, $df = 1$, $P < 0.0001$; Fig. 6). Common Terns dove more successfully in Common flocks (39%) than in Roseate flocks (28%; $\chi^2 = 6.63$, $df = 1$, $P < 0.01$). Common Terns made more aborted dives per minute while fishing in Roseate flocks (Kruskal-Wallis $\chi^2 = 18.29$, $df = 1$, $P < 0.0001$; Fig. 6). Common Terns engaged in more agonistic interactions within Common flocks (Kruskal-Wallis $\chi^2 = 4.63$, $df = 1$, $P < 0.03$; Fig. 6). There was no difference in the mean rate at

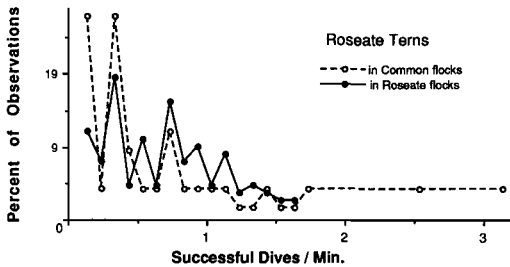


Fig. 7. Overlap in the success frequencies of Roseate Terns foraging in Roseate and Common flocks.

which foraging Common Terns left the area while fishing in Common flocks as compared with Roseate flocks.

Interspecies comparisons between flock types.—Roseate Terns foraging in Roseate flocks had a higher frequency of successful and completed dives than Common Terns that foraged in Common flocks (Kruskal-Wallis $\chi^2 = 11.49$, $df = 1$, $P < 0.001$; $\chi^2 = 33.52$, $df = 1$, $P < 0.0001$). Common Terns in Common flocks were successful on a slightly higher proportion of completed dives than were Roseate Terns in Roseate flocks (Kruskal-Wallis $\chi^2 = 3.37$, $df = 1$, $P < 0.07$). There was no interspecies, interflock difference in the rate at which birds left flocks.

The only difference found between Roseate Terns foraging in Common flocks and Common Terns foraging in Roseate flocks was that the Roseate Terns completed more dives per minute than did Common Terns (Kruskal-Wallis $\chi^2 = 5.29$, $df = 1$, $P < 0.02$). For all data pooled, Roseate Terns had a higher frequency of fish captures than did Common Terns (Kruskal-Wallis $\chi^2 = 7.05$, $df = 1$, $P < 0.01$).

DISCUSSION

The prediction that habitat characteristics differed between species was consistent with these data. These differences may occur through differential decision rules. Very large flocks, dense flocks, or flocks in shallow water could all have contained ratios of each tern species that reflected the ratio in the population, yet they did not. Further, Roseate Terns often absolutely outnumbered Common Terns in foraging flocks. This indicates clear differences in foraging habitat through differential selection by each species.

Roseate Terns were more successful in Roseate flocks than in Common flocks, and they

were frequently absent from Common flocks. They also left Common flocks more frequently than did Common Terns. However, a degree of overlap in success frequencies by Roseate Terns in both flock types (Fig. 7) suggests that, despite their relative specialization, Roseate Terns must continue to sample both situations in order to maximize their net energy intake (Sih 1982, Heinrich 1983).

My second prediction was that each species' foraging efficiency would be greater in their principal foraging situations. This was clearly the case for Roseate Terns, which caught fish at a higher rate in Roseate flocks than in Common flocks. It was less clear for Common Terns, for which there was no such difference. However, Common Terns may have expended more energy per fish caught in Roseate flocks, which reduced each fish's profitability, because they dove more frequently but caught fish less successfully while in Roseate flocks. These are mean comparisons; each species occasionally foraged profitably in each flock type, which maintained their tendencies to mix to some degree. Common Terns' subtler mean between-flock differences in efficiency may indicate that their foraging is more often profitable in Roseate flocks than is Roseate Terns' foraging in Common flocks, and this may manifest itself in the relatively generalized foraging habits of Common Terns (Lemmetyinen 1976, Erwin 1977, this study) compared with Roseate Terns.

The pattern of specialization and resource use in the two species is also consistent with a model of competition-based resource partitioning (discussed by Pimm and Pimm 1982) in which intraspecific competition causes generalization whereas interspecific competition causes specialization. Numerical dominance can lead to competitive dominance in interspecific behavioral interactions (Burger and Gochfeld 1984). Common Terns frequently interfere with each other in foraging flocks (Safina and Burger 1988). According to the model then, Roseate Terns should be specialists and Common Terns generalists, as was the case. Roseate Terns were more successful in Roseate flocks than were Common Terns in Common flocks, which may help explain why populations of Roseate Terns persist despite their numerical inferiority.

Roseate flocks were in areas that were shallower, closer to shore, and had warmer water than Common flocks' areas. I suspect that the water temperature is a function of depth, as

water ran over shallow sand flats where Roseate Terns often foraged. Common flocks were often in areas where depths changed abruptly from 100 m to 10 m, and where tidal currents were strong, which presumably produced much upwelling and mixing of cold, deep water with warmer surface water.

I found Roseate flocks' proximity to shore contrary to Nisbet's (1981) report. It appears that Roseate Terns' distance from shore or from their colony is related to the distribution of the physical features that attract them, not to any innate tendency to commute farther. For example, Roseate Terns that bred at Cedar Beach did not travel as far as Common Terns did. The colony is close to the Fire Island Inlet, the preferred Roseate foraging area, while Common Terns often ranged far into the ocean (Safina and Burger 1988). Conversely, Roseate Terns that bred on Great Gull Island often traveled considerably farther than Common Terns because of the position of their preferred foraging locations with respect to the colony.

Wind speed was greater around Roseate flocks. Roseate Terns are less able to hover than Common Terns (Nisbet 1981, Hatch 1985), and they have higher disc-loading (Duffy 1986). Both Common and Sandwich (*Sterna sandvicensus*) terns' success is enhanced by moderate wind, which apparently aids hovering (which often immediately precedes diving) and impairs fishes' ability to detect terns through its effect on the water's surface (Dunn 1973). Wind would seem to aid Roseate Terns more than Common Terns in both hovering and prey detection. Because predatory fish activity was greater under Common flocks, detection of birds by fish would presumably allow fish to withdraw from the surface more frequently in Roseate flocks than in Common flocks, where the prey fish's attention may more often be on the immediate threat of pursuing predatory fish.

Roseate flocks were more dispersed than Common flocks. Duffy (1986) presumed that Common Terns' denser groups foraged over denser prey, and that dispersed groups of Roseate Terns foraged over more dispersed prey. My impressions were that prey under Common flocks was very dense in small patches but not dense over the area covered by the flock. In contrast, prey under Roseate flocks seemed relatively evenly distributed and denser over the area covered by the flock. Confirmation or refutation of these impressions is lacking, but prey

were visible more frequently under Roseate flocks than under Common flocks, which suggested higher density, greater abundance in the upper few meters of water, and broader distribution. Duffy (1986) reported that Roseate Terns were the more aggressive of the two tern species, a finding based on a very small sample size and contradictory to mine.

Predatory fish activity was much lower in Roseate than Common flocks. Prey fish tend to avoid the surface when predatory fish are not present (Safina and Burger 1988). A possible reason that Roseate Terns are more successful than Common Terns in these situations is their apparent ability to dive slightly deeper, as measured by submergence intervals (Duffy 1986). This may account for both the lower success of Common Terns than Roseate Terns in Roseate flocks and also the fact that Roseate Terns forage over shallow water, where prey's downward movement is limited. Predatory bluefish, which were more active under Common flocks, cause prey in deep water to come close to the surface where they are accessible to terns, but bluefish also profoundly affect the system by driving down overall prey density and abundance (Safina and Burger 1985, 1988, 1989), leading to increased prey patchiness.

Roseate and Common terns forage differently. Although the question of whether competition caused the evolution of these differences cannot be answered conclusively with these data (Ashmole 1968, Levin 1970, Schoener 1974a, Wiens 1977, Connell 1980, Thornhill 1987), I believe that the presence of foraging differences and the incomplete overlap of foraging abilities of the two tern species in various situations lessens the potential severity of trophic competition. Both Ashmole (1968) and Diamond (1978) believed that seabird numbers were related to the area of exploitable foraging habitat. The demonstration of foraging differences between Roseate and Common terns, Roseate Terns' more specialized foraging abilities, and their more physically restricted foraging locations suggest that Roseate Terns in this population have been less numerous than Common Terns throughout their recorded history because their foraging habitat is smaller in area.

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