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Foraging at patches: interactions between Common and Roseate Terns

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In foraging groups in the Long Island Sound area of the eastern United States, Roseate Terns *Sterna dougalli* plunged for longer periods and from greater heights than did Common Terns *Sterna hirundo*. Roseate Terns were rarer than expected in dense feeding groups where they tended to occur at the peripheries but they were more common than expected in more dispersed groups. Roseates were also more successful per plunge than were Common Terns in dispersed groups. The species appeared to partition food on the basis of patchiness: Common Terns were more successful in large groups over presumably larger patches of prey while Roseate Terns had more success in smaller groups feeding on more dispersed prey.

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1. Introduction

A growing number of studies have demonstrated the importance and complexity of seabird foraging aggregations at local concentrations of prey (e.g. Ashmole and Ashmole 1967, Sealy 1973, Erwin 1977, Hoffman et al. 1981, Porter and Sealy 1981, Gochfeld and Burger 1982, Schneider 1982, and Duffy 1983). Interactions between species at patches include mutualistic locating and herding of prey, kleptoparasitism, species' dominance interactions, and disruption of prey shoals (e.g. Hulsman 1978, Hoffman et al. 1981, Duffy 1983). Studies of how seabirds partition food resources, based on 'traditional' measurements such as prey species, prey size, and distance foraged may be incomplete or even misleading because behavior at sea, especially at patches of prey, may be the main source of partitioning, causing the other differences.

This paper reports on interactions of Common Terns *Sterna hirundo* and Roseate Terns *S. dougalli* over patches of prey in the waters of eastern Long Island and western Block Island sounds off the states of New York, Connecticut, and Rhode Island, United States. Although solitary foraging occurred, most feeding was done by groups of birds, over shoals of prey. This paper investigates these groups, with particular attention to: (1) whether the two species fed in the same areas or at the same distances from the breeding colony; (2) whether the size or density of the group affected the relative abundances of the two species; (3) whether frequency or success of foraging attempts were affected by group density; (4) whether the species fed at the same depths, based on duration of plunges; (5) whether they took the same sizes and species of prey; (6) whether interspecific interactions between species occurred and what effect these had on group foraging.

2. Methods

The study area covered the area between the Connecticut-Rhode Island border and the Connecticut River in the north and between Montauk Point (N.Y.) to the east and Shelter Island (N.Y.) to the west (Fig. 1). During the study period from 1973 to 1979, ap-

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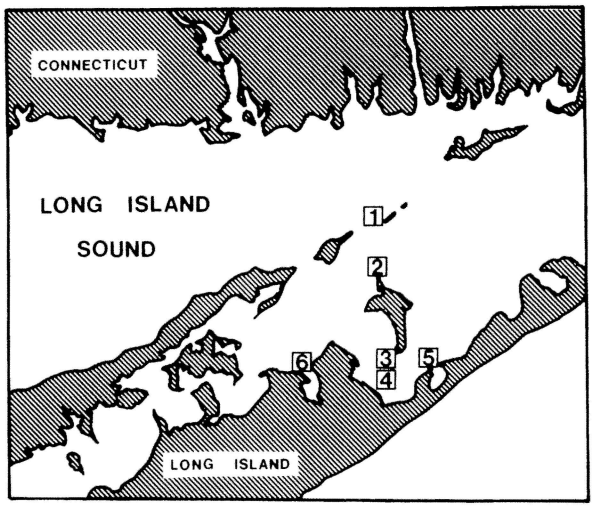

Fig. 1. The study area in Long Island and Block Island Sounds. Numbers indicate breeding colonies: 1. Great Gull Island; 2. Gardiner's Point ruins; 3. South Point, Gardiner's Island; 4. Cartwright Island; 5. Hicks Island, Napeague; 6. Three Mile Harbor.

proximately 3650 pairs of Common Terns nested at 12 sites in the study area (data from 1975: Duffy 1977). Approximately 70% of these nested on Great Gull Island. Colonies of over one hundred pairs also occurred at Three Mile Harbor, Gardiner's Point ruins, the south point of Gardiner's Island, Cartwright Island, and Hicks Island, all on eastern Long Island (Fig. 1, Duffy 1977). Approximately 1000 pairs of Roseate Terns nested at 8 sites in the study area but over 90 % nested on Great Gull (Duffy 1977). Limited numbers of Least Terns *S. albifrons* also bred in the area, primarily on mainland sand-dunes at the mouths of salt ponds or estuaries (Duffy 1977). Least Terns generally foraged inshore near their colonies (cf. Atwood and Minsky 1983) or in salt ponds and did not occur frequently with foraging Common and Roseate Terns (pers. observ.) so they are not considered here. Also excluded are other species such as Osprey *Pandion haliaetus,* Snowy Egret *Leucophoyx thula,* Laughing Gull *Larus atricilla,* Herring Gull *L. argentatus,* and Parasitic Jaeger *Stercorarius skua* which made up less than one percent of all birds in flocks.

Observations were made opportunistically during each breeding season, except in 1976 when a small boat was available. I observed groups of foraging terns offshore from Great Gull and Gardiner's islands (Fig. 1), as well as from a 6 m outboard motorboat. The boat was used to reach areas where terns frequently fed but could not be viewed from land.

I observed terns from 5 to 100 m distances. I did not attempt to calculate the absolute frequency of feeding groups of different sizes because larger groups were disproportionately visible, and feeding by solitary birds was sporadic and sometimes difficult to distinguish from opportunistic plunges while travelling to or from nesting colonies.

At each feeding group, I counted the number of both species present and their apparent food source. I estimated the densities of feeding groups, dividing them into three classes: dense, where birds typically were less than one m apart; dispersed, where birds were at least 10–20 m apart, in a loose flock; and intermediate where densities were intermediate.

I measured the height from which plunges began when some scale of reference was available, such as a dock or boat. I measured duration of plunges from first contact with the water to emergence of the head from the water; the frequency and success of feeding attempts; and the number of aggressive interactions over one-minute periods in groups of different densities. I attempted to alternate observations between the species and usually did not collect more than ten observations per feeding group. Not all measurements could be made at each feeding group, so the sample sizes vary for the different parameters.

I made descriptive observations of the structure of foraging groups: which species arrived first, where the species occurred in groups, and how birds reacted to changes in prey availability at a feeding group. Many of these observations did not lend themselves to quantification but facilitated interpretation of the quantitative results.

Previous workers (e.g. Nisbet 1977) determined sizes and species of prey carried by flying terns over breeding colonies, estimating size with reference to mandible length. While this may be possible at colonies, it is much more difficult at sea. In addition, larger, more conspicuously-colored or shaped species may be observed more frequently. To avoid these problems, I used fish collected by researchers during daily checks of nests of both species at Great Gull Island. Fish were usually dropped near nest sites by parents or young during feeding. Others were dropped by young which were satiated during periods of local food abundance. Still other fish were recovered after being dropped during kleptoparasitic attempts. Finally, some fish were simply too large for young, especially newly-hatched individuals, to swallow. Such larger fish might bias estimates of fish size upwards. This is also, however, likely to be true to some extent of size estimates of fish carried by flying birds. I preferred the use of fish found in colonies since actual specimens were available for measurement and identification to species, rather than relying on the possible idiosyncracies of individual observers.

Using wing-tracings provided by G. Schnell, I measured the spans and areas for single wings of 21 Common and 22 Roseate Terns. These measurements and the masses of the birds were used to calculate the average wing-loading (mass divided by wing area), chord (wing area divided by wing span; Greenwalt 1975) and buoyancy (wing area^{-2} divided by mass^{-3}; Hartman 1961).

3. Results

3.1. Distance foraged from colony

Seventy % of Common and 90% of Roseate Terns in the study area nested on Great Gull Island (Duffy 1977). I assumed that the percentage of each species at five sites at different distances from Great Gull represented the foraging ranges of the two species (Fig. 2). In 1976, the 46 observations of 1444 Common and 651 Roseate Terns showed no evidence of consistent differences in foraging distance. The overlap (Horn 1966) was 0.89. Both species fed most commonly at a site 5.5 km from the colony.

3.2. Group size and density

Feeding groups of terns observed in the study ranged from three to 330 birds although groups of up to several thousand were seen at other times. The frequency of Roseate Terns decreased slightly, but not significantly, with increasing group size ($r = -0.13$, $p > 0.05$, Fig. 3). Since the largest group of Roseates seen (34 of 35 birds in a flock) represented less than 2% of the total Roseate Tern population in the area, the decrease was not an artefact of a small population size becoming a proportionally smaller part of larger feeding groups.

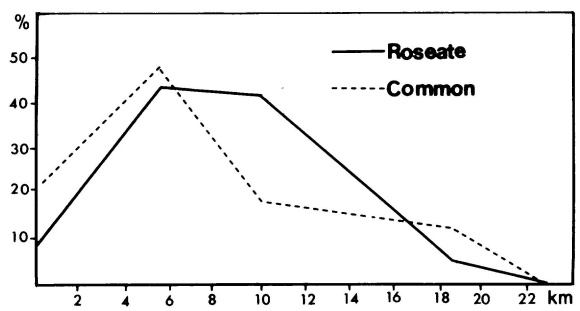

Fig. 2. Percentage of Common and Roseate Terns feeding at different distances from Great Gull Island in 1976.

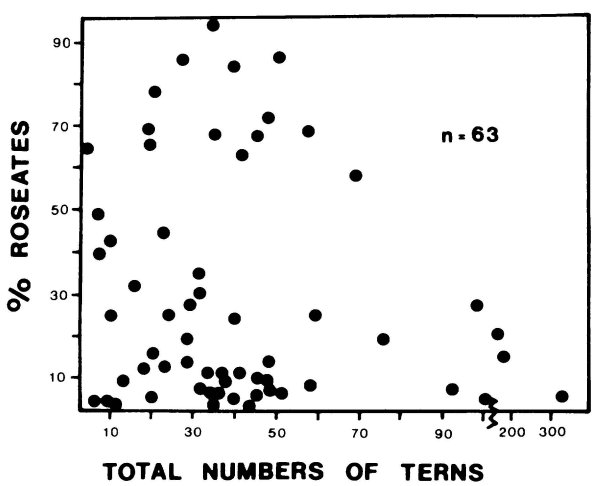

Fig. 3. The percentage of Roseate Terns in feeding flocks of different sizes.

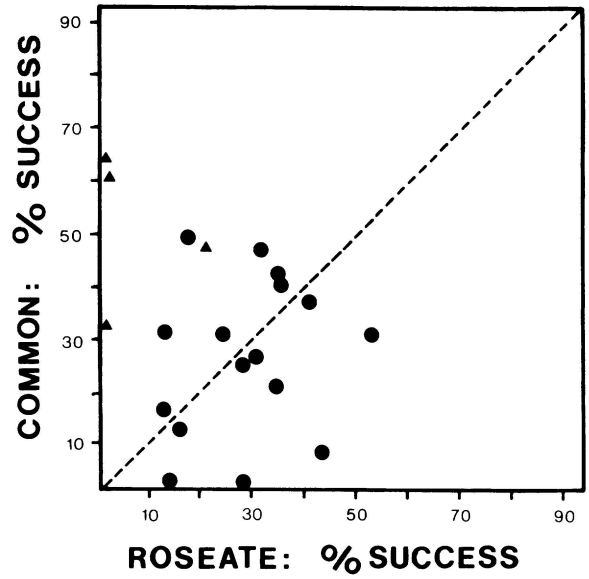

Fig. 4. Success per plunge by Common and Roseate Terns in feeding situations of differing degrees of crowding. ●: dispersed and intermediate feeding, ▲: dense feeding.

If the relative proportions of Roseate and Common Terns in feeding groups of different densities are considered (56 groups, 2161 Common, 655 Roseate Terns), then 63% of Common Terns were in dense groups ($n = 22$), 23% in medium groups ($n = 12$) and 14% in dispersed groups ($n = 22$), but the reverse occurred for Roseate Terns: only 12% in dense groups, 19% in medium groups, and 69% in dispersed groups. These differences were statistically significant ($p < 0.05$, 2×3 contingency table). Roseate Terns were less common than expected in dense groups, but the reverse was true in dispersed groups.

3.3. Foraging attempts and group density

Common Terns were more successful, catching more fish per plunge, than Roseate Terns in dense feeding groups ($n = 4$) but the reverse was true in dispersed and medium groups ($p < 0.05$, $n = 16$, Wilcoxon signed-ranks test; Siegel 1956; Fig. 4). Roseate Terns had more successful plunges per minute than Common Terns in dispersed situations ($p < 0.05$, $n = 9$, Wilcoxon signed-ranks test; Fig. 5), but there were only two dense feeding situations where success per minute was measured and the results are ambivalent.

3.4. Foraging depth

Both species fed by plunging head-first from heights of several metres. Roseate Terns appeared to submerge

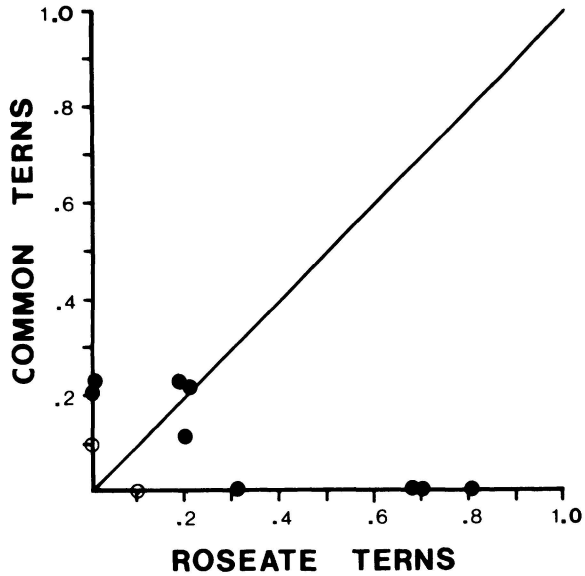

Fig. 5. The number of successful plunges per minute by Common and Roseate Terns feeding together in flocks of differing degrees of crowding. ●: dispersed and intermediate feeding, ○: dense feeding.

more frequently than Common Terns. Common Terns frequently plunged, landing on their bellies, snatching prey from the upper few centimeters. I assumed duration of contact of head with the water was a measure of the duration and depth of dive.

Mean duration of plunges by Common Terns was 0.8 s (SE = 0.02; n = 213) compared with 1.2 s (SE = 0.03; n = 202) for Roseate Terns. The longest Roseate plunge was 2.2 s but the longest Common plunge was only 1.6 s. When feeding together (Fig. 6), Roseates had longer durations than Common Terns in 12 of 14 foraging situations. When known heights were available for reference, Roseate Terns began their plunges from higher (4.4 m, SE = 0.2, n = 31) than Common Terns (2.6 m, SE = 0.3, n = 18; data gathered from dense, medium and dispersed groups).

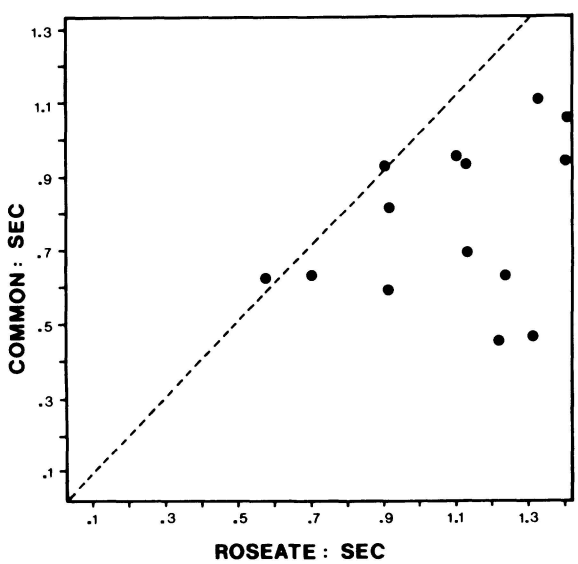

Fig. 6. The duration(s) of plunges by Common and Roseate Terns feeding together in flocks of differing degrees of crowding.

3.5. Prey size and species-composition

Although Common Terns took slightly larger prey than did Roseate Terns, the difference was not significant except in 1973 (Tab. 1) when small fish were taken by both species. Common Terns consistently took more types of prey than Roseate Terns within years. Between 1973 and 1977, Common Terns averaged 15.8 types of prey per year while Roseate Terns took only 6.8 types (Tab. 2). Roseate Tern diets overlapped greatly with those of Common Terns. In all years except 1976 (Tab. 2), a few species appeared to be heavily exploited by both species, with Common Terns taking a wider variety of relatively rare taxa.

3.6. Species' interactions

Within a feeding flock, aggressive encounters were frequent. Birds attempting to feed were interrupted or displaced. Following single birds within groups, I found

Tab. 1. The lengths (snout to caudal peduncle) in mm of fish captured by Common and Roseate Terns, based on fish found in the colony at Great Gull Island, 1973–1977.

Year	Common Tern			Roseate Tern		
	n	mean	S.D.	n	mean	S.D.
1973	233	59	4	141	39	1
1974	295	84	1	192	79	1
1975	106	82	2	40	79	3
1976	83	86	3	42	84	5
1977	133	89	2	18	87	8

Tab. 2. Number of prey taxa (identified to species or genus) taken by Common and Roseate Terns, based on specimens recovered in the colony at Great Gull Island, 1973 to 1977 (sample sizes in Tab. 1). Overlap index from Horn (1966): a score of 0.0 indicates no overlap and a score of 1.00 indicates complete overlap.

Year	Common Tern	Roseate Tern	Both species	Overlap
1973	18	6	5	0.91
1974	18	11	11	0.88
1975	19	9	8	0.95
1976	14	5	4	0.57
1977	10	3	3	0.91
Mean	15.8	6.8	6.2	0.84

Tab. 3. Single-wing dimensions (defined in text) and masses of Common (n=21: and Roseate Tern (n=22) (means plus one standard deviation).

Measurement	Common Tern	Roseate Tern
Wing span (m)	0.345 (0.010)	0.304 (0.010)
Wing area (m^2)	0.022 (0.014)	0.017 (0.009)
Chord (m)	0.064 (0.003)	0.056 (0.003)
Mass (kg)	0.117 (0.006)	0.017 (0.007)
Wingload (kg m^{-2})	5.318	6.294
Buoyancy index	1.406	1.297

that Common Terns were involved in 2.6 encounters min^{-1} (SE = 0.51, n = 5) and Roseate Terns 3.0 min^{-1} (SE = 0.54, n = 5) in dense feeding situations; in intermediate situations, Commons 0.46 encounters min^{-1} (SE = 0.27, n = 15), Roseates 0.53 (SE = 0.21, n = 15); and in dispersed situations, Commons no interactions observed (n = 15), Roseates 0.2 (SE = 0.18, n = 15). While the samples were small, they showed that, at all three feeding densities, Roseate Terns were involved in more aggressive encounters per bird than were the Common Terns feeding with them. Dense situations produced more than 15 times the encounter rate of dispersed groups for Roseate Terns.

Dense situations frequently resembled inverted cones, with a few birds at the base close to the water and a more dispersed, wider group of birds at increasing distances from the surface. Prey appeared to be available in many cases only briefly in dense situations, and then only in a small area under the cone. Birds might spend several minutes jockeying for position, hovering close to the surface waiting for prey. When prey became available, most of the birds in the lower part of the cone would plunge into the water. The lowest birds appeared to have the best chance of taking prey, with higher birds frequently landing on them and attempting to steal fish. Roseate Terns rarely occurred in the centers of cones. They were most frequent at the peripheries of cones. Cones of birds might persist for up to an hour, but most broke up and reformed several times in ten minutes. In contrast, dispersed situations appeared to be longer-lasting, with no concentrations of birds or pulses of hovering. Birds would circle over a wide area rather than hovering. Feeding was confined to individuals or groups of two or three rather than the mass activities of dense groups.

Roseate Terns had shorter, narrower wings which supported a heavier wing-loading than did the wings of Common Terns (Tab. 3). In flight, Roseate Terns appeared to have deeper, more frequent wing-beats. Roseates were only rarely seen hovering, either while feeding or at the colony whereas Common Terns frequently hovered. The heavier wing loading and lower buoyancy would make hovering, slow flight and maneuvering more difficult (Hartman 1961).

4. Discussion

Roseate Terns were less frequent in dense feeding situations than expected. They were involved in more aggressive interactions than were Common Terns in all feeding situations but such interactions were most frequent in dense feeding groups. Aggressive interactions appeared to interfere with foraging and might explain the Roseate Tern's reduced foraging success compared with that of Common Terns in dense groups. Roseate Terns plunged from a greater height, had longer plunge-durations, and presumably plunged deeper than Common Terns. Fish taken by the two species were the same size but Common Terns exploited a wider variety of prey species.

Like the Brown Noddy *Anous stolidus* and Sooty Tern *S. fuscata* in the tropical Pacific Ocean (Ashmole and Ashmole 1967) and the White-capped Noddy *Anous minutus* and Black-napped Tern *S. sumatrana* in Australia (Hulsman 1978), Common and Roseate Terns in the study area differed primarily in their exploitation of patches of prey. Common Terns hovered, were heavier, broader-winged, and were involved in fewer aggressive interactions than were Roseate Terns. Common Terns were more successful and appeared better able to compete in dense groups of birds over very rich patches of prey that are temporally or spatially restricted. On the other hand, Roseate Terns, with their deeper plunges and greater heights from which they began plunges, were perhaps better able to take prey from the peripheries of groups or exploit prey that were dispersed over a wide area, but not locally common enough to produce feeding aggregations of birds. The greater height of plunges of the Roseate Tern would also allow a larger area to be searched for prey while foraging. In contrast to the foraging of Sooty Terns and Brown Noddies, the two terns on Great Gull Island did not appear to forage at different distances from the colony .

While this may explain the distribution of foraging Roseate Terns in the study area, different mechanisms may operate elsewhere, especially where different prey or tern species are present. For example, Roseate Terns very rarely stole food from Common Terns at sea or at the breeding colony at Great Gull Island (pers. observ.), but Roseates are apparently more frequently parasitic at some colonies in Britain (Dunn 1973) and Australia (Hulsman 1976) where different tern species are present. In South African waters, Roseate Terns fed in "small compact flocks numbering about 80 birds" which were joined by Common and Sandwich Terns *S. sandvicensis* (Randall and Randall 1978).

Given the taxonomic similarities of tern species, the major difference being size, and the different combinations of species present in different areas, studies of the foraging ecology of tern communities should provide useful insights into the marine ecology of seabirds, especially their use of patchy resources.