COLONIALITY IN TERNS: THE ROLE OF SOCIAL FEEDING

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Coloniality in ground-nesting seabirds is believed by most workers to have evolved primarily as an adaptation to avoid predation (Tinbergen 1953, Cullen 1960, Kruuk 1964, Lack 1968). Because locations free of mammalian predators are limited, many marine species breed in dense congregations. Birds in large breeding colonies may effectively reduce avian predation either because many individuals jointly mob an intruding predator (Kruuk 1964) or because nests in the center of the colony are relatively invulnerable to predators ("selfish herd" phenomenon of Hamilton 1971). The upper limit in colony size is presumably set by local food supply (Ashmole 1963, Bourne 1963, Lack 1968, Nelson 1970).

Recent evidence suggests that food-finding is another important function of coloniality (Ward 1965, Horn 1968, Fry 1972, Ward and Zahavi 1973, Krebs 1974, Emlen 1975). When food is unevenly distributed and unpredictable, individuals may learn about good feeding sites by observing the flight direction and success of individuals nearby (Turner 1964). In this view, colony size per se might be an important selective factor because large colonies provide more "sources of information" about food location than small ones.

Ward and Zahavi's (1973) "information-centre" hypothesis predicts that, given equal habitat and predation factors, species which depend upon food that is unpredictable in space and time and/or distributed over large areas should nest in larger colonies than species feeding on a more uniformly-distributed food source close to the nest site. Also, gregariousness and group feeding should be more highly developed in species relying upon "local enhancement" (Thorpe 1956) to find dispersed food patches over large feeding areas. To test the hypothesis, I compared the six abundant beach-nesting tern species along the Atlantic coast of the United States: Arctic Tern (*Sterna paradisaea*), Common Tern (*S. hirundo*), Roseate Tern (*S. dougallii*), Least Tern (*S. albifrons*), Royal Tern (*S. maxima*), and Gull-billed Tern (*Gelochelidon nilotica*). Sandwich Terns (*S. sandvicensis*) were not included because of their low numbers and the lack of information about their feeding ecology. Five of the six species are primarily piscivorous (i.e., all except Gull-billed Terns), and all nest primarily on beaches or rocks of open islands. Breeding space seldom appears to be limited and most colonies are on sites free of ground predators. This comparison of species within a subfamily should more rigorously test a hypothesis which originally depended upon selected examples from a variety of distantly related avian species.

METHODS

During the course of another study on seabird feeding ecology in 1973 and 1974, I collected data on foraging range, habitat use, and group feeding of Common, Royal, Least and Gull-billed terns in coastal Virginia (see Erwin 1975, 1977a for details). Foraging zones were divided into four categories: (1) onshore (terrestrial feeding); (2) adjacent (inlets, beach and marsh shallows); (3) middle (up to several kilometers from colony); (4) distant (> 20 km from colony). When more than one feeding zone was used, relative usage was estimated. At selected observation stations, I recorded the species and numbers of individuals feeding during periods of 0.5 to 3.0 h. I arbitrarily called a feeding "group" any assemblage of two or more individuals whose members were within 30 m of their nearest neighbors. Because the number of feeding birds fluctuated during every observation period, the maximum number was chosen for each period. Data on the feeding behavior and ecology of the Arctic Tern were extracted from studies in Maine, and of the Roseate Tern from studies in Massachusetts and New York.

Coastal censuses of Virginia's beach-nesting tern colonies were made concomitant with my field studies by J. Weske, R. Clapp, and M. Byrd. Because there were only two Royal Tern colonies in Virginia, 1975 census data were obtained from J. Parnell and R. Soots in North Carolina where Royal Terns are more abundant. Other census information for Arctic, Roseate, and Least terns was obtained from published accounts. The mean, median, and range of breeding pairs per colony were calculated from census data. Median/abundance ratios were also computed to provide another index of relative size.

Insufficient information on fish abundance and distribution prevented examination of food pattern differences among the species. In the following comparison, I emphasize species differences in foraging area rather than food predictability in testing the hypothesis.

SPECIES ACCOUNTS

Table 1 compares colony size, foraging range, and feeding behavior among the six species. Gull-billed Terns usually nest in small colonies with more than three-fourths of the Virginia colonies having fewer than 50 nests. These terns are almost exclusively terrestrial feeders, preying upon various crabs, lizards, and in-

TABLE 1.   Relationship between colony size and foraging attributes among six Atlantic coast tern species.[a]

Species	Location	Total breeding pairs[b]	Colony size (prs) Mean	Colony size (prs) Median	Median/abun-dance[c]	Foraging area[d]	Feeding group size
Gull-billed Tern	Virginia	940(21)	45	8	.009	1	Solitary
Least Tern	Virginia	540(24)	18	20	.037	1,2	Solitary or very small groups
Common Tern	Virginia	3,310(31)	95	60	.018	1–4[e]	Varies from solitary to large groups
Arctic Tern	Maine	ca. 7,200(11)	668	100	.014	1–4[e]	Probably similar to Common Terns
Roseate Tern	Massachusetts	2,280(8)	285	150	.066	2,3,4(?)	Groups somewhat smaller, more diffuse than Common Terns
Royal Tern	Virginia North Carolina	2,400(2) 15,995(11)	1,415	1,106	.060	2,3,4	Varies from solitary to large groups

[a] Sources for colony data: Gull-billed, Least and Common terns (1974 censuses by Weske, Clapp, Byrd); Arctic Terns (H. Tyler, unpubl. data); Roseate Terns (Nisbet 1973); Royal Terns (Virginia by Weske and author, North Carolina by J. Parnell and R. Soots, 1975 census).
[b] Number of colonies given in parentheses.
[c] Abundance refers to the total number of breeding pairs.
[d] 1, terrestrial; 2, adjacent waters; 3, middle; 4, distant.
[e] Insects (terrestrial) also taken by Common and Arctic terns (Bent 1921, Palmer 1941, Pearson 1968, Lemmetyinen 1973, 1974).

sects (Bent 1921). They usually feed alone, never in groups of more than 2–3 birds (Table 2). I never saw them feeding over water away from the colony. Similar observations were made in North Carolina colonies where, in 15 cases, 10 were of single birds feeding, and 5 were of pairs (H. Sears, unpubl. data).

Least Terns also nest most commonly in very small colonies in Virginia, ranging from 5 to 50 nests. In the northern part of their breeding range in Massachusetts, most colonies are also comprised of fewer than 50 pairs (Fisk 1974, Blodget 1978). Palmer (1941) stated that Least Terns are "unlike other (larger) terns which only nest in large aggregations." They feed on small fish or insects (Bent 1921) close to shore, preferring shallow marsh channels and inlets in Virginia. I never recorded Least Terns at observation stations 13 and 21 km from shore even though they bred commonly in the area. This inshore, shallow water feeding preference has also been found in New York (D. Duffy, unpubl. data)

TABLE 2.   Feeding group size among four tern species in coastal Virginia, May–July 1974 (all foraging zones pooled).

Species	Group size 1–2	Group size 2–10	Group size 10–50	Group size >50	N
Gull-billed Tern	14	2	—	—	16
Least Tern	13	5	—	—	18
Common Tern	9	12	6	5	32
Royal Tern	7	6	7	6	26

and California (Massey 1974, pers. comm.). Feeding in coastal Virginia is usually performed alone or in pairs (Table 2).

Common Terns usually nest in much larger colonies than either Gull-billed or Least Terns. Three Common Tern colonies in 1974 exceeded 400 pairs, whereas, 275 was the largest colony of either of the other species. Foraging is concentrated mostly near beaches and inlets, but Common Terns were frequently seen at distant locations (> 20 km) from colonies (Erwin 1975, 1977a). This plasticity in feeding range was also noted by Hopkins and Wiley (1972) at a Maine ternery. On Long Island, Raynor (1972) found that Common Terns flew 24 km over land to feeding areas. Numbers of foraging individuals varied considerably, ranging from one to more than 200 at two Virginia colonies (Table 2). Dense feeding congregations of Common Terns also occur in Maine (Palmer 1941, Hopkins and Wiley 1972) and New York (Duffy 1975, unpubl. data).

Royal Terns nest in the largest, densest colonies of any of the Atlantic coast species. The two Virginia beach colonies (800 and 1,600 pairs) were combined with those in North Carolina (range 44–3,867 pairs) to calculate colony size measures (Table 1). Buckley and Buckley (1972) found that Royal Terns fed commonly at distances of 20–30 km from their colonies in both Virginia and North Carolina. I also found Royal Terns feeding relatively more often at distant sites than Common Terns

in Virginia (Erwin 1975, 1977a). Feeding group size was variable, ranging from 1 to 150 (Table 2).

Arctic Terns, censused between 1968 and 1973 by W. Drury (H. Tyler, unpubl. data) range in colony size from 2 pairs to about 5,000 with a median somewhat larger than that of the Common Tern. The unusually large colony on Machias Seal Island biases the mean colony size (Table 1). Despite considerable overlap, Arctic Terns appear to be more pelagic than the Common Tern (Hopkins and Wiley 1972, Nisbet pers. comm.). Feeding groups are common in this species (Bent 1921, Hawksley 1957, Hopkins and Wiley 1972), but no quantitative data on frequency and size of groups are available.

Roseate Tern colonies ranged from 6 to 1,100 nests in Massachusetts in 1972 (Nisbet 1973). Despite a paucity of published data, this species appears to be intermediate morphologically and ecologically between Arctic and Common terns, and the larger, crested Sandwich and Royal terns (J. Cullen as indicated by I. Nisbet pers. comm., Langham 1974). By comparing duration of parental feeding trips, Duffy (1975) found that Roseate Terns fed farther from colonies than Common Terns on Long Island, but did not feel the difference to be of sufficient magnitude to separate the species. However, he assumed that the two species have equivalent flight speeds while Nisbet (pers. comm.) has evidence that Roseate Terns are much faster than Common Terns, hence capable of feeding over a larger area. Roseate Terns also feed in groups but these are often smaller and more diffuse than are those of Common Terns (Duffy 1975, unpubl. data). Possible reasons for this will be discussed below.

DISCUSSION

A definite correlation is evident among distance to foraging area, gregariousness when feeding, and colony size. Species which feed at greater distances from the colony site also nest in larger colonies (Fig. 1) and are more gregarious (larger groups) than the more solitary, small colony, inshore-feeding terns. The large differences in colony size among the species apparently reflect true social differences, not merely abundance differences. Common Terns in Virginia were 50% more abundant than either Royal Terns or Roseate Terns (in Massachusetts), yet their colonies are generally smaller. Similarly, Gull-billed Terns are twice as numerous as Least Terns in Virginia, but their median colony size is small-
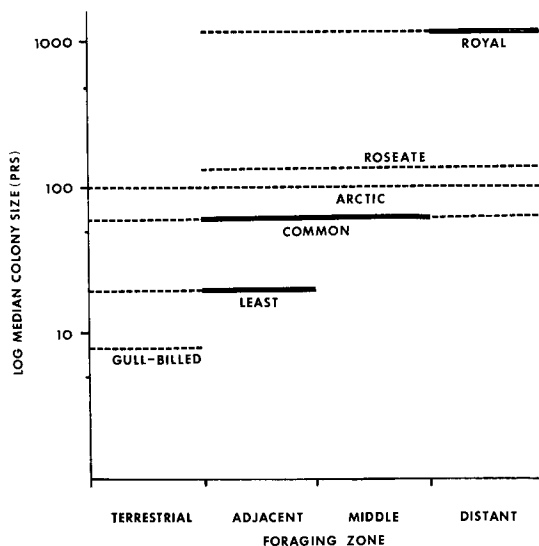

FIGURE 1. Relationship between median colony sizes and comparative foraging zone use by six Atlantic coast terns. Foraging zones are arbitrarily divided into a terrestrial zone and waters adjacent to, at middle distances from, and distant from the colony site. Dark bars indicate areas of heaviest use (see text). Relative use of zones by Arctic and Roseate terns is not well-documented. Table 1 lists median colony size for each species.

er. Comparing median/abundance ratios, however, reveals that Least Terns are more clumped than the other small terns (Table 1). The fact that most colonies are located adjacent to inlets where feeding is concentrated suggests that some degree of site limitation may exist for Least Terns.

Lack (1968) asserted that the high productivity of plankton and fish in North Temperate waters during the summer precludes food competition for most seabirds. However, a mobile, patchy fish resource, no matter how abundant, is more difficult to locate for species who feed over larger areas than for those who restrict their search area (Ward and and Zahavi 1973). Under these conditions, it would be advantageous for a bird to be in a large colony, with many "information sources." Indeed, as shown above, the more distant-foraging species nest in the largest colonies.

While correlations may strongly suggest causal relationships, direct proof of the "information-centre" hypothesis requires measures of food distribution patterns, evidence of communication, and comparisons of feeding success at varying group sizes. The first requirement presents great logistical difficulties for seabird researchers. I previously analyzed the results of scientific and commercial fish collections (Erwin 1975, 1977a) and found a

tendency for inshore fish to be more uniform in distribution than offshore fish. However, these are only crude estimations of availability patterns. Different patterns of prey distribution might select for different modes of predation (Kleiman and Eisenberg 1973). Common Terns seem to feed in dense flocks while Roseate Terns are more diffuse. This may be explained in part by their preferences for different prey or the same prey in different situations. Roseate Terns seem to feed more predictably in smaller numbers at certain locations (e.g., tide rips) than the more opportunistic Common Terns which often follow predatory bluefish (*Pomatomus saltatrix*), waiting for panicking baitfish to surface (D. Duffy, unpubl. data). Terns depending upon this latter "bonanza" would surely benefit more from food "information sharing" than those in the former case. Clearly, more data are needed on prey behavior and hunting methods among species.

A correlation of colony size and foraging range among related tern species was similarly described in Europe (Lack 1967, 1968). The Least (= Little) Tern had smaller colonies than the offshore-feeding Sandwich Tern in Great Britain. Common and Arctic terns were intermediate in both colony size and foraging zone use. Lack's interpretation was that by nesting in smaller groups, Least Terns would be nearer to their food supply when feeding young than if they were in larger groups. However, his argument was one-sided because he failed to explain the energetic advantage accruing to distant feeders nesting in large colonies.

Pearson (1968) found that Sandwich Terns had a maximum feeding range of 24 km, greater than that of either Arctic Terns (20 km) or Common Terns (22 km) in Great Britain. In Eurasia, Gause (1934) related an account by A. Formosov showing spatial segregation of feeding areas near the Crimean Sea, with Gull-billed Terns feeding on land, Least Terns using shallow water areas, Common Terns foraging somewhat further from shore, and Sandwich Terns fishing in open ocean areas. In different parts of Europe, Arctic and Common terns, despite large overlap, may reverse their relative use of shallow and deep water areas (Boecker 1967, Pearson 1968, Lemmetyinen 1973, 1974, 1976).

The six species comparisons I have made may be representative of a widespread adaptation among seabirds. The only other related fish-eating seabird (excluding the omnivorous gulls) breeding in similar habitats along the western Atlantic coast is the Black Skimmer (*Rynchops nigra*). It is strictly an inshore feeder (< 5 km) and seldom forages in groups of more than three or four (Erwin 1975, 1977b). Colony sizes in Virginia averaged 95 pairs (median 90) in 38 colonies (1973–1974 censuses by Weske and Clapp). Skimmer colonies, then, are similar in size to those of Common Terns which also feed mostly close to shore along beaches and inlets.

Sealy (1975) found a similar comparison in coastal island-nesting murrelets in British Columbia. Distant-feeding Ancient Murrelets (*Synthliboramphus antiquus*) nest in colonies, feed in flocks, and shift feeding locations from day to day while Marbled Murrelets (*Brachyramphus marmoratus*) limit their feeding to inshore bays, nest solitarily, and feed either singly or in pairs.

I am not suggesting that the relationship discussed above constitutes critical proof that information-sharing is the "prime mover" in seabird coloniality. As Lack (1967), Crook (1965) and others have shown, breeding distributions often represent responses to a large set of interrelated selection factors including food, predator abundance and hunting technique, habitat structure, etc. However, by attempting to compare related species under similar habitat-predation constraints, I have provided support for what could be an important factor influencing the evolution of coloniality.

SUMMARY

Aspects of foraging and colonial breeding in six Atlantic tern species are compared. Inshore-feeders (Gull-billed and Least terns) tend to have the smallest colonies, mid-range feeders (Common and Arctic terns) have intermediate colonies, while the "distant" foraging Roseate and Royal terns have the largest colonies. Consistencies are also found between group foraging tendency and foraging zone. Species foraging at greater distances feed in groups more readily than inshore-feeders. Similar correlations exist among terns in Europe and alcids in British Columbia, suggesting that the phenomenon may be widespread. Colonial nesting may not only deter predators but also increase searching efficiency over a range of foraging areas where the distribution of food is patchy and unpredictable.

ACKNOWLEDGMENTS

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