

# EFFECTS OF INTERFERENCE COMPETITION ON THE FORAGING ACTIVITY OF TROPICAL ROSEATE TERNS<sup>1</sup>

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**Abstract.** Although difficult to detect, interference competition among foraging birds may affect the fitness of an inferior competitor by lowering foraging success. We studied foraging flocks of Roseate Terns (*Sterna dougallii*) at Culebra, Puerto Rico, in 1990 to examine the effects of small and large monospecific and mixed-species flocks on the foraging success and behavior of this threatened species. Roseate Terns mostly foraged in small flocks with Brown Noddies (*Anous stolidus*). The frequency of foraging attempts in Roseate Terns decreased with increasing size of mixed-species flocks, primarily due to passive interference by Brown Noddies, which foraged just over the water surface and limited the area available to Roseate Terns. The size of monospecific Roseate Tern flocks had no effect on foraging attempt frequency. Roseate Terns also aborted more feeding dives and foraged more by dipping when in flocks with noddies, relative to flocks of only conspecifics. Proportionally fewer Roseate Terns than expected foraged in large, mixed-species flocks (>8 birds), suggesting that they preferentially avoid large flocks that result in lower foraging success. Although Brown Noddies caused a reduction in Roseate Tern foraging attempt frequencies and an increase in aborted dives, we were unable to detect a negative effect on adult survival or reproductive success of this population.

**Key words:** Competition; interference; foraging success; Roseate Tern; *Sterna dougallii*; Brown Noddy; *Anous stolidus*.

## INTRODUCTION

Interference competition among foraging birds may affect the fitness of an inferior competitor by lowering foraging success, particularly when food availability is limited. Interference competition occurs when one species impedes the access of another species to a resource either through active aggression or territoriality (Schoener 1983) or by passive means, such as creating a barrier to the resource (Charnov et al. 1976). Maurer (1984) developed a model that predicts the ecological setting in which interference competition may occur. Despite Maurer's model, only a few examples of passive interference competition exist (Goss-Custard 1980, Waite 1984, Poysa 1985), possibly due to the difficulty in detecting it (Maurer 1984) or in differentiating it from exploitative competition (Anholt 1990).

Aggregations of foraging seabirds provide an opportunity to examine the effects of interference competition for prey resources. Seabirds often congregate in mixed-species flocks over prey fish schools that are patchily-distributed and ephemeral (Lack 1968, Safina et al. 1988, Safina 1990).

Fish schools tend to be monotypic (Breder 1959, Shaw 1970), suggesting that all birds in a flock are vying for the same resource. Further, seabirds use different prey-capture techniques (Porter and Sealy 1982, Hulsman 1989), creating the potential for asymmetrical prey acquisition and passive interference between species. Competition probably does not lead to competitive exclusion (sensu Gause 1934) among breeding seabird species because the guild is only congregated during part of the year. Ashmole (1963) has argued that selection (in terms of mortality) in birds is strongest during the nonbreeding season when resources are more limited. Seasonal fluctuation in food abundance may be a primary determining factor in clutch size (Ricklefs 1980) and breeding success (Uttley et al. 1989). But competition may restrict breeding population size and reproductive success as well, particularly when prey is scarce (Ashmole 1971).

In 1990 we studied a guild of seabirds at Culebra, Puerto Rico, with particular emphasis on the foraging associations, behavior and success of the Roseate Tern (*Sterna dougallii*). Roseate Terns historically nested on several cays in the Culebra Archipelago, but the breeding population has remained consistently small (<225 pairs; Furniss 1983; Burger and Gochfeld, unpubl. data).

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Nearby Roseate Tern colonies at St. Thomas and along the southwest coast of Puerto Rico number up to 1,000 breeding pairs. The low numbers of Roseate Terns at Culebra may indicate that this site is suboptimal for breeding, possibly because of low food availability or because Roseate Terns are inferior competitors to other breeding seabird species in the area.

Our objectives in this study were to quantify the composition of foraging flocks at Culebra that included Roseate Terns, and to compare foraging behavior and success of Roseate Terns between large and small monospecific and mixed-species flocks. A secondary goal of this study was to provide comparative data on the foraging behavior of Roseate Terns in the Caribbean to the well-studied population in the northeastern United States.

#### STUDY AREA AND METHODS

We studied foraging flocks of Roseate Terns in the Culebra Archipelago, Puerto Rico. The study site lies 37 km east of Puerto Rico proper and 25 km west of the U.S. Virgin Islands (see Wetmore 1917, Kepler and Kepler 1978, Furniss 1983, for detailed site descriptions). Roseate Terns nested on two small islands in the archipelago (see Burger and Gochfeld 1988 for nest-site characteristics). The total breeding population at Culebra in 1990 was 102 pairs. Other breeding seabirds in the area included Brown Noddies (*Anous stolidus*), Laughing Gulls (*Larus atricilla*), Bridled and Sooty Terns (*Sterna aethetus* and *S. fuscata*), tropicbirds (*Phaethon aethereus* and *P. lepturus*) and boobies (*Sula leucogaster*, *S. sula* and *S. dactylatra*).

On 14 days from 26 May to 1 July 1990, we observed foraging flocks of seabirds which included Roseate Terns in the Culebra Archipelago. Sites were chosen opportunistically, wherever and whenever groups of birds were foraging over schools of prey fish, but all observations were made from land. Data were collected only when predatory fish were visible at the surface, indicating that prey fish were readily available to foraging birds, and only when birds were actively foraging.

When the above criteria were met, feeding observations were conducted on individual Roseate Terns until the feeding flock dispersed. A feeding observation consisted of first counting the total number and species composition of seabirds in the flock. A test bird was randomly selected by

scanning the flock with  $7 \times 35$  binoculars until the first Roseate Tern was encountered. We then timed the length of the bird's foraging bout with a stopwatch and counted the number of completed dives and aborted dives the bird made. Roseate Terns feed primarily by plunge-diving into the water from variable heights, making feeding attempts easy to quantify. We scored an aborted dive when a tern began a dive but pulled up before contacting the water. Terns aborted dives both when other birds moved between them and the fish school and when their path from the air to the water was clear. We were not certain what caused terns to abort dives in the latter case, but presumably it was related to the target fish becoming inaccessible. Thus, for convention, we hereafter refer to the two types of aborted dives as being caused by birds and fish. We excluded all observations in which we could not determine which situation caused an aborted dive.

In this study we use the frequency of prey capture attempts as a relative measure of foraging success. We were unable to determine capture success because we often observed flocks from a considerable distance and because prey fish were quite small ( $<20$  mm standard length; Shealer, unpubl. data). In 1991, we observed Roseate Terns foraging in a shallow tidal lagoon in southwestern Puerto Rico and found that capture success frequency was highly correlated with capture attempt frequency (Fig. 1). Our 1991 study only validated this relationship up to four capture attempts per minute, whereas capture attempt frequencies in the present study were always higher. A possible reason for this difference is that in the 1991 study, terns were foraging on larger fish ( $>30$  mm standard length) and in the absence of predatory fish. Thus, search and handling times were almost certainly greater, resulting in a lower capture attempt frequency. Search and handling times in the present study were presumably negligible since the surface thrashing of predatory fish indicated the presence of prey and the smaller fish were easier to swallow. Salt and Willard (1971) found that Forster's Terns (*Sterna forsteri*) swallowed small fish "almost immediately, sometimes while the bird was ascending to hunting altitude." Ulenaers et al. (1992) found that handling times of Great Crested Grebes (*Podiceps cristatus*) feeding on small fish did not limit the number of prey eaten per unit time. The few times we observed Roseate Terns catching fish in flocks over predatory fish, we also noted that

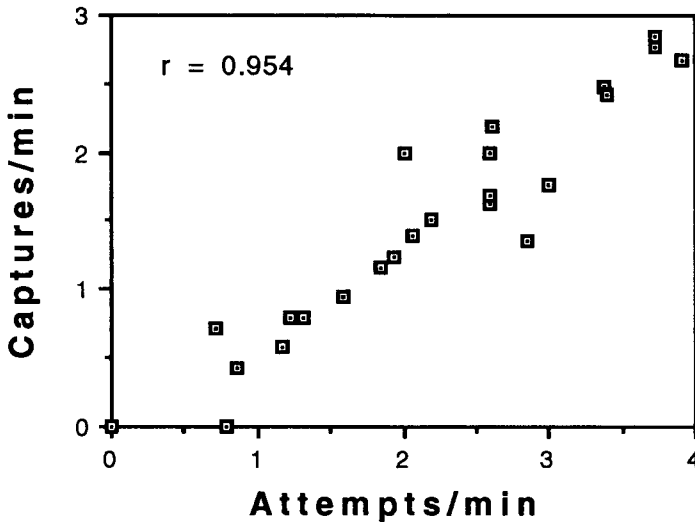


FIGURE 1. Relationship between frequency of plunge dives and captures in individual Roseate Terns. Study was conducted at a Roseate Tern colony in southwestern Puerto Rico in 1991. Points are individual birds followed for  $\geq 4$  min each.  $R^2 = 0.911$ ,  $df = 23$ ,  $P < 0.01$ .

fish were swallowed immediately upon the bird's emergence from the water. For the above reasons we do not believe that handling times would affect the linear relationship between capture attempt and success frequencies beyond four attempts per minute.

A single Roseate Tern was followed until it either ceased foraging or it was lost from the field of view. Thus, bout lengths were not consistent between individuals and ranged from 18–173 sec. Bout lengths and capture attempt frequencies were summed for each flock size and analyzed to examine individual species effects.

## RESULTS

### FLOCK COMPOSITION

We conducted 277 feeding observations (288 min) on Roseate Terns in foraging flocks. Of the breeding seabirds in the area, Brown Noddies fed most frequently with Roseate Terns (Table 1). Bridled Terns, Laughing Gulls and Brown Boobies occurred less frequently in smaller numbers. Sooty Terns and tropicbirds never foraged with Roseate Terns. Roseate Terns and Brown Noddies comprised 96.5% of all individuals in feeding flocks; however, participation of the two species in flocks differed according to flock size ( $\chi^2 = 201.5$ ,  $df = 5$ ,  $P < 0.001$ , Fig. 2). Proportionally more Roseate Terns than expected foraged in small flocks while fewer foraged in large flocks.

### FORAGING BEHAVIOR AND SUCCESS

Roseate Terns and Brown Boobies were the only species in the foraging guild to use plunge-diving as the primary prey capture technique; 95.4% of all Roseate Tern attempts were plunge dives. Brown Noddies, Bridled Terns and Laughing Gulls foraged exclusively by dipping (Ashmole and Ashmole 1967). Roseate Terns also used the dipping technique in 4.6% of all feeding attempts.

To compare foraging behavior and success we divided our data set into two groups: monospecific Roseate Tern flocks and mixed-species flocks that were comprised of Roseate Terns and at least one Brown Noddy. Because all other species were so infrequent in flocks, we excluded them from further analysis, and hereafter we refer to the two flock types as "Roseate flocks" and "Mixed flocks."

Roseate Terns used the dipping technique more frequently in Mixed flocks (87/124.02 min) than in Roseate flocks (26/113.92 min,  $\chi^2 = 27.0$ ,  $df = 1$ ,  $P < 0.001$ ). When scaled to account for observation times, Roseate Terns aborted more dives because of bird interference in Mixed flocks (26/107.77 min) relative to Roseate flocks (12/102.32 min), although the difference was only weakly significant ( $\chi^2 = 3.88$ ,  $df = 1$ ,  $P < 0.05$ ). No differences were found between the two flock types for aborted dives presumably caused by

TABLE 1. Frequency of occurrence by seabird species in foraging flocks with Roseate Terns in the Culebra Archipelago in 1990. Sample size = 277 flocks.

Species <sup>a</sup>	Number of flocks with Roseate Terns	Frequency of occurrence	Number per flock ( $\bar{x} \pm 1$ SD)
Brown Noddy	160	.578	6.5 $\pm$ 5.2
Laughing Gull	33	.119	2.0 $\pm$ 2.0
Bridled Tern	26	.094	1.5 $\pm$ 0.8
Brown Booby	3	.011	1.0 $\pm$ 0.0

<sup>a</sup> See text for scientific names.

the evasive response of fish (Mixed flocks, 47/107.77 min; Roseate flocks, 60/102.32 min;  $\chi^2 = 2.04$ ,  $df = 1$ ,  $P > 0.10$ ). Roseate Terns occasionally collided with noddies below them and directed aggressive calls towards nearby birds, but we did not observe any prolonged fights or chases between the two species.

Foraging success (measured in terms of prey-capture attempt frequencies) in Roseate Terns declined as the size of Mixed flocks increased (Spearman rank correlation,  $r_s = 0.632$ ,  $df = 16$ ,  $P < 0.001$ , Fig. 3A). Exclusion of all other species except Brown Noddies strengthened the relationship ( $r_s = 0.718$ ,  $df = 16$ ,  $P < 0.001$ , Fig. 3B). There were no significant density-dependent relationships in monospecific Roseate Tern flocks ( $r_s = 0.063$ ,  $df = 16$ ,  $P > 0.75$ , Fig. 3C), although the data suggest that foraging success may peak

at a flock size of eight birds. The mean number of Roseate Terns in flocks in this study was  $6.9 \pm 5.3$  individuals, very close to the flock size associated with maximum foraging success in both Roseate and Mixed flocks.

We determined differences in Roseate Tern foraging success between small and large Roseate and Mixed flocks using eight birds as the cutoff. The frequency of Roseate Tern dives did not differ between small Roseate and Mixed flocks (Wilcoxon matched-pairs signed-rank test,  $t = 13$ ,  $n = 8$ ,  $P = 0.242$ ) but was significantly different in large flocks ( $t = 7$ ,  $n = 9$ ,  $P = 0.033$ ). Thus, Roseate Terns foraging in mixed-species flocks of more than eight birds were less successful than when foraging in monospecific flocks of more than eight birds (Fig. 3).

## DISCUSSION

Our evidence for interference competition between foraging Brown Noddies and Roseate Terns is indirect but is based on several findings. First, the frequency of prey capture attempts by Roseate Terns showed a significant negative relationship to the number of Brown Noddies in the flock. No such relationship was apparent in monospecific flocks of Roseate Terns. Second, flocks consisting of more than eight noddies resulted in significantly lower capture attempt frequencies for Roseate Terns relative to monospecific flocks of more than eight Roseate Terns.

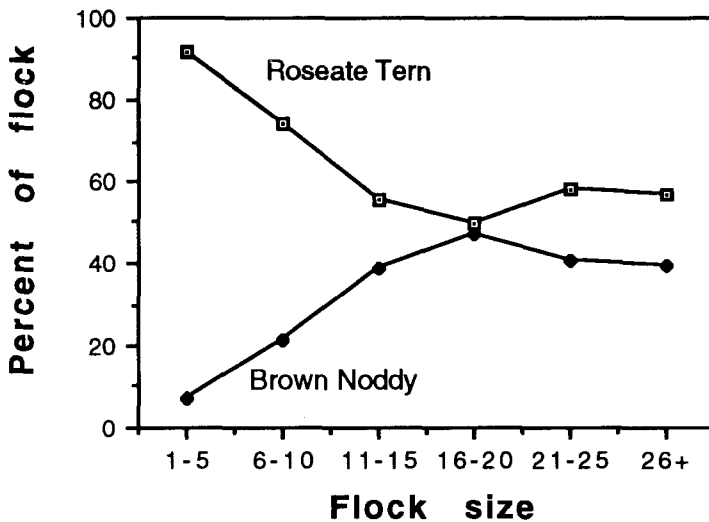


FIGURE 2. Inverse relationship between total foraging flock size and percent of Roseate Terns and Brown Noddies comprising flocks of particular sizes.

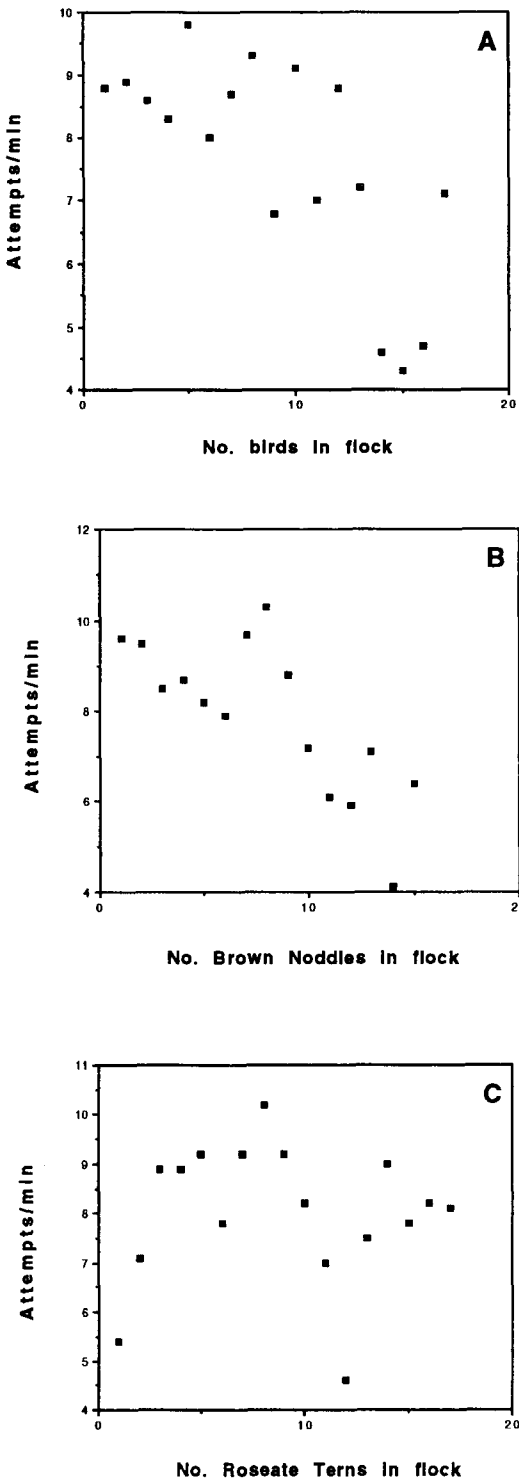


FIGURE 3. Relationship between the frequency of Roseate Tern prey capture attempts and (A) total num-

ber of birds (excluding Roseate Terns) in a foraging flock, (B) the number of Brown Noddies in a foraging flock, and (C) the number of Roseate Terns in a foraging flock. Points are means for flocks of a particular size.

Third, Roseate Terns were more likely to abort feeding dives in Mixed flocks than in monospecific flocks. Fourth, Roseate Terns altered their foraging behavior when in Mixed flocks by using the dipping technique a higher proportion of times than when in monospecific flocks. Although we were unable to determine prey capture success rates in this study, we have supplied evidence that in certain situations, prey capture success frequency is directly and positively related to capture attempt frequency in Roseate Terns (Fig. 1). We recognize that because we were unable to determine capture success rates in our present study, interpretation of our results must be cautious.

Although Roseate Terns aborted a higher proportion of dives in Mixed flocks than in Roseate flocks, the absolute number of aborted dives caused by bird interference was less than 2% of all attempts. Although this seems in and of itself to be a low cost, we contend that the most important cost to Roseate Terns foraging in flocks with Brown Noddies is not the number of aborted dives per se, but rather the reduction in foraging attempt frequency. Prey patches in this study appeared to be quite ephemeral, and the loss of even a few seconds of foraging time may be significantly detrimental to foraging terns.

Hulsman (1989) first described the mechanism by which noddies may interfere with other foraging seabirds. Black Noddies (*Anous minutus*) in Australia forage in flocks less than 1 m over the surface, essentially limiting the foraging area for other birds that plunge dive into the water from greater heights. Brown Noddies in the Caribbean forage in a similar manner to Black Noddies in Australia. Our data suggest that at Culebra in 1990, Roseate Terns suffered the effects of passive interference competition from Brown Noddies, as access to prey fish was limited by the blanket of noddies below them.

Roseate Terns occurred more frequently than expected in smaller-sized flocks, whereas noddies were more abundant in larger flocks, suggesting that Roseate Terns preferentially avoid large Mixed flocks that result in lower foraging

success. Our findings support the work of Duffy (1986), who found that Roseate Terns in the United States tend to avoid large, dense flocks containing Common Terns because in this situation, Roseate Terns are less successful in prey capture relative to foraging in dispersed flocks.

Roseate Terns are specialists in prey selection compared to other terns (Randall and Randall 1978, Richards and Schew 1989, Safina et al. 1990). Indeed, over 90% of prey items we could identify at Culebra were small (<20 mm) silver-sided fish (probably *Jenkinsia* sp. or *Opisthonema oglinum*). Roseate Terns confined their foraging activity to areas around the islands of Culebra. We never saw them feeding farther than 2 km from land, despite occasional surveys from a boat. Brown Noddies at Culebra and elsewhere are more generalist feeders and more plastic in their feeding habitat requirements, feeding both inshore and offshore along shelf breaks (Brown 1975, Harrison et al. 1983, Morris and Chardine 1992). When a generalist and a specialist use the same resource, theory predicts that the specialist is more likely to suffer any adverse effects of competition (Pianka 1969, Roughgarden 1972), consistent with our findings for Roseate Terns in terms of reduced foraging success.

We did not measure prey patch sizes or fish densities under foraging terns as Safina and Burger (1985, 1988) and Safina et al. (1988) have done with terns in North America. Prey abundance almost certainly varied between trials and may have been correlated with the size of the feeding flock. We believe, however, that variation in prey abundance could only obscure the effects of competition, not reveal it when it does not exist. For terns, the important factor in foraging success is not prey abundance per se, but rather prey availability. Prey fish may be abundant in the water column but distributed in such a way as to be unavailable to foraging seabirds. Some species of terns rely heavily on predatory fish to herd and drive fish schools to the surface (Hulsman 1978, 1989; Safina and Burger 1988). Thus, even though predatory fish may facilitate seabird foraging success, the same fish also deplete prey stocks, resulting in seasonal declines (Safina and Burger 1988). In our study, we conducted observations only when predatory fish were thrashing about at the surface, in effect controlling for prey availability. If the prey resource was depleted during the course of our study, the result would have been to increase the likelihood

of competitive interactions between seabird species, not reduce them, since Brown Noddies and Roseate Terns were presumably vying for the same prey resource in flocks in which both species occurred.

A decline in foraging efficiency with increasing flock size in birds feeding on depletable patches has been shown both theoretically (Clark and Mangel 1984) and empirically (Hake and Ekman 1988), although some exceptions have also been found (Gotmark et al. 1986, Høglund 1985). Our findings for Roseate Terns foraging in monospecific flocks are quite similar to those of Gotmark et al. (1986), who found that the foraging success of captive Black-headed Gulls (*Larus ridibundus*) increased with increasing flock size up to at least eight birds. Our data show almost exactly the same trend in Roseate Terns (Fig. 3C). Mean size of monospecific Roseate Tern flocks in our study was seven birds, suggesting that this species generally forages in groups that maximize individual prey capture success.

In North America, Roseate Terns are at a competitive disadvantage when foraging with Common Terns over prey fish brought to the surface by Bluefish (*Pomatomus saltatrix*), because Common Terns exclude Roseate Terns from the center of the flock (Duffy 1986, Safina 1990). Roseate Terns in mixed flocks are less successful in prey capture relative to feeding in monospecific flocks (Duffy 1986), presumably because they are less able than Common Terns to hover for prolonged periods over prey patches (Kirkham and Nisbet 1987). Prey fish in our study were usually mobile, and birds were constantly tracking the patch so that after several minutes, birds would actually fly ahead of the patch and have to circle back around and join the rear of the flock. Thus, we do not believe that hovering difficulties affected foraging success in our study as much as passive interference from foraging Brown Noddies.

Research in progress suggests that Brown Noddies and Roseate Terns do not always forage together in flocks as consistently as we found in 1990. It appears that this association intensifies during years of food shortage or environmental stress (R. D. Morris and J. W. Chardine, pers. comm.; Shealer, unpubl. data). In September 1989, Hurricane Hugo passed directly over the Culebra Archipelago, destroying terrestrial and reef ecosystems. The impact of the hurricane on inshore schooling fishes has not yet been as-

sessed, but presumably the storm caused high fish mortality. Ongoing studies of Brown Noddies at Culebra indicate that 1990 was a poor year for adult survival and reproductive success (Morris and Chardine, unpubl. data). Roseate Terns also suffered heavy losses from eggings and predators (Shealer and Burger 1992), but there were no visible signs of food shortages at the nesting colony. Sizes of fish brought to chicks increased with increasing chick age, while feeding rates remained fairly consistent throughout the chick-rearing period (Shealer 1992). Thus, even though we detected a measurable effect of Roseate Terns foraging in flocks with Brown Noddies, we do not believe that it represents a significant factor in the survival of this threatened population.

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#### LITERATURE CITED

- ANHOLT, B. R. 1990. An experimental separation of interference and exploitative competition in a larval damselfly. *Ecology* 71:1483-1493.
- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-473.
- ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, p. 223-286. *In* D. S. Farner and J. R. King [eds.], *Avian biology*, Vol. I. Academic Press, New York.
- ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of seabirds on a tropical oceanic island. *Peabody Mus. Nat. Hist. Yale Univ. Bull.* 24:1-128.
- BREDER, C. M., JR. 1959. Studies on social groupings in fishes. *Bull. Am. Mus. Nat. Hist.* 117:397-481.
- BROWN, W. Y. 1975. Parental feeding of young Sooty Terns (*Sterna fuscata*) and Brown Noddies (*Anous stolidus*) in Hawaii. *J. Anim. Ecol.* 44:731-742.
- BURGER, J., AND M. GOCHFELD. 1988. Nest-site selection by Roseate Terns in two tropical colonies on Culebra, Puerto Rico. *Condor* 90:843-851.
- CHARNOV, E. L., G. H. ORIANS, AND K. HYATT. 1976. Ecological implications of resource depression. *Am. Nat.* 110:247-259.
- CLARK, C. W., AND M. MANGEL. 1984. Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* 123:626-641.
- DUFFY, D. C. 1986. Foraging at patches: interactions between Common and Roseate Terns. *Ornis Scand.* 17:47-52.
- FURNISS, S. 1983. Status of the seabirds of the Culebra Archipelago, Puerto Rico. *Col. Waterbirds* 6:121-125.
- GAUSE, G. F. 1934. *The struggle for existence*. Williams and Wilkins, Baltimore, MD.
- GOSS-CUSTARD, J. D. 1980. Competition for food and interference among waders. *Ardea* 68:31-52.
- GOTMARK, F., D. W. WINKLER, AND M. ANDERSSON. 1986. Flock-feeding on fish schools increases individual success in gulls. *Nature* 319:589-591.
- HAKE, M., AND J. EKMAN. 1988. Finding and sharing depletable patches: when group foraging decreases intake rates. *Ornis Scand.* 19:275-279.
- HARRISON, C. S., T. S. HIDA, AND M. P. SEKI. 1983. Hawaiian seabird feeding ecology. *Wildl. Monogr.* 85:1-71.
- HOGLUND, J. 1985. Foraging success of Rooks (*Corvus frugilegus*) in mixed-species flocks of different sizes. *Ornis Fenn.* 62:19-22.
- HULSMAN, K. 1978. Reactions of fish to hunting methods of terns: a means of segregation. *Proc. Col. Waterbird Group* 1978:105-109.
- HULSMAN, K. 1989. The structure of seabird communities: an example from Australian waters, p. 59-91. *In* J. Burger [ed.], *Seabirds and other marine vertebrates: competition, predation, and other interactions*. Columbia Univ. Press, New York.
- KEPLER, C. B., AND A. K. KEPLER. 1978. The sea birds of Culebra and its adjacent islands, Puerto Rico. *Living Bird* 16:21-50.
- KIRKHAM, I. R., AND I.C.T. NISBET. 1987. Feeding techniques and field identification of Arctic, Common, and Roseate Terns. *Brit. Birds* 80:41-47.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- MAURER, B. A. 1984. Interference and exploitation in bird communities. *Wilson Bull.* 96:380-395.
- MORRIS, R. D., AND J. W. CHARDINE. 1992. The breeding biology and aspects of the feeding ecology of Brown Noddies *Anous stolidus* nesting near Culebra, Puerto Rico, 1985-1989. *J. Zool. (Lond.)* 226:65-79.
- PIANKA, E. R. 1969. Sympatry of desert lizards (*Crotalus*) in western Australia. *Ecology* 50:1012-1030.
- PORTER, J. M., AND S. G. SEALY. 1982. Dynamics of seabird multispecies feeding flocks: age-related feeding behaviour. *Behaviour* 81:91-109.
- POYSA, H. 1985. Circumstantial evidence of foraging interference between two species of dabbling ducks. *Wilson Bull.* 97:541-543.
- RANDALL, R. M., AND B. M. RANDALL. 1978. Diet of Roseate Tern during the breeding season at St. Croix Island, Algoa Bay. *Cormorant* 5:4-10.
- RICHARDS, S. W., AND W. A. SCHEW. 1989. Species composition of food brought to Roseate Tern chicks on Falkner Island, Connecticut in summer 1984. *Connecticut Warbler* 9:1-5.

- RICKLEFS, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97:38-49.
- ROUGHGARDEN, J. 1972. Evolution of niche width. *Am. Nat.* 106:683-718.
- SAFINA, C. 1990. Bluefish mediation of foraging competition between Roseate and Common Terns. *Ecology* 71:1804-1809.
- SAFINA, C., AND J. BURGER. 1985. Common Tern foraging: seasonal trends in prey fish densities and competition with bluefish. *Ecology* 66:1457-1463.
- SAFINA, C., AND J. BURGER. 1988. Prey dynamics and the breeding phenology of Common Terns (*Sterna hirundo*). *Auk* 105:720-726.
- SAFINA, C., J. BURGER, M. GOCHFELD, AND R. H. WAGNER. 1988. Evidence for prey limitation of Common and Roseate Tern reproduction. *Condor* 90:852-859.
- 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.
- SALT, G. W., AND D. E. WILLARD. 1971. The hunting behavior and success of Forster's Tern. *Ecology* 52:989-998.
- SCHOENER, T. W. 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240-285.
- SHAW, E. 1970. Schooling in fishes: critique and review, p. 452-480. *In* L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt [eds.], *Development and evolution of behavior*. Freeman, San Francisco.
- SHEALER, D. A. 1992. Behavioral and ecological factors affecting reproductive success in a threatened population of tropical Roseate Terns. M.Sc.thesis, Rutgers Univ., New Brunswick, NJ.
- SHEALER, D. A., AND J. BURGER. 1992. Differential responses of tropical Roseate Terns to aerial intruders throughout the nesting cycle. *Condor* 94:712-719.
- ULENAERS, P., J. VAN VESSEM, AND A. DHONDT. 1992. Foraging of the Great Crested Grebe in relation to food supply. *J. Anim. Ecol.* 61:659-667.
- UTTLEY, J., P. MONAGHAN, AND S. WHITE. 1989. Differential effects of reduced sandeel availability on two sympatrically breeding species of tern. *Ornis Scand.* 20:273-277.
- WAITE, R. K. 1984. Sympatric corvids: effects of social behaviour, aggression and avoidance on feeding. *Behav. Ecol. Sociobiol.* 15:55-59.
- WETMORE, A. 1917. The birds of Culebra Island, Porto Rico. *Auk* 34:51-61.