

DIFFERENTIAL RESPONSES OF TROPICAL ROSEATE TERNS TO AERIAL INTRUDERS THROUGHOUT THE NESTING CYCLE¹

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Abstract. We studied a small (63-pair) breeding colony of Roseate Terns (*Sterna dougallii*) at Culebra, Puerto Rico, in 1990 to identify disturbances caused by, and responses elicited by, aerial intruders and to determine the effect of predation on reproductive success of this threatened species. Laughing Gulls (*Larus atricilla*) were the most frequent cause of disturbance to nesting adults and captured at least two chicks. More intrusions occurred during the early stages of the breeding season and in the early morning than at other times. Defensive aggression in nesting Roseate Terns increased until the chick hatching stage, then decreased progressively through fledging. Neither the number of adults nor the number of chicks in the colony influenced aggressive responses against intruders as strongly as the nesting stage, suggesting that this population of Roseate Terns was most aggressive when the young were most vulnerable. Although our findings contrast with traditional parental investment theory, they are consistent with other studies of defensive aggression in seabirds. Most chick losses occurred during or shortly after hatching. Reproductive success of the colony was 0.25 ± 0.50 chicks/pair and may have been low due to egg and chick mortality caused by predatory land crabs (*Gecarcinus ruricola*) that were abundant in the colony. Our findings suggest that although Roseate Terns responded appropriately to potential avian predators at this small Culebra colony, they were unable to successfully defend against certain ground predators (e.g., crabs).

Key words: *Roseate Tern*; *Sterna dougallii*; nest defense; defensive aggression; disturbance; predation; parental care.

INTRODUCTION

Many species of birds actively defend their nests against potential predators (Altmann 1956, Kruuk 1964, Fuchs 1977, Bierman and Robertson 1981, Shedd 1982). Flocking and colonial nesting species exhibit group defense (Siegfried and Underhill 1975, Hoogland and Sherman 1976). Burger and Gochfeld (1988a) have shown that participation in colony defense increases with increasing nest density and colony size, suggesting that larger colonies should suffer less predation than smaller colonies (but see Wilkinson and English-Loeb 1982, Erwin 1988).

Other factors that affect defense are the type of predator (Patterson et al. 1980, Buitron 1983), stage of breeding cycle (Lack 1968, Lemmetyinen 1971, Veen 1977, Burger 1984a, Kilpi 1987), and parental investment considerations (Trivers 1972, Dawkins and Carlisle 1976, Boucher 1977, Weatherhead 1979, Andersson et al. 1980). In addition, some colonial species rely on other species nesting in the area for defense (Nuechterlein 1981, Burger 1984b, Young and Titman 1986).

Disjunct populations provide a unique opportunity to study aggressive behavior and to examine factors that lead to differences. In the Western Hemisphere, Roseate Terns (*Sterna dougallii*) breed in two locations: along the coast of northeastern North America and in the Caribbean region (Nisbet 1980). North American Roseate Terns almost invariably nest in association with Common Terns (*Sterna hirundo*), which usually outnumber them (Spendelov 1982, Kress et al. 1983, Gochfeld and Burger 1987) and which may provide additional predator defense (Langham 1974, Burger and Gochfeld 1988a). In the Caribbean, Roseate Terns nest in monospecific groups and are more aggressive than North American conspecifics (Burger and Gochfeld 1988a).

We investigated the aggressive behavior of Roseate Terns at Culebra, Puerto Rico, during the 1990 breeding season to determine if the difference in aggression between temperate North American and tropical Caribbean colonies is due to differences in the number and types of predators, the frequency of intrusions by potential predators and predation rate. We also examined how aggression varies with time of day and reproductive stage.

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Roseate Tern colonies in North America have been extensively studied, but little is known about the breeding biology or population dynamics of the Caribbean population. North American Roseate Terns are vulnerable to predation by gulls (*Larus marinus* and *L. argentatus*, Hatch 1970), rats (*Rattus norvegicus*, Gochfeld 1976), mink (*Mustela vison*, S. W. Kress, pers. comm.), Great Horned Owls (*Bubo virginianus*, Nisbet and Welton 1984) and Black-crowned Night-Herons (*Nycticorax nycticorax*, Collins 1970). Little is known about the predators that threaten Roseate Terns in the Caribbean region or their effects on reproductive success. This is of particular interest because the Caribbean population has recently been listed as threatened (Federal Register 1987) due to a recent population decline.

STUDY AREA AND METHODS

Observations were conducted on 23 days between 1 June and 20 July 1990 in a small (63 nesting pairs) colony of Roseate Terns at Cayo Ratón (18°19'N; 65°21'W), a 0.8 ha island in the Culebra Archipelago, Puerto Rico. Roseate Terns nested amidst boulders and sedges on the eastern slope of the cay (see Burger and Gochfeld 1988b for a detailed site description). Other species that nested on the cay included Brown Noddies (*Anous stolidus*), Bridled Terns (*Sterna anaethetus*) and Zenaida Doves (*Zenaida aurita*). The entire colony was observed from a small rock located ca. 10 m southeast of the cay using 7 × 35 binoculars and a 15–40 × spotting scope. Arrival at the observation post occasionally caused terns to leave their nests, but they always settled back down within 5 min. Data collection began 15 min after arrival to eliminate the effects of observer disturbance.

During each observation period, data were collected on all aerial intruders that approached the colony. Data recorded included stage of nesting cycle, date, time of day, wind speed and direction, sky condition, number and species of intruder, direction of intruder approach, detection distance by the terns or closest approach of intruder, tern response to the intruder, number of terns responding, duration of disturbance, and outcome. Wind speed and sky condition were not variable enough to warrant analysis and are not discussed further. Detection distances of, and closest approaches by, intruders were estimated using reference points of known distances near

the colony. These included the distance from the observation post to Cayo Ratón (10 m), the height of Cayo Ratón (15 m) and the distance between Cayo Ratón and the nearest cay (ca. 250 m). Therefore, any differences <5 m should be regarded with caution.

Tern responses to intruders were arbitrarily assigned a point value according to the degree of aggression (−1 = dread flight or fleeing from intruder, 0 = no response, 1 = alarm call only, 2 = aerial pursuit of intruder, 3 = attack or aerial mobbing of intruder). Higher values indicate increased aggression of, and risk to, a tern when confronting an intruder (sensu Barash 1975). This procedure allowed quantitative comparisons between intruder species and stage of the nesting cycle. During an intrusion it was possible for terns to exhibit more than one response, but we only scored the strongest response for each intrusion regardless of how many birds responded. Mean bout scores >1.0 were considered to be aggressive responses to intruders, while scores ≤1.0 were considered nonaggressive.

Hourly counts were made of all adults in the colony. To avoid counting the same bird twice, all terns that were in flight either to or from the colony were excluded. We used these counts to derive the mean number of adults that were present in the colony during each stage of the nesting cycle. Counts usually underestimated the number of terns present in the colony because some birds were hidden by rocks or vegetation. Hidden birds may have slightly biased the counts, but relative numbers of terns present in the colony should not have been affected by this procedure. Later in the season we added fledglings to our counts. Fledgling counts, along with the weekly nest censuses, gave us an estimate of reproductive success of the Ratón colony.

Total observation time for this study was 164.75 hrs. The breeding season was divided into five periods (egg-laying, 1–3 June; incubation, 8–12 June; chick hatching, 22–26 June; pre-fledgling, 3–8 July; fledging, 13–20 July). Stage of the nesting cycle was determined by remote observation and by weekly visits to the colony to census nest contents. We classified a new period as having begun when the modal number of nesting pairs had entered the stage. Breeding at Cayo Ratón in 1990 was not entirely synchronous. To reduce the possible confounding effects of overlapping stages in the analysis, we allowed a minimum of four days to pass before collecting data

TABLE 1. Intrusion and disturbance frequencies by species; detection distances and responses by Roseate Terns to intruders at Cayo Ratón in 1990. Total observation time was 164.75 hrs. Values are means with 1 SD in parentheses.

Intruder species	Predator ¹	Number of intrusions (mean per hour)	Number of disturbances (mean per hour)	Total disturbance time (mean per visit) (sec)	Detection distance (m) (mean ± SD)	Number of terns responding (mean ± SD)
Laughing Gull (<i>Larus atricilla</i>)	Yes	95 (0.58)	77 (0.47)	1175 (12.4)	5.2 ± 8.9	5.5 ± 7.9
Magnificent Frigatebird (<i>Fregata magnificens</i>)	Yes	9 (0.05)	5 (0.03)	115 (12.8)	11.3 ± 5.4	5.8 ± 7.2
American Kestrel (<i>Falco sparverius</i>)	Yes ²	6 (0.04)	5 (0.03)	166 (27.7)	5.2 ± 2.6	1.4 ± 0.8
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	Yes	4 (0.02)	4 (0.02)	1214 (303.5)	38.8 ± 36.5	58.3 ± 26.3
American Oystercatcher (<i>Haematopus palliatus</i>)	Yes	5 (0.03)	4 (0.02)	311 (62.2)	27.5 ± 14.8	47.5 ± 19.2
Red-billed Tropicbird (<i>Phaethon aethereus</i>)	No	4 (0.02)	2 (0.01)	25 (6.3)	2.0 ± 0.0	27.5 ± 22.5
Bridled Tern (<i>Sterna anaethetus</i>)	No	1 (0.01)	1 (0.01)	30 (30.0)	1.0 ± 0.0	20.0 ± 0.0
Brown Pelican (<i>Pelecanus occidentalis</i>)	No	1 (0.01)	1 (0.01)	10 (10.0)	20.0 ± 0.0	5.0 ± 0.0
Little Blue Heron (<i>Egretta caerulea</i>)	No	1 (0.01)	1 (0.01)	10 (10.0)	10.0 ± 0.0	3.0 ± 0.0

¹ Observed predator of eggs, chicks or adult seabirds of any species in the Culebra Archipelago.

² Undocumented predator of seabird chicks at Culebra prior to this study. On five occasions (24, 25, 26 June; 7, 19 July) a kestrel flew over Cayo Ratón with a dark seabird chick (probably *Sterna anaethetus* or *Sterna fuscata*) in its talons.

on the next stage. During each colony census, a count was made of all potential viable offspring, defined as the total number of viable eggs and living chicks in the entire colony.

Throughout this paper we use the terms "intrusion" and "disturbance." We defined an intrusion as any visit to the colony by a nonbreeding species that approached within 50 m, whether its presence elicited a response or not. Intrusion time is the length of time an intruder remained within 50 m of the colony. A disturbance is an intrusion that elicited a response from the terns and included dread flights, alarm calls, aerial mobbing or attacks. Disturbance time is the length of time terns were off their nests following an intrusion, whether or not the intruder was still in the area. An intrusion that resulted in no response by the colony was not treated as a disturbance.

Differences in intrusion frequencies and responses by terns between reproductive stages were analyzed by χ -square, Kruskal-Wallis H tests or by Spearman rank correlation. Pairwise multiple-comparisons tests were performed on certain transformed data sets when we wanted to determine which stages were significantly different from others.

RESULTS

INTRUDER SPECIES AND BEHAVIOR

Nine species of aerial intruders made 126 visits to the Roseate Tern colony in 1990; five species are known predators of adults, chicks or eggs (Table 1). Laughing Gulls (*Larus atricilla*) were the most frequent intruder species, making more appearances at the colony than all other intruders combined ($\chi^2 = 13.36$, $df = 1$, $P < 0.001$). No more than four Laughing Gulls ever patrolled the colony at one time. The modal number was one. When scaled to account for observation time, Laughing Gulls made more intrusions during the egg phase (egg-laying and incubation, $n = 43/58.75$ hr observ.) than during the chick phase (chick hatching, pre-fledging; fledging, $n = 52/106$ hr observ. $\chi^2 = 28.8$, $df = 1$, $P < 0.001$). However, Laughing Gulls made more attempts to capture chicks ($n = 17$) than eggs ($n = 1$). We observed them capturing and ingesting two chicks but no eggs in 1990, resulting in an 11% capture success.

The frequency of intrusions in the colony differed significantly among stages (Kruskal-Wallis, $H = 25.9$, $df = 4$, $P < 0.001$), decreasing from egg laying to chick hatching and then increasing slightly through the fledging stage (Fig. 1A). The

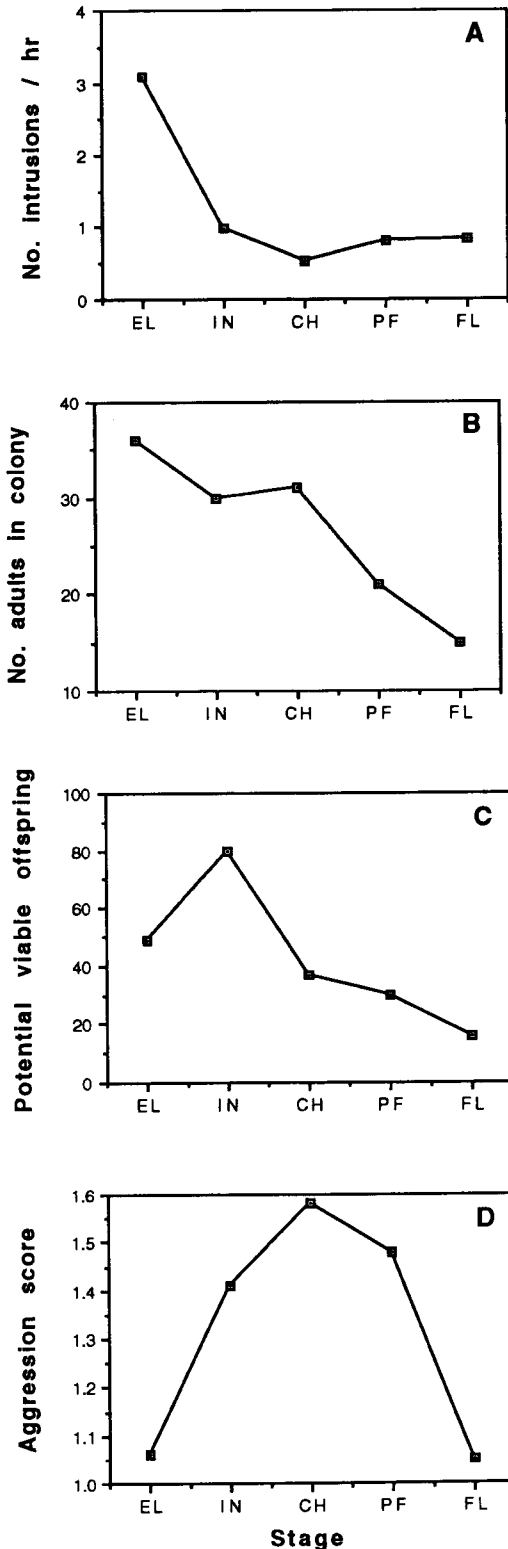


TABLE 2. Number of disturbances to nesting Roseate Terns at Cayo Ratón during each 3-hr period of the diurnal cycle. Observations were conducted from 1 June–20 July 1990.

Period	Hours of observation	Number of disturbances	Disturbances/hr. (\bar{x})
06:00–09:00 (early AM)	36.50	42	1.15
09:00–12:00 (late AM)	61.25	47	0.77
12:00–15:00 (early PM)	47.50	33	0.69
15:00–18:00 (late PM)	23.00	12	0.52

number of intrusions also varied significantly by time of day ($\chi^2 = 6.02$, $df = 3$, $P < 0.05$), with more disturbances occurring during the early morning (06:00–09:00) than during all other periods (Table 2).

ROSEATE TERN RESPONSES

Roseate Terns were aggressive (mean bout score > 1.0) towards intruders in 80 of 126 intrusions (63.5%) and in 80 of 100 disturbances (80.0%). Aggression levels peaked at chick hatching and decreased through fledging (Fig. 1D). Aggression scores differed by stage (Kruskal-Wallis, $H = 14.3$, $df = 4$, $P < 0.01$) with significant differences found between incubation and chick hatching ($P = 0.034$) and between chick hatching and fledging ($P = 0.004$). The two captures of Roseate chicks by Laughing Gulls (5, 7 July) occurred during the pre-fledging period when aggression was declining.

Roseate Terns were more aggressive towards potential predators (mean score = 2.09, $n = 103$) than non-predators (mean score = 0.28, $n = 18$). The number of disturbances by each species of intruder did not correlate with the total or the mean disturbance time per species ($r_s = -0.116$,

FIGURE 1. Relationship between the stage of the breeding cycle of Roseate Terns at Cayo Ratón in 1990 and (A) the frequency of intrusions by all nonbreeding avian species; (B) the mean number of attending adults in the colony; (C) the number of potential viable offspring (eggs or chicks), and (D) mean aggression scores of Roseate Terns at each stage. Stage of breeding cycle: EL = egg laying, IN = incubation, CH = chick hatching, PF = pre-fledging, FL = fledging. See text for corresponding dates.

$P = 0.827$; $r_s = -0.290$, $P = 0.577$, respectively). Total disturbance time, however, correlated with mean disturbance time per visit ($r_s = 0.829$, $P = 0.042$). These findings indicate that the most frequent visitors, i.e., Laughing Gulls, disturbed the colony for shorter periods of time than the more infrequent visitors, such as Red-tailed Hawks (*Buteo jamaicensis*) and frigatebirds (*Fregata magnificens*), suggesting that Roseate Terns may have habituated to certain species of intruder (McNicholl 1973, Veen 1977).

Mean detection distances of intruders by Roseate Terns varied by species, as did the mean number of terns responding to each species of intruder (Table 1). Although sample sizes are small for most species, some trends are evident. Red-tailed Hawks, which pose the greatest threat to adult seabirds in the archipelago (J. E. Saliva, pers. comm.), were detected at the greatest distance and caused the greatest number of terns to respond for the longest time. Detection distances for and the number of terns responding to intruder species which only prey upon eggs and/or chicks (i.e., Laughing Gulls, frigatebirds, kestrels) were considerably less.

Roseate Terns responded to the high, shrill alarm call given by American Oystercatchers (*Haematopus pilliatus*) by dread flights, and terns did not attack or chase these birds. On three occasions, oystercatchers called as they flew past the observer after attempting to land on the observation post. The fourth alarm was given several minutes before a Red-tailed Hawk flew over the tern colony. Thus, the alarm calls given by oystercatchers may warn terns of potential danger.

PARENTAL ATTENDANCE AND REPRODUCTIVE SUCCESS

The mean number of adults in the colony during each stage of the season was not significantly correlated with the number of potential viable offspring ($r_s = 0.70$, $P = 0.037$, Figs. 1B, C). No relationship was found between the number of adults in the colony and aggression levels at each stage ($r_s = 0.30$, $P > 0.50$, Figs. 1B, D) or the number of potential viable offspring and adult aggression levels ($r_s = 0.20$, $P > 0.70$, Figs. 1C, D).

Over 90% of all eggs hatched, but fledging success at Ratón in 1990 was 0.25 ± 0.50 chicks/pair. The majority of losses occurred during the

chick hatching stage (Fig. 1C), when there was the highest level of adult defensive aggression.

DISCUSSION

We suggest that reproductive success was low at Cayo Ratón because of effects of predators. Even though we observed only two chicks being taken by avian predators, chicks disappeared between colony censuses and only 16 of 81 chicks fledged. Several factors may have contributed to the low reproductive success. First, the consistent patrolling and harassment by Laughing Gulls may have disrupted the daily activity pattern of the nesting colony. Second, intruders disturbed the colony much more in the early morning (06:00–09:00) than at other times in the day. The early morning period is the time of highest activity of adults in feeding themselves and their chicks (pers. observ.). Colony defense by adult terns probably reduced the amount of time available for foraging and thus prevented chicks from receiving as much food as they would have in the absence of disturbance.

Defensive aggression in Roseate Terns peaked at chick hatching. Traditional parental investment theory predicts that defensive aggression should increase throughout the breeding season (e.g., Trivers 1972, Dawkins and Carlisle 1976, Boucher 1977). Barash (1975), however, pointed out that while this trend may hold true for altricial species that rely totally on parental care up to fledging, more precocial species adopt an inverted U-shaped pattern, with peak offspring defense occurring at hatching. This is true because precocial young are not helplessly confined to a nest but are mobile and can hide from predators soon after hatching. Barash's distinction between altricial and precocial birds has been supported by studies of seabirds, where adult aggression usually peaks at chick hatching, when the young are most vulnerable (Andersson et al. 1980, Burger 1984a, Kilpi 1987). Our findings with Roseate Terns (Fig. 1D) are consistent with the vulnerability hypothesis and not with traditional parental investment theory. In addition to aggression, the number of adults at the colony decreased as chicks got older, either because both adults of a pair were forced to leave the colony to provide food for older chicks or because as chicks died or were preyed upon, fewer adults were tied to the colony and may have left the area.

Despite the highest adult aggression levels, most chick mortality occurred during the hatching period. We could not positively identify the fates of the chicks that did not fledge because we observed the colony from a considerable distance and entered the colony only once per week. Several lines of evidence suggest that predation, probably by the land crab, *Gecarcinus ruricola*, was the primary cause of chick loss at Cayo Ratón in 1990. Land crab burrows were abundant on Cayo Ratón, interspersed among tern nests throughout the colony. In previous years, Burger and Gochfeld (1988b) witnessed crabs dragging live chicks away from unattended nests at Cayo Ratón and also reported overnight disappearances of several chicks from a small area. On five occasions during this study we observed small groups of terns hovering over a specific area on the ground. Although we could not identify the cause of these disturbances, we suspect that terns were reacting to crabs that had emerged to capture a chick.

We did not investigate possible nocturnal disturbance or predation in this study. The only potential nocturnal predator in the Culebra Archipelago is the Yellow-crowned Night-Heron (*Nycticorax violaceus*). In North America, Black-crowned Night-Herons (*Nycticorax nycticorax*) are notorious predators of tern eggs and chicks (Marshall 1942, Collins 1970, Hunter and Morris 1976, Nisbet and Welton 1984). The nearest known Yellow-crowned Night-Heron nest was on the main island of Culebra, >3 km from Cayo Ratón. We do not believe that night herons visited the Roseate Tern colony because we found no behaviors, such as restlessness or extended periods of nest abandonment, that are characteristic of this type of disturbance (Emlen et al. 1966, Shealer and Kress 1991).

Roseate Terns nesting at Cayo Ratón and other cays in the Culebra Archipelago in the past decade have displayed little site tenacity or group adherence, moving between cays both in the same year, after failing at one site, and between years (Furniss 1983, Burger and Gochfeld 1988b). Egg-ing by locals has occurred in past years at one Roseate Tern colony in the archipelago (Burger and Gochfeld 1988b), as well as in 1990 (pers. observ.), and is a probable contributing factor to colony abandonment.

In North America and in other Caribbean colonies, Roseate Terns appear to be much more

philopatric than they are at Culebra colonies. We suspect that site fidelity in this species may be directly related to predation pressure. In North America Roseate Terns nest in colonies with Common Terns. In this association, Roseate Terns seem to suffer less predation than Common Terns, possibly because their nests are better concealed. At a large Roseate Tern colony (>400 pairs) in southwestern Puerto Rico in 1991, potential predators occasionally flew over the nesting area, but they were always mobbed by many (>50) Roseate Terns at the colony. Reproductive success in this colony was much higher (1.56 ± 0.75) than at Cayo Ratón in 1990.

Our findings suggest that, although the small tern colony at Cayo Ratón responded appropriately to the most conspicuous types of intrusions (e.g., avian), they were unable to successfully defend against certain ground predators (e.g., crabs). Burger and Gochfeld (1988a) found that colony size and density influences defensive aggression by terns toward intruders, with larger colonies exhibiting a higher degree of defense. The number of birds participating in colony defense positively affects success in deterring an intruder (Goransson et al. 1975). Our observations at Cayo Ratón in previous years (Burger and Gochfeld 1988b, unpubl. data), suggest that colony size is not an important factor in preventing crab predation on Roseate Tern chicks. Whereas an approaching aerial predator usually elicits a group response from several terns (Table 1), crab predation is quick and inconspicuous, due to the rocks and vegetation that separate tern nests on Cayo Ratón. Group defense against crabs probably does not occur because most terns in the colony cannot see them. Although a single tern can usually defend its chicks against crab intrusions, crabs take chicks when parents leave the nest to forage or respond to a disturbance. Thus, the persistent disturbances caused by Laughing Gulls may facilitate crab predation of Roseate Tern chicks at Cayo Ratón.

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