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NESTING BEHAVIOR OF THE GULL-BILLED TERN

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INTRODUCTION

The Gull-billed Tern (*Gelochelidon nilotica*) has a scattered distribution, and its breeding behavior has been little studied in the past (e.g., deWaard, 1952; Lind, 1963a; Møller, 1975). I have therefore made a relatively broad study of the breeding behavior of this species. I present my observations on nesting behavior here and discuss the antipredator strategy of the Gull-billed Tern. The species' display behavior will be discussed elsewhere.

STUDY AREA AND METHODS

I spent the springs and summers of 1971, 1972, and 1973 on an unnamed island 0.5 km south of the port at Morehead City, Carteret County, North Carolina. Beaufort Inlet lies to the southeast, and a *Spartina* marsh and Bogue Banks lie to the southwest.

Early during each breeding season, I watched the terns from exposed but distant positions using 8 × 24 binoculars or a 15–60 power zoom telescope. As colonies were established, I positioned burlap blinds at their borders, and observations were made from within the blinds.

I used time-lapse photography to study incubation behavior. A Braun-Nizo S-80 movie camera was positioned on a tripod 20 to 30 m from the nest. It was set to expose one frame every four to five seconds (later determined exactly) and was left in position for up to five hours.

Gull-billed Terns are quite sensitive to disturbance; therefore, I did not trap or mark any terns. This meant I could only rarely recognize individuals. The sexes were not distinguishable, although Lind (1963a) thought he could distinguish males by their heavier bill. No terns were naturally marked in any way, and only twice did I study pairs whose members could be distinguished by tone of voice. I did band most chicks with a Fish and Wildlife Service band, and on a few occasions, I placed a red dye in solution in a small mollusc shell in the bowl of the nest, thereby temporarily marking an incubating adult. Such a mark faded after a few days.

RESULTS

Colony Site and Composition

The island consisted of recently dredged spoil, which provided a variety of nesting substrates, including loose sand, sand mixed with shells, and firmer sand mixed with silt that supported low vegetation of variable density. Gull-billed Terns in this area appeared to prefer a site that had a substrate of fairly rough texture (consisting of shells, sticks, and other debris as well as sand), that was sparsely dotted with vegetation, and that was situated near an area of relatively dense, low vegetation. The initial colonies of 1971 and 1972 were established in such sites. No Gull-billed Terns nested in dense vegetation, and nesting on bare substrate was associated with disturbed conditions. After widespread nest desertion during unusually cold wet weather in 1972, presumed renesting attempts were made on virtually bare sand. Then, during the fall of 1972, the southwestern half of the island was largely buried under fresh spoil, and in 1973, one of the two major colonies was established on bare substrate.

Most of the colonies I studied contained both Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*), as well as Gull-billed Terns. During 1971, the first colony established contained at least 20 Gull-billed nests. Later, a second and a third colony were established, containing about 9 and 3 Gull-billed nests, respectively. These were probably renesting attempts. During 1972 and 1973, two colonies formed initially (9 and 10 Gull-billed nests in 1972 and 9 and 7 Gull-billed nests in 1973), and again those that abandoned their nests apparently renested in smaller colonies in other locations.

In 1973, the average distance between a Gull-billed nest and its nearest neighbor was about 10 m (Table 1). If only conspecific nearest neighbors are considered, the distance was a little greater, 12 m. Of the 32 Gull-billed nests considered, 16 had conspecific nearest neighbors, 10 had Black Skimmer nearest neighbors, and 6 had Common Tern nearest neighbors. I collected no quantitative data on the total frequencies

TABLE 1

Average distance of Gull-billed Tern nests from their nearest neighbors in seven different colonies established during 1973[1].

Colony	Neighbor			$\bar{x}$
	Black Skimmer	Common Tern	Gull-billed Tern	
Far SW	2.7 (3)	—	7.0 (6)	5.6
W (14 May)	8.5 (2)	10.0 (3)	16.5 (2)	11.4
W (6 June)	2.0 (2)	—	4.0 (3)	3.2
Near SW	3.0 (1)	—	—	3.0
N	5.0 (2)	—	8.0 (1)	6.0
NW	—	5.0 (2)	10.0 (1)	6.7
S	—	42.0 (1)	29.3 (3)	32.5

[1] Distances in meters. Number of Gull-billed nests on which each mean is based is given in parenthesis.

of the three species on the island, but the Gull-billed Tern was certainly in the minority, outnumbered by each other species by at least a factor of five. Thus, the Gull-billed Tern tends to nest near conspecifics.

Territory Establishment

Nesting territories are established no more than a day or two before the first egg is laid. Establishment of the territory involves rapid localization of a pair's courtship activity, at which time the nest is scraped out by both members of the pair. The first eggs were laid about 5–7 May in 1971, 1972, and 1973.

Nest Construction

The Gull-billed Tern tends to nest near an object that stands out from the substrate, such as a tuft of grass, a stick, or other piece of flotsam. My study area was unusually bare, being composed largely of fresh spoil, but nearly half the nests established during 1973 were positioned near such a feature.

The nest consists of a depression in the sand, a surrounding rim of sand raised above the level of the substrate, and an accumulation of shells, sticks, or grass blades on and around the rim. The exact nature of the nest varies considerably from nest to nest and from day to day, largely depending upon the area in which the nest is located. At a nest on an open shelly area, many shells are incorporated into the nest and nest rim. At a nest on a shrubby, grassy area, twigs and grasses are used. In open areas, nests become well defined and complex during periods of calm weather but may be obliterated during heavy wind or rain. In protected areas, nests remain deep and the rims conspicuous.

The construction of the nest involves three relatively distinct behavior patterns: scraping, sideways-throwing, and sideways-building. Nest material is not brought to the nest from a distance. A tern begins nest construction by scraping out a shallow depression in the sand. The tern kicks its feet alternately while resting on its breast and so pushes sand backwards and onto the nest rim. Subsequent deepening of this bowl and later clearing it of blown sand involve the same movements.

During sideways-throwing, shells or other items are tossed from the immediate vicinity of the nest toward the nest. The tern stands with wings slightly abducted and drooped. The tern stretches its neck out horizontally, reaches down to the substrate, grasps the item in its bill, and tosses it to one side and backward with a quick and relatively stereotyped turn of the head. The item is tossed as far as a meter to the rear of the bird. Sideways-throwing is occasionally performed by an incubating tern that rises from the nest and walks away, sideways-throwing repeatedly. The tern then walks back to the nest and resumes incubation. Sideways-throwing is also commonly performed during or immediately following the nest exchange. With the repeated performance of this behavior through the incubation period, material is slowly moved from the surrounding area toward the nest.

Sideways-building is a more variable and more well-directed behavior whereby material is actually placed onto the nest rim. It is performed by incubating terns or by terns standing near the nest before beginning to incubate. Although the sideways-throw is relatively stereotyped in form, it is frequently oriented with respect to the nest, just as sideways-building is. Perhaps sideways-throwing and sideways-building are two ends of a continuum. At a distance from the nest, the movement is relatively stereotyped and undirected, but the closer the tern is to the nest, the more deliberate and well-directed the movement becomes (Harrison, 1967).

Clutch Size

The Gull-billed Tern produces clutches of one to three eggs ($\bar{x}$ = 2.0, n = 41). Most of the pairs that established nests at the beginning of the 1973 season (before 15 May) produced clutches of two or three ($\bar{x}$ = 2.5, n = 16). Most of those that nested later produced clutches of one or two ($\bar{x}$ = 1.7, n = 25). A decrease in the average clutch size during the nesting season is a trend found in many birds (Bergman, 1953; Cullen, 1956; Langham, 1968, 1974).

However, these data probably give a biased picture of clutch size in this species because some clutches could have been reduced by predation before I discovered them or could have been abandoned before laying was completed. Pemberton (1927) describes one nest containing four eggs. Bent (1963) reports that the clutch size is two or three, rarely four.

The eggs were laid at a rate of less than one per day. Five three-egg clutches were laid over the course of at least four days, and three were laid over the course of at least five days.

Incubation Spell

An incubation or sitting spell is an uninterrupted period of incubation, separated from the preceding and following spells by such off-the-nest behavior as nest exchanges, sideways-throwing, defecation, or alarm flight.

Using time-lapse photography, I monitored incubation behavior for two to five hours on each of 36 separate occasions at 12 different nests. The duration of the incubation spell ranged from less than 1 minute to over 194 minutes, and the daily mean duration varied almost as much: 5 minutes to 152 minutes ($\bar{x}$ = 42, SD = 30, n = 36).

To explain some of this variability, I measured the degree of association between the daily mean duration of the incubation spell and each of two temporal parameters, date and days since completion of the clutch, and eight weather parameters: daily rainfall, high temperature, and low temperature (taken from *Climatological Data* for Morehead City published by the National Oceanic and Atmospheric Administration) and sky cover, windspeed, wetbulb temperature, dewpoint, and relative humidity (taken from *Local Climatological Data* for Cape Hatteras, N.C. also published by NOAA). I calculated Spearman's Rank Correlation

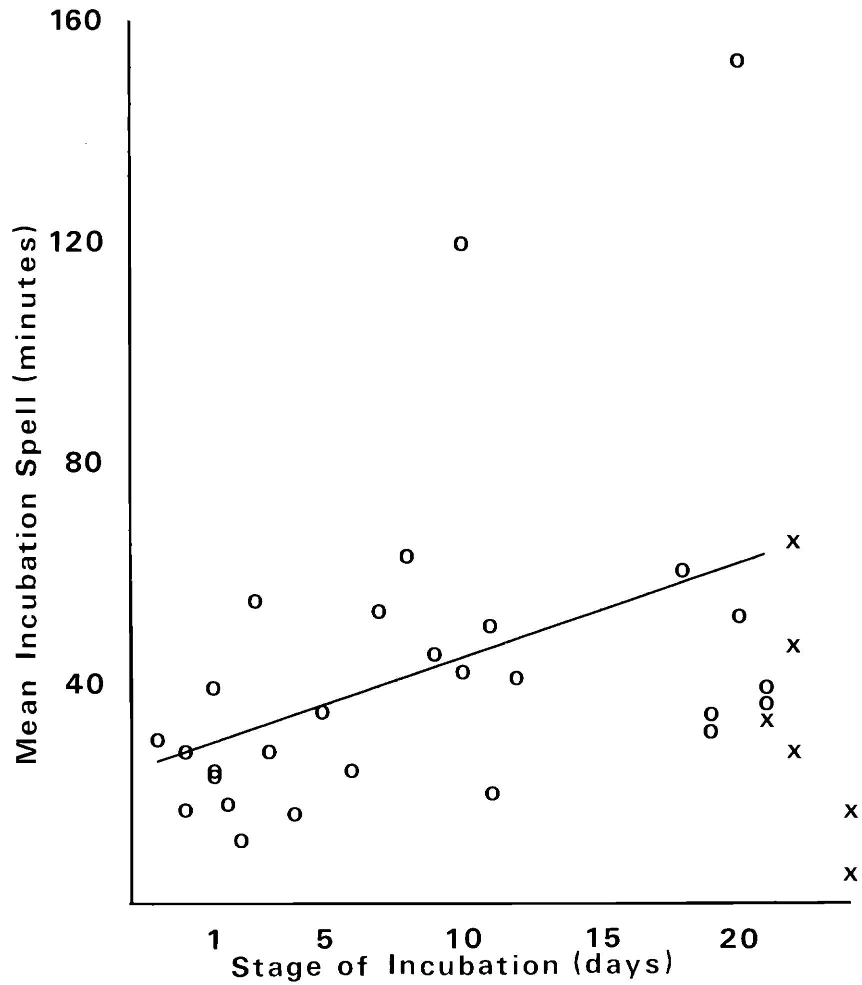

FIGURE 1. The change in the mean duration of the incubation spell through the incubation period (day 1 = first day of incubation of full clutch). The least squares regression line (y = 1.70x + 27.66) was calculated from the data for unhatched clutches only (o = unhatched clutch; x = one or more eggs hatched).

Coefficient for each pair of variables and tested H_0: $r_s = 0$ with a one-tailed *t*-test (Siegel, 1956). Spell duration is not significantly correlated with any of the weather parameters, nor with the temporal parameters when the entire nesting period is considered in the analysis. However, if only the first three weeks of the nesting period are considered, spell duration is significantly correlated with the stage of incubation ($r_s = 0.48$) and therefore with the date ($r_s = 0.37$). Figure 1 illustrates this association in more detail. Spell duration tends to increase through the incubation period, peaks around the time of hatching, and falls sharply thereafter.

The interval separating two incubation spells normally ranges from a few seconds to a few minutes. At the 12 nests discussed above, the relative amount of time a nest was left uncovered ranged up to 8% ($\bar{x}$ = 1.7%, SD = 1.6, n = 36). During the first three weeks of incubation, this variable is significantly negatively correlated with the stage of incubation ($r_s = -0.52$) and with the date ($r_s = -0.39$). During the entire nesting season, it is significantly negatively correlated with daily rainfall ($r_s = -0.38$) and with the high and low temperatures for the day (r_s = -0.41 and -0.38, respectively).

It has often been found that birds become increasingly attentive at the nest as the incubation period progresses and during periods of harsh weather (Cullen, 1956; Beer, 1961; Howell and Bartholomew, 1962; Baerends and Drent, 1970; Drent, 1973).

Defecation and Regurgitation

Adults apparently do not defecate in or near the nest. Feces do not accumulate around the nest, and on several occasions, I saw an incubating tern walk or fly from the nest, defecate, and return. It is also common for a tern, after a nest exchange, to defecate as it walks from the nest.

Adults regurgitate pellets of undigested material onto the nest, however. I collected many pellets from nests, nest rims, and nest vicinities. At some nests, I collected a pellet daily for several consecutive days.

Egg-retrieval

The Gull-billed Tern retrieves eggs that have become displaced from the nest, but it does not do so consistently. On five different occasions, I moved an egg to the rim of a nest or just beyond the rim, leaving one or two eggs remaining in the nest. Three of these experiments resulted in retrieval, but only after 10 to 15 minutes of incubation on the nest, and two experiments were terminated after 30 minutes of incubation without retrieval. On the other hand, I have seen the retrieval of an eggshell, which had been moved to the nest rim during a nest exchange, and the retrieval of a piece of white plastic cup that I had placed on the nest rim. Both of these retrievals occurred soon after the tern settled onto the nest.

During retrieval, the egg is drawn under the body with the bill. The most distant retrieval was performed in two stages, the tern resettling on the nest between them. Distant retrieval in stages seems to be a common technique in terns (Marshall, 1943; Hawksley, 1950; Körner, 1966).

Reactions to Predators

No evidence of predation on adult Gull-billed Terns was seen, but eggs and young were obviously vulnerable. Humans and dogs occasionally came onto the island, and I once saw a dog running along the periphery of a colony carrying a juvenile tern in its mouth. A few rats (probably *Rattus norvegicus*) had burrows on the island, and I once followed rat tracks into a colony and past an empty Common Tern nest that had held eggs the previous day. Occasionally I saw trespassing chicks severely pecked by neighboring Gull-billed and Common terns, and both eggs and chicks were taken by Laughing Gulls (*Larus atricilla*) and by immature Herring Gulls (*L. argentatus*). In addition, I have seen adults react defensively toward the Ruddy Turnstone (*Arenaria interpres*) (in contrast, Wilson's Plovers, *Charadrius wilsonia*, were ignored) and the Red-winged Blackbird (*Agelaius phoeniceus*), which have been known to take tern eggs (Pessino, 1968; Crossin and Huber, 1970; Parkes et al., 1971; Dinsmore, 1972), and also toward the Snowy Egret (*Egretta thula*) and Eastern Meadowlark (*Sturnella magna*). During 1973, nest success was 40% (17 broods/43 nests).

Most gulls flying near the colony elicit no reaction from the terns. I have also seen an adult simply lead its young away from a nearby gull, and in another case, fly closer to its young. An approaching aerial predator elicits aggressive postures and vocalizations. One or more terns then fly up, chase the predator, and continue to vocalize. An approaching ground predator elicits the same aggressive displays, and at least several individuals finally fly up. They hover over the predator and, one by one, dive toward it and then swoop back up to the flock. Calls are often uttered throughout the dive. At the lowest point, the tern often calls, defecates, and strikes the predator with its bill or feet.

The responsiveness of the pair changes through the incubation period. Incubating terns are particularly reluctant to leave the nest around the time of hatching. I have approached or entered the colony and noticed that adults with hatching eggs or eggs about to hatch did not leave their nests, whereas those at other nests did; or that adults with hatching eggs were quickly back on their nests after I entered the blind, whereas others were much slower to return. At the same time, those adults that do respond to intruders do so with increased intensity late in incubation.

The effect of group attack is usually to repel the potential predator. I have seen picnickers approach a colony but turn abruptly and walk back to the shore after a small flock of terns began diving at them. The dog mentioned above was harried by a small flock of terns, and it loped along through the thick vegetation bordering the colony rather than through the open area occupied by the colony itself. Diving terns also occasionally punctured my fiber-board helmet with their bills; a peck of this intensity is probably a real deterrent to potential predators.

Eggshell Removal

Gull-billed Terns seem to have only a weak tendency to remove eggshells. I have seen only two natural cases of eggshell removal. In one case, the tern walked from the nest, carrying the shell, and dropped it two or three meters from the nest. The chick was still wet. In the second case, the adult flew from the nest calling and dropped the shell 30 to 40 meters away. In contrast, I have watched several nests at which the shells were definitely not removed. Shells remained in two nests and within a meter of seven nests for one day after hatching, in one nest and within a meter of three nests for two days after hatching, and within a meter of six nests until after the parents and chicks left the nest.

I introduced a variety of objects into various Gull-billed nests, including tern eggshells, Willet (*Catoptrophorus semipalmatus*) eggshells, white chicken eggshells, a red and brass shotgun shell, and a piece of white plastic drinking cup (about 6 cm in longest dimension). Of the 15 tern and Willet eggshells introduced, seven were removed within the four to five hour observation period and seven were not. At the remaining nest, the pair and their chicks left the nest. Of the seven removals, only one consisted of a long-distance aerial carry. The others were removals to the nest rim or only slightly beyond.

Of the 12 chicken eggshells introduced, seven were carried away and five were not, and the shotgun shell was not moved, even after two days. The piece of plastic lay on the nest rim as the tern settled onto the nest, and the tern immediately retrieved it as if it were an intact egg. Later, the tern's mate arrived to assume incubation. This individual dove at the plastic as if it were a predator and, on the third dive, grabbed the plastic, flew up and away, and dropped it 10 to 20 meters from the nest.

Alarm or disturbance was evident after some of the other experimental introductions. The tern approaching the shotgun shell in the nest assumed an alarm posture, called, and walked back and forth before the nest before finally settling onto it. This reaction or a less intense form of it was also elicited by some of the chicken eggshells. The tern and Willet eggshells did not tend to elicit such alarm behavior.

Thus, the Gull-billed Tern tends to remove conspicuous objects from the nest, but such objects are not always removed, and they are often moved only a short distance. My few experiments revealed no increased tendency to remove objects late in the incubation period.

The wind plays a fairly important part in what removal does occur. I saw a tern apparently unintentionally nudge an eggshell to the nest rim during a nest exchange. The wind then blew the shell away.

Leaving the Nest

The adults and chicks remain at the nest for a few days at most (see below). After this time, the family leaves the nest site for a more sheltered area. During 1972 and 1973, I watched 14 different families for varying periods after this departure.

Usually the adults seem to direct the movement from the nest. They walk from the nest calling repeatedly and occasionally pausing to scrape, and the chicks follow, usually vocalizing. However, the chicks sometimes direct movement away from the nest. At one nest, there was a two-day-old chick and an egg that hatched later that day. I had removed the egg and chick for experimental reasons; upon replacing them, an adult landed, and the chick immediately walked from the nest and continued several meters past the adult. The adult overtook the chick and led it a distance of 45 meters. On another occasion, an adult landed at a nest, called, and led the chick from the nest. After a few meters, the adult stopped and began to cover the chick, but the chick walked on. The adult rose and followed, calling. The chick finally stopped, and the adult covered it. In a third case, an adult led a chick a meter or so and continued to walk and call, but the chick had stopped, and the adult turned and came back to the chick.

Three main factors apparently control the timing, distance, and direction of movement away from the nest: ages of the chicks, disturbance to the family, and distribution of vegetation around the nest. The age of the youngest chick in the brood exercises little control over the timing of departure from the nest. Nests are left as early as one day after hatching, and the interval from the hatching of the first egg to departure is about the same (about 2.5 days) for clutches of one (n = 4) or two (n = 8), and apparently for those of three as well (n = 2). However, the presence of young chicks seems to affect the distance traveled. During the first hour after leaving the nest, broods with one-day-old chicks were led an average of 26 meters (n = 6) and broods with only older chicks were led an average of 80 meters (n = 5).

Disturbance to the adults or chicks often appears to initiate departure from the nest. I witnessed eight of the 18 departures that occurred during 1972 and 1973, and seven were initiated within a few minutes of my arrival. Similarly, my arrival seemed to trigger many instances of post-departure movement. I witnessed 19 movements that occurred at least one day after departure from the nest. Of all 27 observed movements, 19 were initiated within 15 minutes of my arrival, and only eight were initiated later. This distribution is significantly different from a 50:50 distribution, which is a conservative null hypothesis since all observation periods exceeded 30 minutes ($\chi^2 = 4.48$, 1 d.f., $P < 0.05$).

After moving away from the nest, the family tends to settle among relatively thick vegetation. I classified each stopping point during movement following departure from the nest according to presence or absence of vegetation and according to the length of stay at the site (Table 2). Areas of vegetation were occupied about as often as bare sites. Since at least 80% of the nesting area was bare, this alone indicates a preference for sheltered sites. The table also shows that stays in areas of vegetation tend to be longer than those on bare areas ($\chi^2 = 19.9$, 1 d.f., $P < 0.01$).

The young are ultimately led to the beaches and mudflats that make up the shores of the island. I quickly lost contact with some of the families after departure from the nest, but even so, six reached the water, seven reached the sand dike that partially surrounded the island not far above high water, and only five were still on the island interior at the time I last saw them. In all, most families traveled at least a few hundred meters before the young flew. One family moved about a kilometer.

TABLE 2
Relationship between length of stay and presence or absence of vegetation.

	Length of stay		
	<2 hr	>2 hr	Total
Vegetation present	2	23	25
None	16	13	29

DISCUSSION

Features that have the effect of reducing predation on eggs and young (see Cullen, 1960; Tinbergen, 1963 and 1967; and Lack, 1967 and 1968 for pertinent general discussions) can be classified as those that tend to keep predators from the nesting area, those that tend to hide the clutch or brood from predators in the area, or those that tend to repel predators.

A feature of Gull-billed nesting behavior that tends to keep predators from the nesting area is the isolated position of the colony. The island site of the colonies I studied and the surrounding Coast Guard and State Park property greatly reduced land access to the ternery by man and dog, probably the two most important terrestrial predators in the area. Isolation of the colony is much more strongly developed as an anti-predator adaptation in other terns (e.g. *Sterna maximus* and *S. sandvicensis* among temperate species (Lind, 1963b; Kale et al., 1965; Buckley and Buckley, 1972)).

Many more aspects of the Gull-billed Tern's nesting behavior tend to prevent a predator from finding the clutch or brood, once the predator does enter the breeding area. The nests in the colony are relatively dispersed, and several small colonies tend to form rather than one large one. It was clear that the disturbance caused by my activities was partially responsible for this nest distribution. For example, during 1972, my presence appeared to prevent the establishment of a colony in what had been the preferred area in 1971. When I moved my blind to the area that was becoming occupied, further nesting ceased and nesting began in a still less suitable area. My activity in the first colony to form in 1973 triggered the establishment of the second main colony of that year, and my subsequent discovery and census of the second colony contributed to the return of some individuals to the first. The relocation of renesting attempts might also have been due to my presence.

However, the nest distribution I observed was not grossly abnormal. The mean nearest-neighbor distance that I measured (about 10 m) is much greater than the 15 inches (38 cm) to 3 feet (91.5 cm) reported by Cain (1933) and the 1.5 m reported by Lind (1963a), but it is similar to the 20 feet (6.1 m) reported by Pemberton (1927), and it may reflect either the similarly open nature of the two sites or the similarly large area available. Also, although colonies of 100, 200, or even 300 nests have been reported (Glegg, 1931; Buckley, pers. comm.; Dement'ev and Gladkov, 1969), the typical colony apparently contains about 10 to 20 nests (Bent, 1963; Jensen, 1946; Stewart and Robbins, 1947; Lind, 1963a), as many of my colonies did. Thus, nest dispersion and the sensitivity to disturbance that contributes to it are probably adaptations that increase the difficulty the predator has in locating nests.

The tendency to form mixed colonies might contribute to the concealment of the nest and contents. Croze (1970) has suggested that the Sandwich Tern (*Sterna sandvicensis*) derives protection of this sort by its habit of nesting with other species of terns and gulls. The Sandwich Tern is unusual in that it defecates around the nest, producing a whitish background for unusually light eggs. Predators develop a specific searching image (Tinbergen, 1960) for the more common nests of the species with which the Sandwich Tern nests and thus overlook those of the Sandwich Tern itself. Analogously, the Gull-billed Tern (and the Common Tern) tends to accumulate debris about its nest, in which it lays relatively dark eggs, and the Black Skimmers in the colony accumulate no material and lay relatively light eggs. The nests and eggs of the different species are also of different sizes, and this variation within the colony must make it more difficult for a predator to develop a definite specific searching image.

The tendency to nest near a plant or other object might also help to hide the nest, since such a site is relatively visually complex. It might also tend to prevent birds of prey from getting a clean swoop at the nest (Munro, 1960).

Adult Gull-billed Terns do not defecate near the nest, and the comparison between this inhibition and the lack of inhibition associated with the regurgitation of pellets indicates that camouflage, rather than sanitation, underlies the inhibition of defecation. The feces are largely white and if localized thickly about the nest would become obvious to a predator (Cullen, 1960). The regurgitated pellets are dark, mottled collections of vertebrate bones and insect exoskeletons, and they disintegrate quickly to an inconspicuous scattering among the debris about the nest.

Eggshells near the nest can also jeopardize the brood through their conspicuousness to predators (Tinbergen et al., 1962); thus the tendency of the Gull-billed Tern to remove them is also an adaptation that serves to camouflage the nest. However, this tendency is apparently quite weak. Most terns seem to remove the eggshells soon after hatching (Jones, 1906; Marples and Marples, 1934; Palmer, 1941; Hawksley, 1950; Cuthbert, 1954; Goodwin, 1960; Schönert, 1961), and at least the Common Tern removes other conspicuous objects as well (Pettingill, 1939; Palmer, 1941), although the consistency with which this is done is not usually stated. Cullen (1956) noted that Arctic Terns (*Sterna paradisaea*) do not always remove eggshells, although they usually do; Dinsmore (1972) reported that Sooty Terns (*Sterna fuscata*) seldom do, and Buckley and Buckley (1972) reported that Royal Terns never remove the eggshells.

The weak expression of this adaptation in the Gull-billed Tern could be related to the fact that they, like the Royal Terns (Buckley and Buckley, 1972), quickly leave the nest after the eggs hatch. Predation on chicks in the nest might be relatively slight. Most of my observations of predation were made during the abnormally bad weather of 1972, when many pairs abandoned their nests and later renested. Langham (1968, 1972) has shown predation to be an insignificant component of chick mortality in the Common, Arctic, Roseate (*Sterna dougallii*), and Sandwich terns that he studied and that starvation is the most important cause of mortality during the first week after hatching. In contrast, predation does seem to be significant in the Black-headed Gull (*Larus ridibundus*) (Tinbergen et al., 1962).

Thus, many factors associated with the nest and its location appear to hide the nest from predators. The openness of the colony site allows the incubating terns a clear view of their surroundings and the chance to detect an approaching predator while it is still a significant distance away. The existence of many observers in a colony further increases the probability of early predator detection (Siegfried and Underhill, 1975). The conspicuous adult can then fly and thus permit the cryptic features of the nest to have their effect. However, predation is probably not the major selective agent responsible for the present form of the nest. Most nests appear rather conspicuous, and some are quite substantial and stand out clearly against their sand and shell background. The nest is probably also important in protecting the clutch and brood from other stresses, such as wind-blown sand.

Two other aspects of nesting increase the difficulty with which a predator locates the nest or brood. The ease with which the terns relocate nesting attempts, following early failure, might be an adaptation serving to remove the pair from a disturbed area (Buckley and Buckley, 1972), and the tendency to leave the nest quickly after hatching certainly has this effect.

Most ground-nesting terns do leave the nest after hatching, but the distance traveled varies considerably. The Arctic Tern usually remains within a few meters of the nest until fledging, even at nests on open sand (Cullen, 1956). The young apparently remain on the nesting territory and even defend it (Bullough, 1942; Hawksley, 1950). Cullen noted that adults will occasionally try to lead their young as far as 10 to 20 meters from the nest and that they sometimes succeed, but usually, either the adults or the young stop and return to the territory. Similarly, the Sooty Tern abandons the nest but remains near the territory and returns to the territory each night until fledging (Dinsmore, 1972).

The marsh terns (Black and Whiskered) (*Chlidonias niger* and *C. hybridus*) seem to be somewhat less tied to the nest. They leave the nest and swim about in the nearby vegetation only a day or so after hatching, but they remain near the nest for one or two weeks, and the adults sometimes lure them back to the nest during this time (Hoffmann, 1926;

Baggerman et al., 1956; Swift, 1960; Fuggles-Couchman, 1962; Dement'ev and Gladkov, 1969). After this time, the young wander farther until fledging. Goodwin (1960) suggests that nest-area abandonment can be more rapid in the Black Tern and that early abandonment is associated with unusual disturbance of the nest.

In contrast to these species are the Least Tern (Moseley, pers. comm.), the Sandwich Tern (Bickerton, 1912; Dircksen, 1932; J. van den Assem, Ms), the Royal Tern (Buckley and Buckley, 1972), and the Gull-billed Tern (Møller, 1975; this study), all of which leave the nest soon after hatching and wander relatively far from it. Much of this variation can probably be explained by the amount of disturbance to which the terns were subjected and the amount of shelter the surrounding vegetation provided.

Finally, the most conspicuous anti-predator adaptations are those that repel predators which have found the nest or brood or are about to find it. These adaptations are individual threat and attack, the increased tendency to attack late in incubation and during hatching, group attack, and the colonial nesting and synchronous laying that permits group attack (Kruuk, 1964; Patterson, 1965; Sears, Ms; but see Lemmetyinen, 1971 for counter-argument).

SUMMARY

Nesting behavior of the Gull-billed Tern was studied for three seasons in small mixed-species colonies on an island just off the coast of North Carolina. Many aspects of the species' parental behavior appear to protect the clutch or brood from predators. These include: isolated location of the colony, degree of nest dispersion, tendency to form mixed-species colonies, tendency to nest near a plant or other object, tendency not to defecate near the nest, tendency to remove eggshells and other conspicuous objects from the nest, openness of the colony site, ease with which the terns relocate nesting attempts, tendency to leave the nest soon after hatching, threat and attack behavior, group attack, and the colonial nesting and synchronous laying that permit group attack.

Other aspects of the Gull-billed Tern's parental behavior seem to contribute to the production of the pair in other ways. During periods of rain or high temperature, adults cover the nest a greater percentage of the time. Average clutch size decreases through the breeding season; this probably compensates for the inability of late nesters to raise a large brood. Finally, in many respects, adults put increasing effort into incubation as the incubation period progresses. Several different processes might explain this trend, but its adaptive value is clear: the clutch becomes increasingly hard to replace through the incubation period, and at the time of hatching it is maximally vulnerable.

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