

# BULLETIN

of the  
FLORIDA STATE MUSEUM  
Biological Sciences

Volume 16

1972

Number 3

## SOOTY TERN BEHAVIOR

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UNIVERSITY OF FLORIDA

GAINESVILLE

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

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# SOOTY TERN BEHAVIOR

JAMES J. DINSMORE

**SYNOPSIS:** A 4-year study of the breeding behavior of Sooty Terns (*Sterna fuscata*) was made at Bush Key, Dry Tortugas in the southeastern Gulf of Mexico. The results are compared with the behavior of other terns and the differences discussed, particularly in regard to the pelagic environment the Sooty Tern inhabits.

Sooty Terns arrive at the Dry Tortugas some 2 months before eggs are first laid. At first they circle Bush Key at night only, but eventually land and extend the time they spend on the ground, arriving earlier in the evening and leaving later in the morning. After the first eggs are laid, flocking subsides. Aerial display by Sooty Terns consists mainly of the high flight in which two birds ascend, usually by jerk-flying, circle, and then descend together in a coordinated glide. Sooty Terns may have a poorly developed low flight display. On the ground the major display is the parade, similar to that of other *Sterna* terns. Courtship feeding is rare. Terns often interfere with pairs attempting to copulate.

The single egg is incubated about 29.5 days with the male caring for it somewhat more than the female. The birds are attentive over 95 per cent of the time, incubating when it is cool, shading when it is hot, and engaging in other activities such as preening, fighting, and loafing most commonly when they change between incubating and shading. Nest relief usually occurs in the evening after 24 or 48 hours of care. Dipping, in which adults dip their feet, bill and/or breast feathers in the ocean, is common during incubation and may cool the egg or provide it with needed moisture.

Chicks are closely brooded for 4 or 5 days, after which adults seem to recognize them individually and spend progressively less time with them. By the end of the third week, chicks are alone much of the time except when fed. Adults feed the chick by regurgitation, spend about 3.5 hours per foraging trip, and often feed a chick several times after one trip. Males feed the chick somewhat more than females do. Vocal exchanges between parent and chick

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Dinsmore, James J. 1971. Sooty Tern Behavior. Bull. Florida State Mus., Biol. Sci., Vol. 16, No. 3, pp. 129-179.

seem most important in individual recognition. Occasionally adults feed a chick other than their own. Chicks first fly when about 8 weeks old and leave the colony soon after that.

The ground and aerial displays of Sooty Terns are similar to those of other *Sterna* terns, especially the Common Tern. The rarity of the low flight and courtship feeding, both of which are common in other terns, may be due to the different way in which Sooties carry food and the distance they travel to forage.

Sooty Terns have a lower clutch size, longer period of development of the chick, and first breed when older than most other terns, many of which feed in marshes and coastal waters. These characteristics of Sooty Tern breeding biology are similar to those of many other pelagic birds. A distant food supply and high adult survivorship apparently have contributed to these differences from other terns.

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#### INTRODUCTION

In the recent resurgence of work on seabirds, one species that has received considerable attention is the Sooty Tern (*Sterna fuscata*), an extremely abundant bird of tropical and subtropical marine habitats. Recent studies show that Sooties follow a nonannual breeding cycle at some localities (Chapin, 1954; Ashmole, 1963), that perhaps they fly continuously for months on end (Ashmole, 1963), and that juveniles undertake a long migration (Robertson, 1969). Such tantalizing bits of information suggest that further studies of this species would be rewarding.

Although the ethology of several species of terns is well known, the basic studies of Sooty Tern behavior were made over 50 years ago (Watson, 1908; Watson and Lashley, 1915; Lashley, 1915). Most terns that have been studied feed in coastal waters or fresh water, but the Sooties are pelagic. From 1968 to 1971 I studied the behavior of Sooty Terns at the Dry Tortugas. Besides describing their behavior, I have attempted to compare their behavior with that of coastal feeding terns and then to relate the Sooties' behavior to their pelagic habits.

#### ACKNOWLEDGEMENTS

I have benefited greatly from the counsel and interest of many individuals. In particular, the advice and encouragement of Oliver L. Austin, Jr. and William B. Robertson, Jr. have been of great help to me throughout this study. I have also profited from the comments and criticisms of George W. Cornwell, Brian Harrington, Robert W. McFarlane, Frank G. Nordlie, John C. Ogden, Thomas J. Walker, S. David Webb, Glen E. Woolfenden and others, especially many members of banding parties to the Tortugas. Personnel at Fort Jefferson National Monument and Everglades National Park were especially helpful in providing a place for me to live at Fort Jefferson and then making that living enjoyable. Gary D. Schnell generously gave me access to his unpublished data on Sooty Tern flight speeds. The Florida State Museum provided a boat to use at Fort Jefferson. Two grants from the Frank M. Chapman Fund, American Museum of Natural History, and a Louis Agassiz Fuertes Research grant from the Wilson Ornithological Society helped finance the field work. A University of Florida Graduate School Fellowship made it possible for me to spend an extended period at the Dry Tortugas. My wife, Pat, encouraged me throughout the study and typed many drafts of this paper. The text figures were done by Paul Laessle. To all these individuals and organizations, I am grateful.

#### THE DRY TORTUGAS

I studied Sooty Terns at Bush Key, one of seven islands in the Dry Tortugas group at approximately 24° 38' N, 82° 52' W, about 70 miles west of Key West, Florida. The islands are located on a large shallow bank, much of it less than five fathoms deep, in the southeastern Gulf of Mexico (Figure 1). Sooty Terns have nested at the Tortugas since at least 1832 (Audubon, 1844). In recent years some 80,000 Sooties have bred mainly on Bush Key, a low sand island some 20 acres in area. Nesting terns of the Tortugas have had some protection since 1903, and since 1935 Bush Key has been part of Fort Jefferson National Monument. The history of the tern colonies at the Tortugas has been reviewed in detail (Robertson, 1964) and will not be covered further here.

Three small brackish ponds in the center of Bush Key are rimmed by mangroves (*Rhizophora mangle* and *Laguncularia racemosa*) and buttonwood (*Conocarpus erectus*). Around them a thicket of bay cedar (*Suriana maritima*) 6 to 8 feet tall covers much of the island. Outside the bay cedar

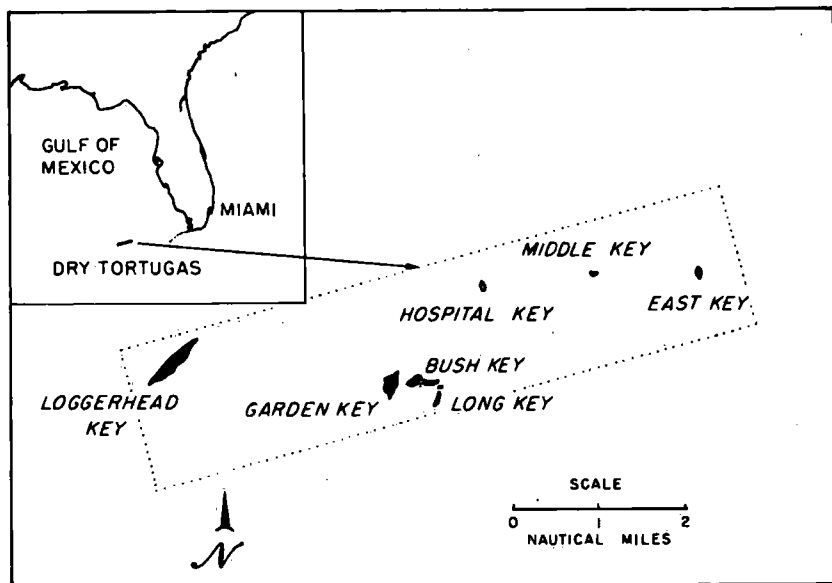


FIGURE 1. Map of Dry Tortugas Islands, based on Coast and Geodetic Survey 585 "Dry Tortugas."

thicket and extending from it to the tide line, the vegetation is relatively low and open. Most Sooty Terns nest on these flats, although some nest in openings in and under the mangroves or the bay cedar. The major plants on the periphery of Bush Key are sea rocket (*Cakile lanceolata*), sea oats (*Uniola paniculata*), prickly pear (*Opuntia* sp.), a grass (*Sporobolus* sp.) and sea purslane (*Sesuvium portulacastrum*) with some sea lavender (*Tournefortia gnaphalodes*) around the edges. The density of these plants varies from year to year, primarily depending on the amount of rainfall.

Royal Terns (*Thalasseus maximus*), Sandwich Terns (*T. sandvicensis*), and Least Terns (*Sterna albifrons*) formerly nested at the Dry Tortugas (Robertson, 1964). Currently several hundred Roseate Terns (*S. dougalii*) nest on the Dry Tortugas and several thousand Brown Noddies (*Anous stolidus*) nest on Bush Key with the Sooties. The only mammals present are the introduced rat (*Rattus rattus*) and a few humans who man the Fort Jefferson National Monument and a nearby Coast Guard lighthouse.

The climate at the Dry Tortugas is best described as hot and dry. Daily temperatures often reach the low 90's (°F) and seldom drop below the low 60's at night (Vaughan, 1918). The intense radiation of heat from both water and the light-colored sand creates a severe microclimate in the layer of air just above the ground, the microhabitat in which Sooty Terns nest. Rainfall averages less than 40 inches per year (Florida State Board of Conservation, 1954), much of it coming in sudden squalls. Several hurri-

canes have struck the Tortugas in recent years. On 8 June 1966 the winds of Hurricane Alma drove water over parts of Bush Key and buried many young terns in the sand. Many died, but overall mortality was surprisingly low (Mason and Steffee, 1966). On 3 June 1968 the center of Hurricane Abby passed about 60 miles west of the islands and heavy winds, rain, and waves belted the islands for several days. The high waves washed away some eggs laid on higher parts of the beaches but did not swamp Bush Key, and mortality was very low. Adults with eggs or chicks sat tight on the scrape throughout the storm, and some eggs hatched during the storm without noticeable detriment.

In recent years much of the work at the Tortugas has centered around long term banding studies of the terns. From 1936 to 1941 some 13,300 Sooty Terns, mainly juveniles, were banded at the Dry Tortugas. Some of these are still alive and provide information on the longevity of the species. In 1959 the National Park Service, the Florida State Museum, and the Florida Audubon Society began a cooperative banding program that to date has banded almost a quarter of a million Sooty Terns on the Tortugas.

#### METHODS

I lived on Garden Key from 29 March to 10 July 1968 and worked almost daily on nearby Bush Key. I erected a blind near a small plot (25 x 30 feet) from which I cleared nearly all vegetation. I captured terns in mist nets and color-marked 182, each with a unique pattern of three-colored leg bands and a Fish and Wildlife Service (FWS) band for individual recognition. The terns gradually became accustomed to my presence in the blind, and their behavior appeared normal once I was out of sight.

I determined the sex of the terns by noting their position in copulation, keeping in mind that male-male mountings may occur. Once the birds were color-marked, I recorded their activities and the roles of males and females in the care of their eggs and chicks. As Sooty Terns spend much of their time flying, I had to limit my studies to their activities at and near Bush Key. After the eggs hatched, I tethered some chicks to prevent them from hiding throughout the day. This altered their behavior, but it was the only way I could keep more than a few chicks in sight after they were about 3 weeks old. In 1969, 1970, and 1971 I spent shorter periods on the island after the young hatched.

#### BREEDING ACTIVITIES

Starting in mid-January, Sooty Terns appear near the Dry Tortugas in numbers at night only, circling, calling, and sometimes landing, but generally are absent during the day (Robertson, 1964; pers. comm.). Gradually the terns start arriving at the Tortugas earlier each evening and also in greater numbers. Finally in late March or April they remain in daylight and land on Bush Key. There they display, copulate, dig a scrape, and

lay the single egg that they incubate 29 to 30 days. The chicks are closely attended for the first week or two and then are alone much of the time except when fed. Chicks first fly when about 8 weeks old and apparently leave Bush Key soon afterward. Some juveniles are flying by late June, and most terns have left the Tortugas by late August or early September.

Little is known of the activities of Sooty Terns away from the colony. Out of some 153,700 chicks banded on Bush Key, about 80 have been recovered away from the colony. After leaving Bush Key juveniles apparently drift west in the Gulf of Mexico and then south along the eastern coast of Central America, finally moving east along northern South America and out across the Atlantic. They spend 2 to 4 years in the Gulf of Guinea off West Africa, and gradually drift back across the Atlantic (Robertson, 1969). A few 3-year-old birds appear at the Tortugas late in the breeding season, but almost certainly do not breed. At least a few 6-year-old birds breed, but some Sooties may not breed until older (B. Harrington, pers. comm.).

Among those banded as adults the recovery rate is lower, with only about 25 recoveries away from the colony out of 81,100 banded through 1970. These recoveries suggest that most adults range over but remain essentially within the Gulf of Mexico throughout the year (Robertson, 1969).

#### FORMATION OF THE COLONY

As the terns assemble and reform the colony, they are very skittish and difficult to follow. Their activities can be divided into periods of aerial flocking and first landing.

#### AERIAL FLOCKING

Robertson (1964) describes a period of night flocking, starting some 2-3 months before eggs are laid. The terns approach Bush Key from the northwest and gather near or over the breeding grounds to call, circle, and land, only to leave around dawn. Ashmole (1963) describes "night clubs" of terns that land on the breeding grounds in groups at night and leave before daylight. Tracks in the sand on Bush Key show that night groups form there too, although I never saw them.

When I arrived at the Dry Tortugas on 29 March 1968, Sooty Terns had not yet laid any eggs, but they were flocking in well-developed patterns every evening. Every morning by about 08:00 (all times are EST) most Sooties had left the island. Occasionally during the day flocks of up to 10 Sooty Terns circled rapidly over Bush Key, giving loud "wide-a-wake" calls or sharp "yip yip" notes as one bird chased another. The birds passed over the island once or sometimes repeatedly, flying low and often in pairs. They flew slowly with deep wing beats. Their flight resembled the low (fish) flight display described for other terns (Palmer, 1941; Cullen, 1960a), except that they did not carry a fish in their bill.



In early evening, between 16:30 and 17:00, the terns gathered to circle and call northwest of Bush Key. Usually they started in a loose flock of 50 to 200 birds circling 50 to 100 feet above the water. They flew with a slow, seemingly exaggerated wing beat, often gliding between beats and drifting along in a circle 100 to 200 feet across. Eventually a few dropped low over the water and, assuming a more rapid wing beat, made a fast circuit over the edge of Bush Key and returned to the flock over the water. Gradually more circled over the island and a few started landing on the open sand beach on the north side of Bush Key. Occasionally all the birds on the beach flew rapidly and noisily back to the flock. There they circled and again started moving back toward the island. Around 18:30 the number of birds gathered on the beach increased. Fewer flew when disturbed, and they returned sooner when disturbed. All this time more terns continued to join the circling flocks and their calls grew louder.

Out over the water the flocking pattern changed slowly. At first all the terns were in one circling flock, from which they flew to the island. As more birds arrived near Bush Key, more flocks formed in a line strung out to the northwest. Presumably birds entered the farthest one first and then moved from flock to flock as they approached the island.

On 5 April at 17:30 I could see three such flocks, one about 1,000 feet north of Bush Key and the other two beyond. Between the flocks lines of birds flew with slow, exaggerated wing beats about 50 feet above the water. Beyond the last flock a line of terns, again about 50 feet above the water, was stretched out for several miles. Perhaps some birds approach Bush Key low over the water as they normally do later in the season, but most drifted in with the flocks described above. Most terns circled northwest of Bush Key but occasionally small flocks formed south of Garden Key. After sundown more terns landed and gathered on the beaches.

At sunrise no distinct flocks were present, although many terns circled and called over Bush Key or stayed on the ground. By 08:00 most birds had left the island, flying to the northwest. The exodus was not so well defined as the approach.

Flocking by Sooties is apparently a significant social activity. Although the adults apparently are spread throughout the Gulf of Mexico during the nonbreeding season, most individuals still commence breeding on Bush Key within a relatively short period of time. Even on Ascension Island where the breeding cycle is nonannual and there apparently is no selection for breeding in one given calendar month each year, the breeding cycles of most birds are still synchronized (Ashmole, 1963). Presumably highly synchronized egg-laying would reduce the time when individuals were vulnerable to predation at the nesting colony. Thus it seems possible that the flocking by terns prior to egg-laying synchronizes the reproductive cycles of individual birds.

### FIRST LANDING

In 1968 the first daylight landings of Sooty Terns appeared to be gradual extensions of time spent on the ground by night groups. Similarly on Ascension Island, after a period during which Sooties were present only at night, they suddenly started to return earlier in the evening and stayed later in the morning, and egg-laying soon followed (Ashmole, 1963).

When I arrived on the Dry Tortugas in late March 1968, the terns had already started staying later in the day so that some were present until around 08:00. Egg-laying started on 1 April 1968 and by 21 April eggs were present virtually throughout Bush Key.

When first landing the terns seemed nervous and were easily frightened. They hovered over open ground, landed briefly, and then flew in a panic almost immediately. Gradually more birds landed and began to fill the available open ground, only to fly at the slightest disturbance and then return and repeat the whole sequence.

As soon as the birds landed and settled down, displaying became common. One display is the parade that will be described later. In another display the bird points its bill down, sometimes almost burying it in its breast feathers (Figure 2). A common posture of Larids, Harrison (1965) calls it the "stare-down" and says it seems to "cut off" or end a low inten-



FIGURE 2. Sooty Tern in stare down, a display that commonly is given almost immediately after the terns land at the colony. (Photograph by O. L. Austin, Jr.)

sity agonistic or conflict situation. Sooties often give a stare-down almost immediately after landing and then preen their back and wings.

Apparently little displaying occurs in the night clubs (Ashmole, 1963) but generally little is known about the birds' nocturnal activities. I made only one night visit to Bush Key during this period, and I found that most terns were quietly resting on the beaches or in open parts of the island with few in the air. Generally the terns were highly excitable at night so I avoided night work and have little information on their nocturnal activities.

### PRE-LAYING ACTIVITIES

All of the displays and activities preceding egg-laying may occur within a few days after the birds first land in daylight. I was marking birds at this time and had few that I could follow through the entire behavioral sequence. I also found that birds were still moving around within the colony, as many color-marked birds immediately left my study plot upon release and never returned. Hence the sequence of events has been pieced together from the few pairs that I could follow throughout this period and also by noting when various activities were most common on my plot.

### AERIAL DISPLAY

Early in the nesting season and to a lesser extent later, aerial displays are a characteristic activity of Sooty Terns. Cullen (1960a) studied aerial activities of the Arctic Tern (*Sterna paradisaea*) in detail and summarized much of the information available on other terns. I follow his terminology for activities he describes that appear homologous to those of the Sooty Tern.

Except for the chases over the colony prior to egg-laying, which may be homologous to the low (fish) flight that is common among *Sterna* terns, aerial display by Sooties seems to consist solely of a high flight similar to that of the Arctic Tern (Cullen, 1960a).

In Sooties the high flight is a slow steady ascent by two or sometimes three terns to a height of several hundred feet and then a rapid gliding descent. I noted two means of ascent. In one the two birds ascended almost vertically in small circles, flapping their wings rapidly as the lower bird chased and occasionally tried to grasp the tail of the upper bird. This seems comparable to the upward flutter, a hostile behavior that Cullen (1960a) describes. I saw the upward flutter at the start of about 36 percent of all aerial displays, but usually it was given only briefly and I may have missed seeing it in other cases. From the upward flutter, the birds changed to seemingly exaggerated deep wing beats that Cullen calls jerk-flying. In many instances the first sign of aerial display was this type of flight, and it was the initial pattern in many high flights.

Flying thusly, the birds continued to climb, though not so steeply as with the upward flutter. Again they stayed close together as if one was chasing the other. In these chases the lead bird gave a rattling "ka ka ka" call while the pursuer gave upward-inflected "wek wek" notes. As they climbed, they flew in long looping circles above the colony and adjacent water, often reaching a height of several hundred feet. They sometimes continued to climb for 2 or 3 minutes, although more commonly they climbed for about a minute.

At the peak of the flight they often chased briefly and then maneuvered close to each other by flapping their wings in slow, almost half beats with the wings barely moving to below the level of the body. Then they began a rapid gliding dive. The angle of descent was usually fairly shallow at first and became steeper as they descended, reaching a maximum of about  $45^{\circ}$  to  $60^{\circ}$  above horizontal. Several times I noted that the pursuer passed the leading bird and took the lead at the start of the glide, and this may be usual, much as Cullen (1960a) reports. In the dive one bird was above and just behind the other, the two about a foot apart. Both held their wings rigid; the lower bird's wings were usually bent slightly at the carpals and the upper one's wings were held almost straight out from the body. They held the long outer rectrices "scissored" together and in those instances where I could see their bills, they pointed straight forward. In this position they dove together, their movements coordinated so that the second bird closely followed the sometimes shifting and dodging flight of the first. Sometimes they started the glide several times, leveled off after descending a short way, and then dove again. At other times they separated and each flew away alone. In a complete display they glided together down to just above water level, swooped up a short ways and then separated, each flying away in a normal flight. Several times I followed both birds after the glide, but I never saw them stay together to repeat the high flight.

I saw numerous variations of the high flight. Of 50 high flights in which I saw all of the display, 18 started with the upward flutter and 32 with jerk-flying; 13 times the birds changed from the upward flutter to jerk-flying. Thus jerk-flying was part of the ascent in 45 of the 50 high flights. The other 5 times the entire ascent was with upward flutter. In 40 high flights the two birds circled after this ascent, mainly by jerk-flying. The birds started a descending glide in 47 of the 50 high flights but continued to glide down to about sea level in only 28. Thus ascending by jerk-flying and descending in a glide are the two most common parts of the high flight, although they do not occur in all of them.

The birds often changed positions, first one leading and then the other. These changes occurred both during the ascent and in the glide. In the glide the change was made by the upper bird moving beneath the lower one. I was not able to determine the sex of the birds during the aerial display.

Except that Arctic Terns sometimes carry a fish in the high flight

(Cullen, 1960a), the high flight of Sooties is very similar to that described by Cullen for the Arctic Tern.

Aerial displays are most common in early morning and from 15:00 to 19:00. Most occurred early in the breeding season in April but I also saw some in May, June, and July when they may have been given by late arriving adults or reneesters. Unfortunately I did not see the events on the ground that preceded the high flight.

The function of the high flight is not known, but Cullen (1960a) suggests that it may be part of pair formation. If so, perhaps the high flights late in the nesting season involve subadults. As Sooties as young as 3 years old visit Bush Key late in the nesting season but probably do not breed for several years, perhaps they pair a year or more before they first breed. It is not known how long Sooty Tern pair bonds last but it would not surprise me if the same birds pair in successive years. Such an extended "engagement" period is known for another long-lived pelagic species, the Laysan Albatross (*Diomedea immutabilis*) (Fisher and Fisher, 1969). Moynihan (1962) saw many aerial displays by Brown Noddies and Inca Terns (*Larosterna inca*) late in the nesting season, and suggests that at least in the Inca Tern these may have been young birds pairing. Brown Noddies at Bush Key also commonly give aerial displays late in the nesting season.

#### GROUND ACTIVITIES

**PARADE.** — Once the birds landed and stopped the almost continuous panicking, displays on the ground began. The most conspicuous ground display of Sooty Terns is the parade in which the tern assumes a distinct posture and displays to other birds by prancing rapidly with short, quick steps. A bird may prance toward, in front of, or around another tern; or two may prance together, moving parallel to each other. Palmer (1941) describes a similar display in the Common Tern (*Sterna hirundo*) and says it takes two different forms, each with a different motivation. Although I saw these two forms in Sooties, I saw much variation in posture between the two extremes.

In the parade posture, a Sooty extends its head and neck far forward, often sleeking the feathers. The wings are usually held well away from the body, particularly at the carpals, and are sometimes lowered until they drag on the ground (Figure 3). Occasionally the wings are held tight against the bird's sides. Usually the tail is tilted upward and often the tips of the primaries cross under the base of the tail.

If the bill is pointed upward, it is called the erect posture and Palmer (1941) says the display shows submission. Sooties may point the bill horizontally or slightly above horizontal, but they seldom point it straight up as some other terns do. Sooties also tilt their head to the side, especially when displaying with or to another bird. Then they tip their head away from the other individual but seem to lean the body even more toward it so that the near wing often drags on the ground.

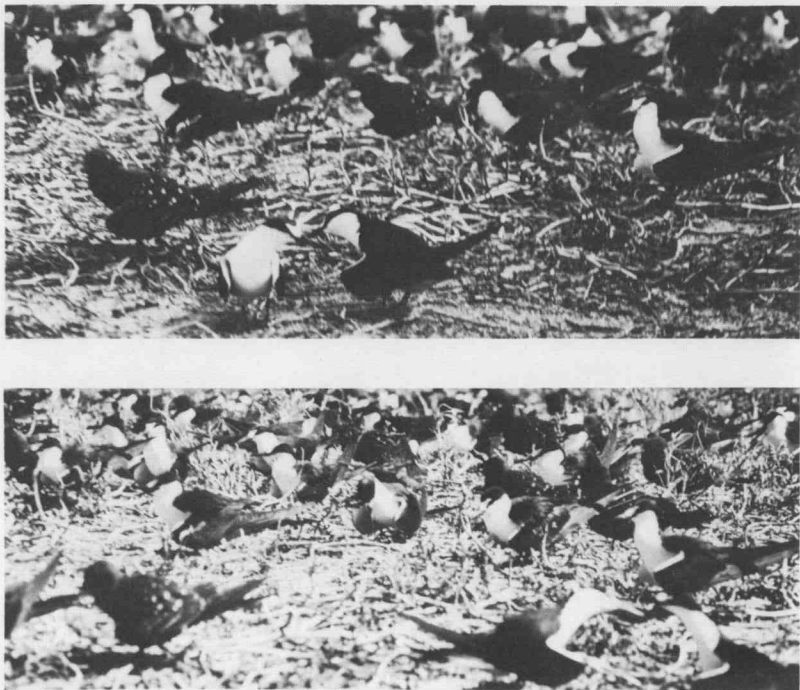


FIGURE 3. Parade display by Sooty Terns. In the top photograph one adult is parading around a second tern, the parading bird holding its wings well away from the body and the head tilted away from the other bird. At the bottom the two birds in the right foreground are parading around each other, each holding its wings away from the body and the head and neck extended forward with the head tilted away from the other bird. (Photographs by O. L. Austin, Jr.)

I saw Sooties give this display almost immediately after landing. Often it preceded copulation, but at other times two birds separated after parading. Both sexes gave the erect form of the parade, but when one bird circled and obviously displayed to another, whenever I could determine the sexes it was always the male that did so. The erect form of the parade was common almost immediately after birds landed and before they established territory, and seems to be part of pair formation.

In the other form of the parade the tern points the bill down, but Sooties seldom point it directly at the ground. Palmer (1941) calls this the bent position and says it is given when a tern tries to intimidate another tern. Sooties do not take so extreme a posture here, usually not holding the wings so far away from the body or stretching the neck so far forward. Several times I saw a parade start with the bill pointing

upward and end with it pointing toward the ground. Thus the position of the bill varies considerably, although the basic wing and body postures are similar in the bent and erect forms of the parade.

Both Palmer (1941) and Cullen (1960a) note these two bill positions occurring in aerial displays of terns. In aerial displays Sooty Terns always seemed to point the bill straight forward, the aerial position apparently comparable to the erect on the ground. In the high flight Sooties usually fly away from the Island, so I may just have been unable to see the birds well enough.

The only calls I heard associated directly with the parade were occasional low "wuk wuk" notes, but usually the birds were silent. Once I noted the throat of a parading male vibrating rapidly, but although I was only 10 feet away I heard no sound. Notes too low for me to hear may accompany the display.

Several times I saw a bird on the ground raise its head and give a loud "ke-wat-ic" or "wan-dick" call that was answered by a second bird in the air. After the two exchanged several calls, the second bird landed and then the two paraded. In one exchange a male called to a female in the air, she landed, they paraded and then the two copulated. In such exchanges the erect form of the parade was most common and it seemed to be part of pair formation.

**COURTSHIP FEEDING.** — I saw courtship feeding only 17 times, mainly from 13 to 20 April but once as late as 17 June. Not all of these terminated with the actual transfer of food. In five instances where the sex was known, the female always begged. Generally she crouched, turned her head toward the male, and uttered a rapid series of low chuckling "ka ka" or "yip yip" notes, raising her open bill toward him, and biting at his bill, much as a young tern begs for food. A few times I actually saw the male transfer food to the female, sometimes repeatedly in one bout of courtship feeding.

Occasionally the parade preceded courtship feeding, but the latter is certainly not a regular component of the parade. Courtship feeding is a typical precopulatory behavior in most Larids (Cullen and Ashmole, 1963) but in Sooty Terns courtship feeding is relatively rare and only occasionally precedes copulation.

**COPULATION** — The parade commonly precedes mounting and copulation. The male parades in front of and around the female, stops beside her, and then mounts. The female crouches, holds her wings out from her sides, raises her tail, and stretches her head forward. The male then moves back on the female, crouches, and copulates. After coitus the male dismounts, and the two usually fluff their body feathers and then preen.

Copulation was commonest on my plot from 6 to 23 April. Of 226 times I noted a male trying to mount a female, in only 60 (26.5 percent) did they seem to copulate. In 77 (34.1 percent) attempts the male fell off the female, the female did not crouch, or he simply dis-

mounted without trying to copulate. More commonly (89 times, 39.4 percent), another bird interfered and either knocked the male off the female or the male dismounted and fought with the intruder. Interference from other birds was especially common from 11-20 April. Then almost half of the attempted copulations ended with interference by another bird and few pairs could copulate without other birds interfering. Several times I saw two to six males try to mount one female.

#### ESTABLISHING TERRITORIES

Sooty Terns apparently do not establish territories until after copulation. Even then the territory is not permanent until they dig a scrape and the female lays an egg. Normally Sooties claim an area spanning little more than what they can reach while sitting on their egg. The scrape itself is a shallow hollow some 3 to 4 inches in diameter and about an inch deep. Although Sooty Tern nest throughout Bush Key, they nest in greatest concentration outside the bay cedar thickets and mangroves of the central part of the island.

**SCRAPE-BUILDING.**—By 10 April scrape-building was common on my plot and from then until 16 April it was the bird's most conspicuous activity. Although scrape-building obviously provides a site for the egg, the incipient scrape-building behavior associated with it often occurs before copulation and seems to be part of courtship in Sooties, much as it is in Common Terns (Palmer, 1941).

Pairs of Sooties usually spend some time selecting a site and may make several false starts over a period of several days. While selecting a site they walk together, poke at the ground, pick up bits of gravel, shell, or vegetation and then drop them, start work at one site only to abandon it shortly, and continuously give low "puck puck" calls.

Nearly always a pair works together to dig the scrape. Typically they stand close together, point their bills toward the ground, then lower their bodies, and kick dirt back with their feet. They often give low "puck puck" notes as they poke at the ground. Usually the male does most of the digging but the female helps at least occasionally. As they work at the scrape, they pick up small pebbles, shells, twigs, or other small objects and sometimes drop them into the scrape.

Scrape-building generally stops once the female lays her egg, but the birds occasionally work on the scrape after it contains an egg. Several pairs that lost their chick shortly after it hatched began work on new scrapes, but I did not see any bird lay again.

**FIGHTING.**—Conspicuous fighting started around 11 April when scrapes were being dug. In fighting, two birds face each other, sometimes approaching each other with their heads and bodies held low and forward or else upright, the head erect and the crown feathers raised. The two hold their wings out from the body and usually hold the tail up. Usually each jabs at the head and bill of the other bird or grips the other bird's bill and then both shake their heads vigorously. Occasion-



ally one beats the other with a wing, but normally they use the wings only for balance. Sometimes they give low rasping growls. Finally the two release each other and each retreats to its own scrape.

While some fights ended with one bird clearly supplanting the other, I often saw them end differently: The two birds stopped scuffling and faced each other with wings against the body, bills forward. First one and then the other lowered its bill into the bent posture, turned its head slowly away, and then broke off the altercation (Figure 4). Occasionally they gaped at each other before lowering the bill. Gaping apparently is an aggressive signal (Moynihan, 1962) as is the bent position. Thus the aggressive display apparently ended the fight.

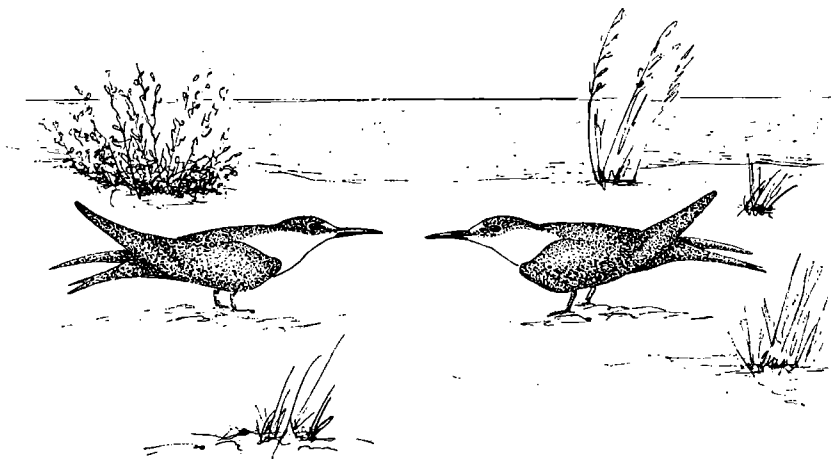


FIGURE 4. Face off between two Sooty Terns. After staring at each other, the birds will lower their bills, turn away from each other, and end the fight. (From photograph by Brian Harrington)

The stare-down posture described earlier also occurs commonly after fights. After a paired bird drove off an intruder, it commonly gave the stare-down upon returning to its mate. Again the aggressiveness seemed to end with the stare-down and the bird turning its attention back to its mate.

Thus the sequence of events preceding egg-laying seems to be as follows: First the terns flock near and land on Bush Key every evening in a mass social activity, perhaps synchronizing the breeding cycles. Gradually they spend more time on the ground and, as flocking decreases, they begin individual sexual activity. Males seem to land, perhaps near where they bred in previous years, and call to try to attract females to them. The parade and high flight that follow probably contribute to pair formation. Pairs continue courting with parading and incipient scrape-building until they copulate. The two then dig a scrape and begin to defend the area immediately around it.

## INCUBATION PERIOD

## EGG-LAYING

After copulating and then working on a scrape for several days, the female Sooty Tern lays a single egg. All 14 eggs whose time of laying I was able to determine accurately were laid in the afternoon: 5 between 12:00 and 14:00, 5 between 14:00 and 16:00, and 4 from 16:00 to 18:00. Ridley and Percy (1958) and Ashmole (1963) also note that Sooty Terns usually lay their egg in the afternoon.

After the first eggs were laid on 1 April 1968, egg-laying gradually spread through the island. The first eggs were laid on my plot on 9 April and the peak of laying there was 15 April.

Usually both members of a pair are present when the egg is laid. The female crouches low in the scrape while the male stands nearby, occasionally walking around her or poking at the ground. After laying the egg the female almost immediately leaves, walks around it, and the male takes over. He pokes at the egg, rolls it into the scrape if it was laid on the edge, and in general worries over it before finally settling down to shade or incubate it. Usually the female flies within about 10 minutes, apparently to drink and dip, as she often returns with her breast feathers wet. The two then stay near the egg, first one and then the other shading or incubating it. Exchanges now, as later in incubation, consist of one bird forcing the other off the egg and then taking over care of it. Exchanges are frequent during the first few hours after the egg is laid, but by early the following morning the male assumes care of the egg and the female is absent, presumably feeding.

During incubation and to some extent after hatching, besides noting which adult cared for the egg and the adult's general behavior, I maintained records of activity patterns of 15 pairs in the following manner: I made a complete catalog of the bird's activities, described below. I knew the date of laying and I could distinguish the sexes of each of these pairs. In the activity records, every 30 seconds I made a 1-second "spot" observation and record of the bird caring for the egg, assigning the bird's activity to one of several readily identifiable categories (e.g. incubating, shading the egg, off the egg and preening, etc.). I used this method to make 120 observations per hour per nest for 1-hour periods throughout incubation.

One fault of this method is that by cataloging activities, some slightly different activities must be grouped in a single category. The categories with the most variety are those that occur when the adult is off the egg, and as the adults either incubate or shade the egg more than 90 percent of the time, this variation is only a small fraction of all the birds' activities.

I analyzed these activity records by sex, hour of day, and date in the incubation cycle, excluding all 1-hour watches in which exchanges occurred. During incubation, I have records for 1,632 bird-hours, each

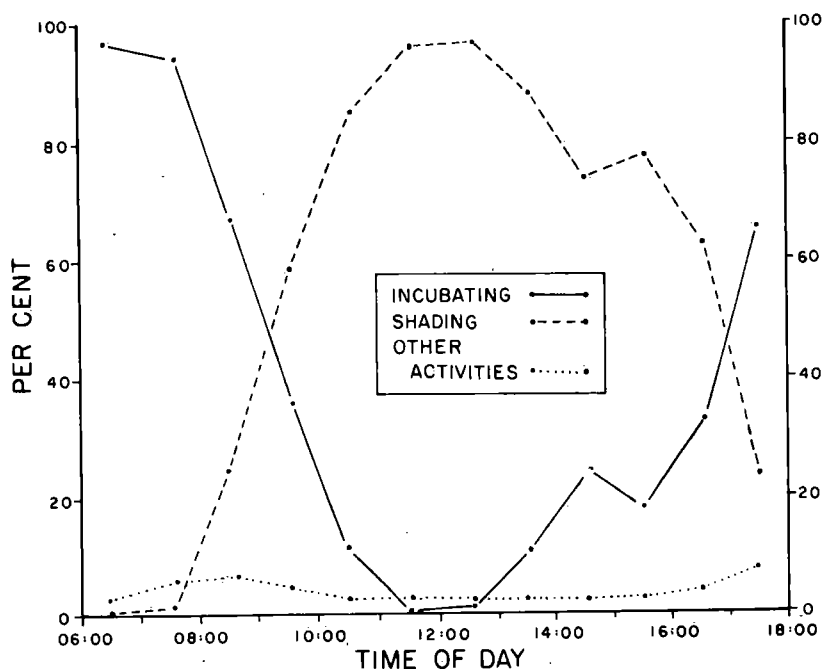


FIGURE 5. Activities by adult Sooty Terns during incubation, showing the percent of time they spend incubating or shading the egg.

including 120 spot observations for a total of 195,840 spot observations. These include at least 1 hour of watching for each sex for each of the 12 daylight hours for most days during incubation, and for some I have many more. These were used to prepare Figure 5 and Table 1.

#### BEHAVIOR DURING INCUBATION

During incubation Sooty Terns primarily tend the egg or perform a few maintenance activities during brief spells away from it. I categorized their activities into several types.

Sooty Terns incubate, placing one of their two brood patches against the egg, mainly at night, in the early morning, and in late afternoon (Figure 5). As the air temperature increases in the morning, adults gradually rise up off the egg so that most days by around 10:00 they are shading the egg rather than incubating it. They usually continue to shade the egg until around 17:00, when they gradually change back to incubating again (Figure 5.) To shade the egg the adult stands over it and keeps it in its shadow. As the sun changes position during the day, the birds turn to keep their backs toward the sun. This keeps the maximum surface area of the body exposed to the sun and, as the upper sur-

TABLE 1. SOOTY TERN ACTIVITIES DURING INCUBATION OTHER THAN INCUBATING OR SHADING

Activity	Spot observations	Percent
Preening	4258	48.4
Poking at egg	1540	17.5
Standing beside egg	1171	13.3
Walking	886	10.1
Fighting	673	7.6
Away from scrape	276	3.1
Total	8804	100.0

face of a Sooty Tern is black, would seem to present problems of heat load for the bird. However keeping the back toward the sun best insures shading of the egg. The adults probably reduce their heat load by erecting their backfeathers and holding their wings out from their sides, increasing insulation and the area for heat loss (Figure 6.) They also gape widely and pant, apparently dissipating more heat than in normal breathing. Another common activity is dipping as described below.

The change from incubating to shading and back again is very gradual and proved my most difficult choice in recording activity. Figure 5 indicates when this change is made. Both incubating and shading involve direct care of the egg. All other activities in which the adult is not actually caring for the egg are shown as the bottom line in Figure 5.

Among these other activities the most frequent is standing at the side of the egg and preening (Table 1). Incubating adults commonly rise up off the egg, poke at it, and apparently turn it. Other times the

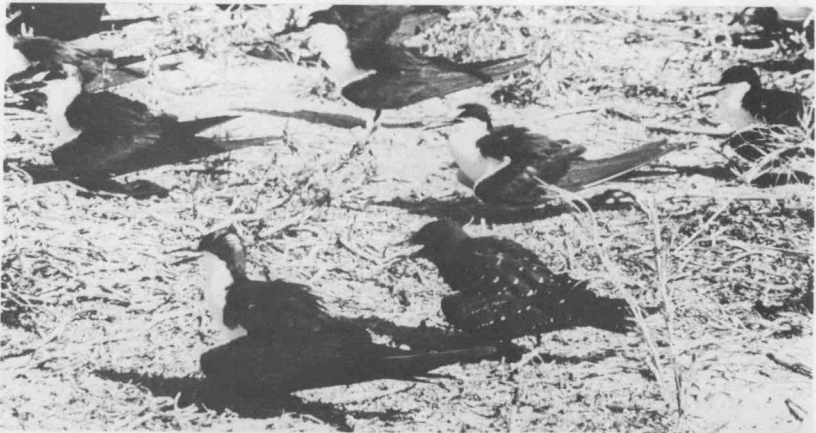


FIGURE 6. Typical sunning posture by adult Sooty Terns. Note the erect back feathers, lowered wings, and open bill. The chicks in this photograph are close to fledging, but the adults assume a similar posture when they are shading eggs. (Photograph by O. L. Austin, Jr.)

adult walks around the scrape or to the edge of its territory and stands. Occasionally a bird leaves its egg to spar briefly with another tern, either a neighbor or one that has come too close. Generally Sooty Terns are much less bellicose during incubation than they are at other times in the nesting cycle. Perhaps home ground is permanently established and recognized, and the absence of chicks to intrude on others' territories enhances stability.

Adult Sooties commonly defecate near their egg. They walk to the edge of their territory and turn to face the egg before defecating. Sometimes the bird stretches both wings vertically above the body, leans forward with head outstretched, and defecates, thus stretching and defecating in almost the same motion.

Another activity of adults during incubation is suddenly flying away leaving the egg unattended. On some occasions the birds fly away when panicked and return almost immediately. Other times their absence seems to be associated with the aerial activity called dipping, described below.

#### ATTENTIVENESS

Sooty Terns are closely attentive during incubation. The percentage of time adults spend incubating or shading differs only slightly between sexes. Females spend a little more of their time incubating and males a little more shading, but with incubating and shading combined, the total attentiveness, analyzed by hour, differs by less than 1.2 percent between sexes. In all, the adult caring for the egg spends over 95 percent of the daylight hours either incubating or shading and only about 4.5 percent in a variety of other activities (Table 1). These other activities are commonest from 07:00 to 10:00 and from 17:00 to 18:00, the times when birds shift between incubating and shading (Figure 5). Presumably at these times egg and air temperatures are much the same, and care by the adult is not so critical. Sooties are most attentive from 12:00 to 15:00 and spend over 98 percent of their time directly caring for the egg, mostly by shading. This is certainly the time when the environmental temperatures are highest, and presumably when adult care is vital to the embryo's survival.

#### DIPPING

An activity of Sooty Terns at Bush Key that is especially noticeable during hot midday hours, but occurs occasionally throughout the day, entails their flying rapidly from the island, briefly dipping their bill, feet, or breast feathers into the water, and returning to the island. When only the bill is skimmed along the water's surface, it seems obvious that the birds are drinking, but dipping the breast feathers requires another explanation.

Usually each tern flies directly and rapidly from the colony at a height of about 10 feet. It then drops down, dips the bill in the water,

TABLE 2. SUMMARY OF 113 DIPPING FLIGHTS BY SOOTY TERNS

Where flight ended	Total flights	Flights that included dipping:			Number of times body parts were dipped:			Total
		Feet	Bill	Breast	Feet	Bill	Breast	
On beach	35	13	34	0	22	60	0	82
In colony	78	45	74	19	102	158	49	309
Totals <sup>§</sup>	113	58	108	19	124	218	49	391

and sometimes almost lands momentarily, wetting the feathers in the process. About 100 to 300 feet offshore the bird turns abruptly and flies back to the island. An individual may dip from 1 to as many as 10 times on one flight. In 113 flights between 13 May and 7 June in which I recorded all dipping movements, and also whether the bird landed back in the colony or with groups of terns sunning on the beach, over 80 percent of all dipping occurred on the flight out. In about 95 percent of the flights the birds dipped the bill at least once (Table 2), and in only about 17 percent they dipped their breast feathers. As one dipping motion might result in more than one part of the body being dipped, I recorded the number of times each part of the body was actually dipped (Table 2). The number of times a bird dropped down to dip is somewhat less.

None of the flights that ended with the bird landing on the beach among terns sunning or resting included dipping the breast feathers, while about 25 percent of the flights that ended with the bird going into the colony where eggs and young were present included dipping the breast feathers (Table 2). This suggests that dipping the breast feathers

TABLE 3. FLIGHTS AWAY FROM THE EGG BY ADULT SOOTY TERNS

Time	Number seen during:		Total
	First 15 days of incubation	Second 15 days of incubation	
06:00—07:00	4 <sup>1</sup> (4) <sup>2</sup>	1 (1)	5 (5)
07:00—08:00	6 (3)	0 (0)	6 (3)
08:00—09:00	8 (7)	5 (4)	13(11)
09:00—10:00	31(24)	4 (3)	35(27)
10:00—11:00	31(25)	11 (8)	42(33)
11:00—12:00	24(18)	5 (5)	29(23)
12:00—13:00	21(19)	17(15)	38(34)
13:00—14:00	24(20)	14(11)	38(31)
14:00—15:00	23(20)	4 (4)	27(24)
15:00—16:00	18(12)	3 (3)	21(15)
16:00—17:00	20(14)	1 (1)	21(15)
17:00—18:00	0 (0)	1 (1)	1 (1)
Totals	210(166)	66(56)	276(222)

<sup>1</sup> Number of times in activity records birds were away from egg.

<sup>2</sup> Number of actual flights represented, i.e., one flight might involve two or more spot observations in activity records.

possibly has some relevance to nesting, something also suggested by behavior I noted at the scrape itself.

Often during the hot midday hours, I saw a single bird fly from its egg, not in a panic, and head toward the water (Table 3). After about a minute it returned, flying low and rapidly toward the scrape. As the bird settled back on the egg, I often could see that its bill, feet, and sometimes the breast feathers were wet. Obviously these direct flights from the egg were the start of the dipping flights that I watched over the water. As dipping is most common when the day is hottest, it seems possible that this behavior is thermoregulatory, both for the adult and the egg. As both sexes dipped with equal frequency (139 to 137), I combined their records. Dipping by incubating adults is most frequent during the first 15 days of incubation (Table 3).

Watson (1908) mentions an activity similar to dipping but says the terns were bathing. The Ashmole (1967: 62) note that incubating Sooties sometimes fly off to drink. Brian Harrington (pers. comm.) has seen Sooties dip at Johnston Island in the Pacific but less frequently than at the Dry Tortugas. Simmons (1970) also noted aerial drinking by Sooties at Ascension Island. Both Tompkins (1942) and Hardy (1957) report Least Terns dipping their breast feathers during incubation and suggest that it provides water necessary for the eggs.

#### TEMPERATURE REGULATION

Howell and Bartholomew (1962), working on Midway Island in the Pacific, show the delicate role that parental care plays in preventing Sooty Tern eggs from approaching the high and probably lethal temperatures they would reach in open sunlight. On Midway the adult terns maintain the egg temperature above that of the surrounding air and below that of the surrounding sand, but it is not stated whether the adult is incubating or shading the egg.

I attached thermisters to several eggs and monitored surface temperature of the egg and air temperature at about 4 inches above the ground for parts of several days. Unfortunately the eggs I worked with were close to my blind, and the adults caring for them were easily disturbed by my movements. Also the wire attached to the egg hindered the tern in turning it and affected the bird's behavior.

I obtained useful information from a 24-day-old egg on 8 June and conflicting information from the same egg the next day. On 8 June, in 23 temperature readings taken between 10:20 and 13:05, the egg averaged 101.5°F (range 99 to 105°F), and the air at 4 inches averaged 105.5°F (range 103 to 108.5°F). The highest egg temperatures occurred when the adult left it to dip or flew off in a panic. In both cases the adult dipped the breast feathers before returning to the egg. The next day in 35 readings the egg temperature averaged 105.2°F, somewhat above the air temperature that day (105°F) and 3.7°F above the egg's

temperature on the 8th. Although the adult repeatedly left the egg to dip, it seemed unable to lower the egg's temperature. As the egg cracked later that day and proved infertile, perhaps the heat of decay foiled the adult's attempts to lower the egg temperature.

On the 8th the adult had been able to maintain the egg's temperature 4°F below the air temperature. When the adult flew off to dip, the exposed egg's surface temperature rose 1 to 2°F while the bird was absent but then dropped 2 to 5°F within a few minutes after the adult returned. The adult did not hold the wet breast feathers against the egg, but held them right above the egg.

Although I have limited information, I suggest that dipping the breast feathers by incubating terns helps regulate either the egg's temperature or humidity. Some adults dipped often during incubation while others did so only rarely. If dipping the breast feathers is thermoregulatory it is puzzling that the tern does not hold the wet, cool feathers directly against the egg. Possibly the water dripping off the feathers onto the egg provides any moisture the egg may need.

Late in the breeding season adults continue to dip but seldom dip their breast feathers. On 27 June 1970 when most chicks were 6 to 8 weeks old and few eggs were present, nearly all of the hundreds of adults flying out from Bush Key dipped only their bill or occasionally their feet.

#### NEST RELIEF

Most of the 61 nest reliefs observed during incubation occurred during early morning or late afternoon (Table 4). Generally the adult lands near its scrape and walks up to its mate on the egg. The bird on

TABLE 4. NEST RELIEF DURING INCUBATION

Time	Number of exchanges	Hours of Observation	Exchanges/hour Observation
06:00—07:00	13	21.52	0.60
07:00—08:00	4	27.92	0.14
08:00—09:00	4	29.03	0.13
09:00—10:00	3	23.50	0.12
10:00—11:00	5	19.33	0.25
11:00—12:00	1	13.38	0.07
12:00—13:00	1	10.33	0.09
13:00—14:00	3	10.25	0.29
14:00—15:00	1	10.97	0.09
15:00—16:00	3	14.78	0.20
16:00—17:00	12	16.98	0.70
17:00—18:00	6	17.00	0.35
18:00—19:00	3	4.50	0.67
19:00—20:00	2	1.17	1.70
Total	61	220.66	0.28



the egg either steps off the egg so the second bird can incubate, or else the newcomer pushes the incubating bird off the egg and then takes over care of it. No elaborate ceremony occurs. The relieved bird generally flies away within a few minutes, presumably to drink, but often returns to the scrape and lingers for several hours or more before leaving Bush Key. Sometimes this bird forces its way back onto the egg so several exchanges occur before the new bird finally takes over and the other leaves the island. I never saw an adult feed another one at a nest exchange during incubation.

Although I saw some exchanges in midday (Table 4), most birds return to the colony in the evening and relieve their mate then. Instead of circling near Bush Key as they do earlier in the nesting cycle, returning adults fly directly to the island and presumably to their scrape. The number of hours I watched in early evening is much smaller than for other times. Otherwise I certainly would have seen more exchanges then.

At Bush Key few adults regurgitate when mist-netted in the morning or early afternoon, but many do so in the late afternoon, indicating they just returned from foraging. The exchanges I saw around sunrise may have been pairs making a final exchange after several exchanges during the night, and the relieved bird was at last leaving to feed. Much as when the colony is forming, the noise gradually diminishes and by about 08:00 few birds are in the air. Those that remain at the colony generally incubate quietly from about 08:00 to 16:00.

Ashmole (1963) found nest relief most frequent between 21:00 and 06:00. He reasons that arriving at that time means that they fed during daylight and then flew some 5 to 8 hours to arrive at the colony in the middle of the night. I have no records of changeovers from 21:00 to 06:00, but the massive influx of terns early in the evening suggests that changeovers are commoner then than late at night as they are on Ascension Island. If Ashmole's reasoning holds, then Bush Key Sooties feed within a few hours flight of Bush Key at most and can return quickly when finished feeding.

#### LENGTH OF INCUBATION SHIFTS

To determine the length of incubation shifts (the length of time one adult cares for the egg without relief), I recorded which adult incubated each day for 13 of the nests on which I kept activity records. I found that the bird present in the morning usually remained there until at least late afternoon. Because most adults seemed to return and exchange in early evening, I assumed this was true unless I had evidence to the contrary. I may have missed a few exchanges, but the pattern I found is generally true of incubation shifts at Bush Key. Watson (1908) also notes that most Dry Tortugas Sooties return in the evening and that incubation shifts generally are 24 or 48 hours long.

Of 231 incubation shifts computed as multiples of 1-day periods, 148 (64.1 percent) were 1 day in length, 70 (30.3 percent) were 2 days

long, and only 13 (5.6 percent) were 3 days long. Figured differently, the Sooties did 45.3 percent of their incubating in 1-day shifts, 42.8 percent in 2-day shifts, and 11.9 percent in 3-day shifts. Even though 1-day shifts are more than twice as common as 2-day shifts, the two contributed about equally to incubation.

Some pairs alternated daily throughout incubation, while others alternated regularly in 2-day or, in a few cases, 3-day shifts. Others seemed to follow no set pattern of relief. Overall on the basis of these records, males spent somewhat more time (175 to 152 days) caring for the egg than did females, but the difference is not statistically significant ( $X^2=1.62$ ,  $P>0.20$ ). In the hourly activity records, males again were present more often (880 to 752 hours), the difference being statistically significant ( $X^2=10.04$ ,  $P<0.005$ ). As the female left the egg shortly after laying and the male cared for it on the first shift, some of this difference occurred then, but even excluding the records for the first day of incubation, the male still cared for the egg more than the female ( $X^2=3.95$ ,  $P<0.05$ ).

Watson (1908) found Sooty Tern incubation shifts on the Tortugas averaged somewhat over a day long with the longest a little over 3 days, well within the range I found in 1968. On Ascension Island incubation shifts average 132 hours (Ashmole, 1963), over twice as long as those on the Dry Tortugas. On Christmas Island in the Pacific, incubation shifts are about 7 days long (Ashmole and Ashmole, 1967); on the Seychelles they vary from 2 hours to 3 days (Ridley and Percy, 1958).

The striking differences in incubation shifts between Bush Key Sooties and those at two other colonies are probably related to food availability and its distance from the island. At Ascension many young died of starvation one year, apparently because of a failure in their food supply (Ashmole, 1963). On the Dry Tortugas Sooty Tern chicks have never been known to experience heavy mortality from food shortage (Robertson, 1964). The shorter incubation shifts seem to indicate that the terns have an adequate food supply near the island.

#### INFLUENCE OF WEATHER

The most obvious effects of weather on incubation patterns of Sooty Terns are the shifts from incubating to shading and back to incubating, depending on the ambient temperature (Figure 5). On hot days when clouds rapidly lower the air temperature, shading birds quickly change to incubating or move away from the egg to preen or perform other maintenance activities. Once the clouds pass and open sunshine returns, the birds again shade the egg. On normal clear hot days an adult virtually never leaves its egg between 11:00 and 15:00 except to dip. The few records I have of terns performing other maintenance activities during those hours nearly always occurred on cloudy days.

Rain also changes activity patterns. At the start of a rainstorm, swarms of Sooty Terns rise and circle over the colony, calling noisily

As nearly all birds that are caring for an egg incubate throughout the storm, it is primarily free birds that circle over the colony.

Apparently Sooty Tern feathers are not water repellent and are easily soaked by rain. After rain Sooties preen their body feathers and flap their wings vigorously. This apparently helps dry the feathers to permit flight. Sooties have difficulty taking off in the early morning after a heavy dew has soaked their feathers. The flocks of terns rising at the start of rainstorms are probably birds getting airborne before they become waterlogged. Once in the air, many remain there until the storm is over, the motion of their wings preventing them from getting soaked.

### FLEDGLING PERIOD

#### HATCHING

Sooty Terns incubate their eggs 29 or 30 days (mean 29 days  $12.3 \pm 2.4$  hours, range 28 days 22 hours to 30 days for 16 eggs). This agrees well with Ashmole (1963) who found that usually the egg is incubated 28.5 to 30 days. Watson's (1908) figure of 26 days seems somewhat short, though Ridley and Percy (1958) claim Sooties incubate for 26 to 29 days on the Seychelles.

The chick may pip the egg as much as 36 hours prior to hatching, but usually does so only the day before hatching. For eggs that I could determine the time of hatching exactly, most hatched around sunrise or around noon.

Once the egg pips, adults continue to care for it very closely. The only time that Sooty Terns ever actually mobbed or struck me in the colony was when eggs were hatching. Howell and Bartholomew (1962) show that a piped egg is particularly sensitive to heat stress and the chick's survival is thus dependent on care by the adult.

Adults appear indifferent to the presence of the empty egg shell in the scrape and sometimes continue to sit on it after the chick has emerged. While I saw adults pick up and carry off a piece of egg shell perhaps 20 times, often one from a neighboring scrape, usually they let the empty shell roll around until it is crushed.

Sooty Tern eggs (like those of most terns) are speckled and camouflaged on the outside, whereas the white inside lining contrasts sharply with the sand background of the nesting colony. Tinbergen et al. (1962) show that rapid removal of the empty shell has definite survival value for Black-headed Gull (*Larus ridibundus*) chicks. In a colonial species like *fuscata*, removing the egg shell probably makes little difference to chick survival. Any predator reaching the colony would have little trouble finding a chick, whether the white inside lining of an empty egg marked the scrape or not.

#### ATTENTIVENESS

My data on parental care of chicks are less complete than those for

care of the egg. Every time I entered my blind the chicks more than a few days old scattered and hid under the nearest cover. It sometimes took them several hours to return to their scrapes where I could watch them again, and some never returned.

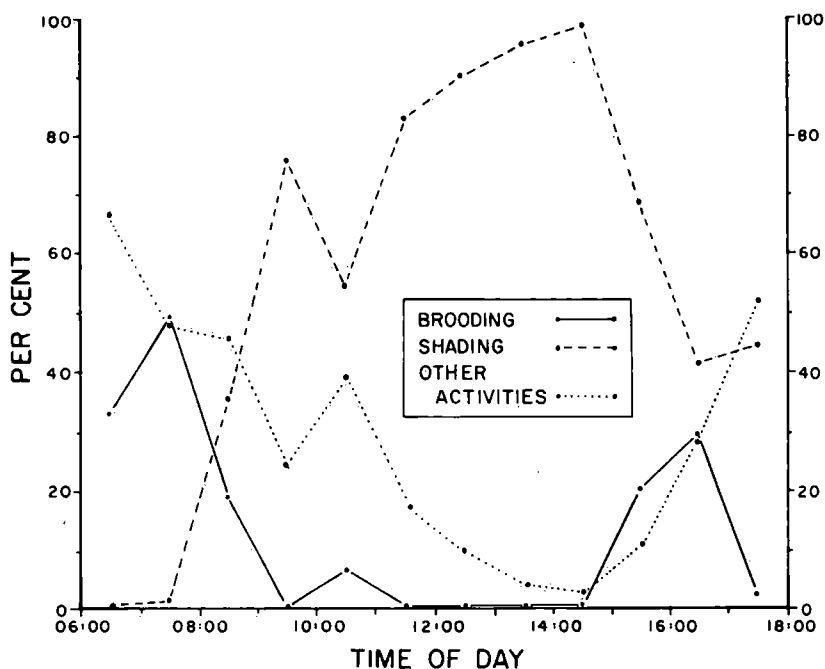


FIGURE 7. Activities by adult Sooty Terns during the first two weeks of caring for the chick, showing the percent of time they spend brooding or shading the chick.

The records I do have, summarized for the first 2 weeks of the chick's life, indicate that the adults are most attentive during the midday hours, much as they were when caring for the egg (Figure 7). As in incubation, adults rise up off the chick to shade it in hotter hours of the day and brood it when it is cool. Females spent somewhat more time with the chick than males did (157 to 132 bird-hours), but statistically these are not significantly different ( $X^2=2.16$ ,  $P>0.10$ ). I found little difference between males and females in care of chicks, and I have combined the records in Figure 7.

Generally adults are less attentive when caring for the chick than when caring for the egg. They often stand to the side of the chick for an hour or more, and their attentiveness decreases as the chick grows older. After the chick is about 3 weeks old, the adult spends very little time actually caring for it other than feeding it, although they may stand

near it during the day. From then on chicks even seem to spend the night unbrooded by an adult.

### FEEDING

Chick care centers around the provision of food. Sooty Terns feed almost exclusively on fish and squid (Ashmole, 1963; Ashmole and Ashmole, 1967). They catch much of this food when schools of tuna, mackerel, or other large predacious fish drive smaller fish to the ocean surface. The Sooties dip down to seize food from the surface or the air above it, and seldom if ever dive headlong into the water for their prey as most other terns do (see Ashmole and Ashmole, 1967).

The Dry Tortugas Sooties have been reported eating fish of the families Carangidae and Clupeidae (Watson, 1908). In recent years Robertson has collected many fish and squid that Sooties and Brown Noddies regurgitated when mist-netted. At present only the Scombridae have been analyzed (Potthoff and Richards, 1970).

I saw one chick fed about 4 hours after hatching, and they may be fed even earlier. The adult stands near the chick and points its bill down. The chick then either grips and bites the adult's bill or else pecks at it. The chick also may beg with some rapid "cheep" calls. This action seems to release regurgitation by the adult. The adult stretches its neck and head upward, tips the bill down, gags, and then brings up a fish. The adult may hold the fish in its bill before feeding the chick, or it may slide the fish directly down the bill and into the chick's mouth. Sooty Terns returning to the colony always carry the food internally and then regurgitate it for the chick.

Older chicks seem to beg more by opening their bills and giving rapid "cheep" calls than by pecking at the adult's bill. They also grab at the fish while the adult is still holding it, sometimes leading to tugs-of-war between the two.

In nearly every case where I could see clearly the exchange of food from adult to chick, the fish was regurgitated and passed to the chick tail-first. Many of the fish seemed to be scaleless, and in some cases they were partly digested or fragmented, especially the last ones fed to the chick (presumably the first ones the adult caught). The regurgitated food is often coated with mucus, which may retard digestion of the food while the adult carries it back to the colony (Ashmole and Ashmole, 1967).

A chick might get six or more fish in one feeding, depending on the size and degree of digestion of the food. Several times I saw an adult feed a chick six times in 3 to 4 minutes, each time passing one fish. Other times a whole meal might be one large bolus containing several fish.

Of 349 occasions when I definitely saw a chick fed, the majority occurred from 06:00 to 10:00 and from 16:00 to 18:00 with many of the rest occurring just before or after those periods (Table 5). Passing several fish to a chick in the space of a few minutes is counted as one feeding. As the number of observation hours varied during the day, the number of feedings

TABLE 5. FEEDING OF YOUNG SOOTY TERNS

Time	Number of times fed	Adult feeding young				Extra adult present	Hours of obs.	Feedings per hour
		Male	Female	Both	Undet. sex			
06:00—08:00	74	22	21	9	22	16	54.78	1.35
08:00—10:00	58	27	23	1	7	27	34.33	1.68
10:00—12:00	26	13	8	0	5	5	16.82	1.54
12:00—14:00	12	5	6	1	0	5	14.42	0.83
14:00—16:00	44	18	6	1	19	8	22.88	1.92
16:00—18:00	85	34	34	4	13	29	33.48	2.53
18:00—20:00	50	19	4	1	26	1	20.83	2.40
Totals	349	138	102	17	92	91	197.54	1.77

per hour of observation (Table 5, last column) is a more valid comparison. This shows that peak chick feeding occurred in late afternoon and early evening with a smaller peak early in the morning. These counts were made from 16 May to 10 July, the time when chicks were present on my plot.

In about 5 percent of the feedings both adults fed the chick; far more commonly two adults were present but only one actually fed it. Of 240 cases in which I knew the sex of the bird feeding the chick, the male did so more often than the female (138 to 102) and the difference is statistically significant ( $X^2=5.40$ ,  $P<0.025$ ).

In addition I recorded some 240 occasions where a chick begged and an adult tried to feed it without actually doing so. Sometimes the adult regurgitated and held food in its bill and then reswallowed it, even when a chick begged loudly. The adult might do this several times, but usually eventually fed the chick. At other times an adult was unable to regurgitate any food.

With small chicks the adult places all food directly in the mouth. Any that drops on the ground remains there unless an adult picks it up to eat or feed to the chick. The youngest chick I saw pick up food from the ground was about a month old, but they may do so when younger. These older chicks pick up food from the ground on scrapes other than their own. Once as an adult held a fish in front of a chick, I saw another adult seize the fish and swallow it.

#### FREQUENCY OF FEEDING

Sooty Terns on Bush Key feed their young infrequently enough to make it difficult to obtain good information on the rate of feeding. Although I watched many chicks continuously for long periods, I have few good records of an adult feeding a chick, leaving it to forage, and returning to feed it again. A major complication is that rather than immediately giving a chick all the food it has in its esophagus, an adult may return to the island and feed the chick several times over a period of several hours. I saw one adult regurgitate and feed its chick some 5.5 hours after it returned to the colony. Thus if an adult fed a chick, flew away and returned in 4 or 5 hours and fed it again, I could not be sure whether the adult had left the island to forage in that time or if it had just loafed elsewhere on Bush Key before returning to the chick. Consequently I have determined the rate of feeding two ways.

Continuous observations on 26 May produced five records of an adult leaving a 2 to 8-day-old chick and returning later to feed it. The length of time the adult was absent (foraging time) averaged 3.87 hours and ranged from 2.63 to 5.30 hours.

I also tabulated the number of times chicks were fed during long periods of continuous observation, separating these into chicks less than 15 days old and ones 15 to 27 days old (Table 6). After listing the total number of times the chick was fed, I subtracted those extra feed-

TABLE 6. ADULT SOOTY TERN FORAGING RATES

Age of chick	Number of feedings	Probable number of foraging trips	Bird-hours of observation	Hours per foraging trip
1—15 days	144	113	369.42	3.27
16—27 days	20	19	84.58	4.45
Totals	164	132	454.00	3.44

ings that occurred when an adult fed a chick more than once after returning to Bush Key. This gives the probable number of foraging trips. Dividing this into the bird-hours of observation gives a rough estimate of the time an adult spent foraging, about 3.44 hours. Apparently foraging trips are about an hour longer when the chicks are older, but the sample size is small and the adults may just loaf part of the time. Note that here time is in bird-hours of observation whereas in Table 5 it is hours of observation, during each of which I watched about 15 chicks.

The two estimates are close enough to indicate that Sooty Terns at Bush Key probably forage 2 to 5 hours at a time when they are feeding their chicks. Adults seem to pass food to older chicks more rapidly on their return. Rather than standing with the chick and feeding it several times in a few hours, they seem to give it all the food they have and then leave.

Often I saw exchanges that appeared to be after foraging trips of 4 to 8 hours, but the birds may have exchanged in shorter intervals when I was not watching. Thus my records of foraging time are biased for shorter periods. Watson (1908) gives 4 to 7 hours as the interval between feedings by Dry Tortugas Sooties.

Sooty Tern chicks on Bush Key are fed more frequently than those in other colonies that have been studied. On Ascension Island and Christmas Island it appears that chicks are fed only about once a day, or even less frequently, but good information is lacking (Ashmole, 1963; Ashmole and Ashmole, 1967).

As the chicks grow, the adults become less attentive and often gather by the hundreds on the Bush Key beaches and sun much of the day. Other adults soar over the island during the hotter times of day. Perhaps adults away from their chicks spend part of their time in these groups. They must spend some of their time foraging but exactly how much is difficult to determine.

At Bush Key more adults are present and the colony is noisier in the evening than at any other time of day. Hence I think that both adults are probably in the colony at night, though both may not be with the chick at all times. Elsewhere Sooty Terns feed at night at least occasionally (Gould, 1967), but at Bush Key, with the noticeable influx of birds in the evening and exodus in the morning, I doubt that many



adults feed at night. As during incubation, mist-netted birds regurgitate far more frequently in the evening than at other times.

The average flight speed of Sooty Terns is about 27 mph (Schnell, unpublished). Thus on longer trips they may forage as much as 100 miles from Bush Key, but the average foraging trip of about 3.5 hours gives them a maximum range of about 47 miles. Sooties from Bush Key usually fly toward the west when they leave the colony and return from that direction. How far they go is unknown but they easily could fly to the nearby Florida Current and forage there.

At about 3 weeks of age the chicks begin to wander from their scrape. They may spend much of the day alone, being accompanied by an adult mainly when being fed. Some adults seem to check their chick periodically during the day, landing beside it, possibly feeding it, and then flying off only to return in an hour or so. These adults probably spend much of their time loafing on the beaches or soaring.

I was not able to visit Bush Key during the height of Hurricane Abby (3 June) but on 4 June it was obvious that the tern's normal schedule had been disrupted as few adults were present until that evening when they started to stream into Bush Key and continued to do so until the evening of the 5th. They probably had been unable to forage during the storm and had left as soon after the storm as possible to obtain food for themselves and their chick. Mason and Steffe (1966) noted a similar disruption after Hurricane Alma. Some of the returnees undoubtedly were birds displaced by the storm.

#### INDIVIDUAL RECOGNITION

As the chick grows, its physical appearance changes and it may wander farther from the scrape. As the colony has thousands of chicks, adults undoubtedly have problems locating and feeding their own (or adopted) offspring. Sooty Tern chicks and adults evidently learn to recognize each other so the chick can be located and fed.

Much as Lashley (1915) and Burckhalter (1969) report, I found that parents apparently do not recognize their chicks individually at first. In the first 4 or 5 days chicks often return to the wrong scrape and are readily accepted and reared by foster parents. After that they are pecked savagely if they intrude near another scrape, and some are killed. Thus recognition seems to develop when the chicks are about 4 to 5 days old. As Davies and Carrick (1962), Hutchison et al. (1968), and Stevenson et al. (1970) suspect for other terns, this recognition probably is based largely on calls between the adults and chicks.

After a disturbance, typically the adult tries to attract its chick back to the home scrape with a combination of bill movements and low calls. The call is a low two syllable "kraa-unk" note accompanied by bowing movements of the bill and head, ending with the bill pointing down toward the breast feathers. Often an adult uses such behavior to lure the chick back to the scrape, backing away from the chick and toward the

scrape until the two are finally back at their own scrape. Once I watched an adult hold a fish in its bill and back away from its chick, apparently using the fish to lure it back to the scrape.

By 3 weeks of age most of the chicks on my plot spent much of their time hiding under the nearby bay cedar. By removing most of the vegetation from the nesting plot I may have forced them to move to this cover. Typically these older chicks emerged from the bay cedar late in the afternoon and stood at its edge or ran out to their scrape. The chicks ran swiftly to a spot and stopped, seemingly knowing where they could stop and not be attacked by other chicks and adults. Once on the scrape, they stood and waited for an adult to come and feed them. Whenever I caught one of these chicks, it was always at the scrape where it had been reared and thus had "homed" correctly. Also when an adult fed the chick, normally the adult was one of the pair that had used that scrape. Hence the chicks apparently knew their home scrapes and returned there to be fed.

Sometimes the adult landed at the scrape before the chick arrived. At first the adult circled 10 to 15 feet over the scrape and delivered loud "wid-ik" or "ka-wid-ik" notes from the air until it was answered by a loud piercing "che-up" call from a chick hidden under vegetation. The two birds exchanged calls several times and the adult landed. The chick then ran out to the adult, begged, and was fed. As the chick approached the adult, the adult often gave what appeared to be a greeting, flying straight up 2 to 5 feet in the air, giving a loud "wide-a-wake" call at the peak, and dropping back down to the ground to feed the chick. These "fly-ups" occurred in other situations and are discussed later. Occasionally the adult pecked the begging chick sharply. I was not able to determine the relationship of the two in these cases, but I suspect that the two had made a mistake in recognition and the adult did not realize it until the chick came close.

Although chicks are usually fed by their parents (or by adults that adopt them in shuffles before chicks are individually recognized), at least eight times I saw a tern feed a chick other than its own. In five of these instances an adult that had lost its chick or whose egg had failed to hatch fed a chick, usually at an adjacent scrape. Three times an unmarked adult fed a chick whose parents were both marked and thus recognizable.

Some chicks seemed to approach and beg of any adult that came near. Although these chicks were not marked, I am fairly sure that some were fed by adults other than their parents. Often the adult pecked the chick and drove it away, but at times the adult tried to regurgitate, and occasionally it brought up food and fed the chick. Possibly these chicks had lost their parents in the shuffle of chicks in the first few days of life, and no adult recognized them as its own. The adults that fed them or tried to feed them may have been their lost parents, or other adults that had lost their chick or egg.

Thus older chicks seem to find their parent both by knowing where

the home scrape is and by recognizing the adult's voice. Although I think Sooty Tern adults and chicks do recognize each other individually, I believe that much of this recognition is done by the adult, while the chick may try to get food from almost any adult that comes near.

#### CHICK BEHAVIOR

Sooty Tern chicks can walk almost immediately after hatching and stand and beg for food within 4 hours. For the first few days they are closely brooded by one of the parents, the chick resting either between the parent's feet or crossways in front of them. At first they walk by half crouching with the body low and almost on the ground, but they soon walk upright like adults. After a disturbance these small chicks frequently end up in the wrong scrape. I often saw two small chicks under one adult that seemed to accept both of them. The extra chick eventually returned to its own scrape, usually when called by an adult. A common alarm response of these small chicks is to lie flat on the ground with the head and bill extended forward. Chicks apparently do this to avoid being pecked by adults, as adults peck and sometimes kill strange chicks that come close. Chicks 5 days old preened and voided with movements typical of adults.

For the first 2 weeks one adult nearly always stays at the scrape with the chick. During the 3rd week this attention gradually diminishes, and by the end of this week the chick is often alone. Chicks defend the scrape, pecking at and driving off other chicks and Brown Noddies that intrude.

Most chicks stay close to their scrape until they can fly, but older chicks that wander or are moved can find their way back to the scrape when displaced several hundred feet (Burckhalter, 1969). Chicks from scrapes close to the beach may sun and rest with adults in large flocks on the beaches during the day, and then disperse in late afternoon. Generally the chicks congregate just above water level and the adults assemble higher on the beach. Occasionally adults feed chicks in such flocks but usually chicks seem to return to their home scrape or some other nearby place to be fed.

I saw 6-week-old chicks jumping into the air and flapping their wings vigorously. I lack exact records of when they begin to fly, but one chick flew several hundred feet on 4 July and others were doing so within a week. If that chick had hatched from one of the eggs laid on 1 April (it was in that part of the colony), it would have been about 9 weeks old. In 1971 some chicks at Bush Key were flying at 8 weeks of age. One year chicks at Ascension were flying when about 8 weeks old and the next year, when food apparently was scarce, birds around 9 weeks old still could not fly (Ashmole, 1963). Burckhalter (1969) saw 8-week-old chicks flying on the Hawaiian Islands, but they stayed at the island another 2 to 3 weeks.

Most of the chick's activities before it starts flying seem to be related to feeding and temperature maintenance. Obviously the adults help with the latter when the chicks are small, but 3- to 4-week-old chicks start assuming their juvenal plumage and are largely independent. When placed

in open sunlight, their body temperatures rise to the lower range of black-bulb temperature and then level off (Howell and Bartholomew, 1962). Chicks may help stabilize body temperature by panting, facing away from the sun, drooping the wings, and erecting the back feathers, much as adults do when it is hot. A few of my tethered chicks died in open sun when about this age, apparently from heat stress. Thus body temperature must closely approach lethality when chicks are exposed to open sun.

Juveniles seem to leave the colony soon after they learn to fly, as there seldom are many flying juveniles at Bush Key at any given time. As they do not feed near Bush Key, little is known of their activities. In all probability, the adults stay with the young and continue to feed it until it can capture food by itself (Robertson, 1964; Burckhalter, 1969) as do adult Royal Terns and other terns (Ashmole and Tovar, 1968). Bush Key adults cannot feed flying Sooty Tern young more than about 2 months, as all juveniles leave the range of adults by mid-October and some have done so by early August (Robertson, 1969). This certainly must be a difficult time for young Sooties, as they must learn to capture food while on the wing, a skill requiring good eyesight, coordination, and timing. Perhaps the long fledgling period of Sooty Terns in comparison to those of coastal terns (see Table 7) is an adaptation to compensate for the reduced period of time when adults can care for the young.

#### OTHER AERIAL ACTIVITIES

##### THERMAL SOARING

Sooty Terns at Bush Key commonly soar in dense circling columns during midday hours on hot days. Possibly at these times updrafts or thermals develop near Bush Key. The columns approach 200 feet in diameter and may go as high as 1,000 feet in altitude, although most birds are usually below 200 feet. Within the columns the birds circle as they climb and may then soar off to join another column. Most common late in the breeding season, these columns of soaring birds are taller and the birds appear to fly faster than in the flocks seen as the colony forms. Usually the terns are silent as they soar but occasionally one gives a "wid-ik" call.

Soaring often continues for several hours, although the composition of the flock changes continually and birds join or leave it. The columns often move laterally and two may merge into a single column. Magnificent Frigatebirds (*Fregata magnificens*) and occasionally Brown Pelicans (*Pelecanus occidentalis*) and Laughing Gulls (*Larus atricilla*) (Harrington, pers. comm.) join these flocks, but I did not see Brown Noddies do so.

##### FLY-UPS

A rather common activity in Sooty Tern colonies, especially when chicks are present, is for one or more adults to fly straight up 1 to 5 or more feet, give a loud "wide-a-wake" call at the peak, and drop back to the

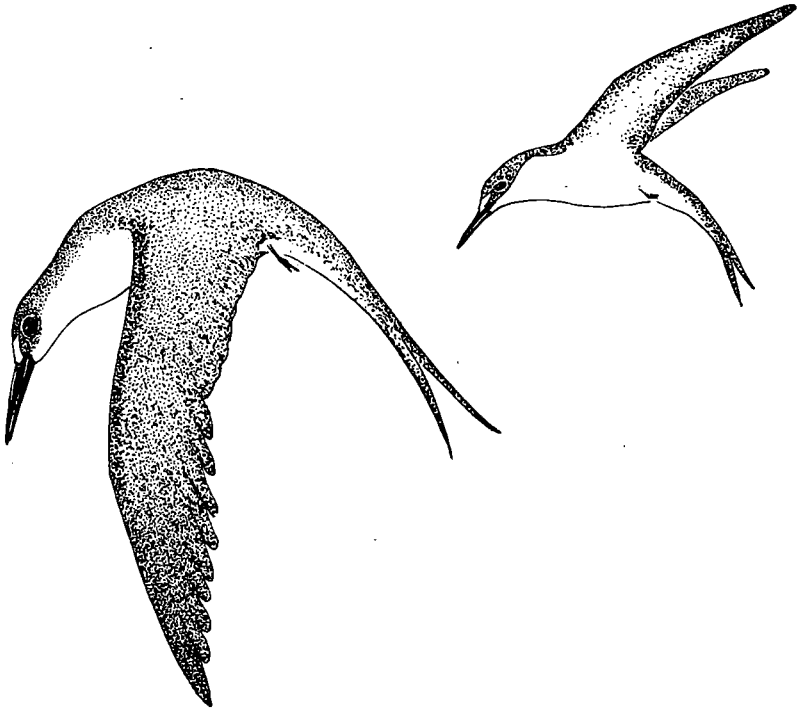


FIGURE 8. A fly-up by Sooty Terns. Just after the peak the birds have the somewhat humpbacked appearance shown here. (From drawing by Brian Harrington)

ground (Figure 8). I call these flights "fly-ups", and I believe they are a type of social behavior, often used in greeting. Besides the birds that actually fly, other birds around them often raise their wings vertically over the body in a flight intention movement, but do not fly. These fly-ups usually involve a small group of terns. During a fly-up, other nearby birds become very active and noisy for 15 to 60 seconds and then gradually quiet down.

The few fly-ups I saw during incubation usually occurred when an adult arrived at the colony to assume care of the egg. Other adults near the arriving tern's scrape might fly up, seemingly in excitement over the arrival of another bird at the colony. Burckhalter (1969) also reports this group activity when an adult arrived at the colony.

Once the chicks were present, I often saw fly-ups when an adult landed to feed a chick or had started feeding it. Again several adults flew up in the air in a sudden burst of activity and then quieted down.

Fly-ups were rather common when the chicks got fairly large. Then

I often saw adults fly up when a chick ran out from cover and approached them. As the chick approached, the adult usually flew up, called, and then landed to feed the chick. In these instances the chick seemed to stimulate the fly-up. Several times I saw a chick run past several adults, each one flying up in turn as the chick approached, until the chick finally came up to an adult that fed it. Thus the adults seemed to react as if the chick were their own while the chick went by and approached another adult, presumably its parent, to be fed.

#### PANICS

Sooty Terns exhibit two distinct types of disturbance flights, commonly called panics. Of these, dreads apparently include the flights Palmer (1941) calls dreads and panics for Common Terns while those termed alarms are similar in both species.

**ALARMS.**—When an intruder openly approaches the colony, the birds stand upright with the neck and head stretched vertically. As the intruder comes closer they fly, calling as they do so, and then circle and hover over the intruder until it leaves the vicinity of the scrape. Unlike many other terns, Sooties seldom actually strike an intruder, but rather hover near it or dive at it without striking it. I did see Sooties attack Cattle Egrets (*Bubulcus ibis*) and once a Purple Gallinule (*Porphyryla martinica*) that had broken a tern egg.

A loud, long alarm call, usually a downward inflected "kee aa" or "kerr aa" often precedes the alarms. Most alarms are quite local, involving relatively few birds in the colony. Occasionally though, they spread throughout the colony and virtually all of the terns fly. Alarms seem to start from an intrusion that is not sudden, but anticipated for a short time. The circling and calling by Sooties during rain are probably just a form of the alarm. Other disturbances are caused by less tangible factors such as a loud sound (e.g., sonic boom, boat whistle) or a sudden movement. These elicited a different response — the dread.

**DREADS.**— In dreads the terns suddenly become silent and fly rapidly from the colony to the water, darting and swooping as a unit silently down low over the water. At the end of the swoop, they rise up, start calling loudly, and gradually drift back to the colony. Thus if a bird is on the ground when the dread starts, it flies rapidly out over the water, and those birds that are already in the air suddenly swoop out over the water. This seems to be a high intensity form of panic.

One final, poorly defined alarm reaction is that in which virtually the entire colony flies up from the ground, either at once or, more often, in a gradually spreading group from one end of the island to the other. In the air the birds call loudly and drift out over the water and then gradually move back to the colony. This delayed alarm seems to start as an alarm in one part of the colony, and as those birds fly, they scare up birds near them and so on until the whole colony is in the air.

Lind (1963) suggests that in Sandwich Terns these disturbance flights

may have several functions, including synchronizing reproductive behavior, but I have no evidence of this for Sooty Terns.

### INTERACTIONS WITH OTHER SPECIES

#### PREDATORS

The isolation of most islands where Sooty Terns nest means that they come in contact with few vertebrate predators. Probably the most serious predator of adult Sooties at Bush Key is the Peregrine Falcon (*Falco peregrinus*). In 1968 I saw a peregrine swoop at Sooty Terns 23 times without capturing a bird, but I did find the decapitated remains of four Sooties that the falcon almost certainly had killed.

At the Tortugas several other bird and animal species prey on the eggs and young of Sooties. I have seen both Ruddy Turnstones (*Arenaria interpres*) and a Purple Gallinule break and eat eggs, and the former has done so elsewhere (Ridley and Percy, 1958; Crossin and Huber, 1970). Rats are also known to take Sooty Tern eggs and chicks (Russell, 1938; Kepler, 1967).

Frigatebirds are perhaps the greatest threat to Sooty Tern chicks. At the Dry Tortugas Magnificent Frigatebirds have taken many chicks some years (Beard, 1939; Sprunt, 1948) while in 1968 I saw only one chick taken. When frigatebirds do prey on tern chicks, it seems to be a prey preference of only a few individuals rather than of all the frigatebirds present (Robertson, pers. comm.). Ashmole (1963) reports *Fregata aquila* taking many young Sooty Terns on Ascension Island, and *F. minor* does the same on Christmas Island (Ashmole and Ashmole, 1967).

On the Dry Tortugas migrating Cattle Egrets experience an extreme shortage of food and feed on almost anything they can find including an occasional Sooty Tern egg or chick (Robertson, pers. comm.) as well as fish dropped by the terns. Cattle Egret predation on Sooty Tern eggs and chicks is also known at the Seychelles (Ridley and Percy, 1958). The Great White Heron (*Ardea occidentalis*) also has been reported preying on Sooty Terns at the Tortugas (Robertson, 1962).

More commonly the Cattle Egrets forage on insects on Bush Key and in doing so disturb the adult terns from their care of their egg or chick, an activity that can be fatal to the offspring. Typically as an egret approaches a tern with an egg or chick, the tern faces the egret and gives a series of low, hoarse "wuk wuk" notes. As the egret comes closer the tern rises up off its egg or chick, erects the crown feathers, and continues to direct "wuk" calls at the egret, the calls becoming louder and more rapid and often changing to rapid "ka ka ak" calls. If the egret comes within a few feet of the tern, the tern flies from the scrape and circles over the egret until it departs. A few times a tern stretched its head and bill forward, raised the wings almost vertically, and ran at the egret.

Cattle Egrets often fly low over nesting terns, eliciting a long,

drawn out "kaaa" note from the terns and sometimes starting a panic. The Sooties often chase egrets in the air and dive at them, mobbing them more commonly in flight than when the egret is on the ground. Brown Noddies frequently join the Sooties in these attacks on Cattle Egrets and the Noddies are much more aggressive, striking them on the ground and in the air, and chasing them farther than the Sooties do.

A few Herring (*Larus argentatus*), Ring-billed (*L. delawarensis*), and Laughing Gulls frequently linger around Bush Key. I never saw one enter the Bush Key colony to prey on tern chicks or eggs, although they could do so easily. Watson and Lashley (1915) saw Laughing Gulls prey on Sooties at the Tortugas.

Adult Sooties often peck and kill chicks that wander onto their scrape and can be a serious cause of mortality.

Despite the isolation of most Sooty Tern colonies, humans still collect eggs for food at some of them (Cott, 1954; Ridley and Percy, 1958), but National Park Service protection eliminated eggging at Bush Key after 1935.

I could not help disturbing the birds every time I entered or left my blind. Although they soon habituated to this and rapidly returned to the scrape once I was out of sight, I occasionally stepped on eggs or separated chicks from their parents. Such mortality is inevitable whenever a human works extensively in a Sooty Tern colony.

Disturbances such as sonic booms, boat whistles, and low flying airplanes may cause the birds suddenly to leave the island in a dread. However I did not see any of these disturbances keep the birds away from their scrape for more than a few minutes unless they were repeated.

#### OTHER TERNS

Sooty Terns and Brown Noddies are abundant and widespread in the tropics and nest together on many islands. On Bush Key the Brown Noddies nest primarily along the edge of the bay cedar, but also in other low vegetation and occasionally on the ground. Although some Sooties nest under the bay cedar, they always nest on the ground and hence are usually vertically segregated from the Noddy nests. Most Sooties nest in the open flat parts of the island outside the bay cedar, again separating them from the Noddies. Some Noddies nest in low vegetation within inches of Sooty scrapes. I often saw young of both species in such situations, so apparently they can breed successfully in close proximity.

Early in the nesting season Noddies often searched for nest material on my study plot. In all 35 instances of direct supplanting between these species that I saw on my study plot, the Sooty drove off the Noddy. In two of these a Sooty chick drove an adult Noddy off the plot. Generally the Sooty stretched its head and neck forward, held the wings either tight against its sides or slightly away from the body, and advanced toward the Noddy until the Noddy retreated or flew. I never saw a Noddy fight back or withstand the attack long. Once I heard a Sooty give a low



growling "urr" note as it advanced at a Noddy but usually both were silent. The few times I watched for the reverse encounters, I saw Noddies drive off Sooties that had come close to Noddy nests.

Noddies arrive at Bush Key at about the same time as Sooties, but start work on their nest almost at once instead of having a pronounced flocking period as Sooties do. In 1968 Noddies started laying somewhat after Sooties (10 April) and as their incubation period is longer than the Sooties (35 to 36 days, Thompson, 1903), Noddy eggs hatched later than the Sooty eggs. Young Noddies mature faster than Sooties and many were flying by late June, well before most Sooty chicks.

Both species forage in a similar manner, dipping down to capture food at the ocean's surface, although Noddies occasionally plunge to the surface or rest on the water to capture food. The Ashmoles (1967) show that Sooties and Brown Noddies have very similar diets on Christmas Island, but the Brown Noddies seem to forage much closer to the island. They suggest that the wing of the Brown Noddy, broader than that of Sooties, perhaps gives it greater maneuverability and allows it to forage more efficiently near the island, whereas the narrower wing of Sooties enables them to forage farther from their colonies.

At the Tortugas Noddies often forage within sight of Garden Key, dipping down and capturing food at the sea surface. The incubation shifts (30 minutes to 5 hours) and to some extent the intervals between feeding their chick (2 to 4 hours) (Watson, 1908), are shorter for the Noddy than for the Sooties. The fact that Sooties seldom forage within sight of Bush Key and the somewhat shorter foraging times of Sooties, especially during incubation, suggest that the two terns forage in somewhat different waters. The two species apparently forage in different zones at colonies in the Pacific and Indian Oceans (Ashmole and Ashmole, 1967; 65-66; King, 1970).

In recent years the few hundred Roseate Terns at the Dry Tortugas have nested in the coral rubble on Long Key and on the open sand on some of the other islands, habitat quite different from that the Sooties use. When they have nested on Bush Key, it usually has been at the far east end away from most Sooties. Roseates usually arrive later than Sooties and in 1968 did not start nesting until mid-May when Sooty eggs were hatching. The incubation and fledging periods of Roseates are much shorter than those of Sooties, so young Roseate Terns were flying well before any Sooty Tern chicks. Roseate Terns often forage within sight of Bush Key and probably avoid competition with Sooties by foraging in different areas. They dive from the air and plunge into the water, thus capturing food that is unavailable to the Sooties.

## SITE TENACITY

Common Terns have been shown to have a tendency to return to the same nest site year after year (Austin, 1949). Later sightings of the 182 Sooties I color-banded on my small study plot on Bush Key in 1968, provide some information on the species' site tenacity. I later saw 106 of the 182 (58.2 percent) in the general area of banding, and most of them probably nested in that general part of the colony.

From 28 April to 2 May 1970, O. L. Austin, Jr. sat near the plot for several hours each day to watch for and record color-banded birds. He saw at least 100 birds with color bands on the plot or immediately adjacent to it. I saw three more in June and July, and four others were caught in other parts of Bush Key. Of the 103 birds on the plot, 73 could be identified individually; the others had lost some of the bands and were not caught to read the FWS band. Of the 73 individually recognizable Sooties, 53 (72.6 percent) were among the 106 that had been seen on the plot in 1968 after banding. Thus, of 106 color-marked birds that probably nested on or near the study plot in 1968, at least half of them (53 of 106) were on the same plot 2 years later. The 30 birds that could not be identified individually in 1970 may well have included birds that nested on the plot in 1968. Thus 50 percent is a minimum figure and perhaps 70 percent is a more meaningful estimate of site tenacity. These data suggest that individual birds had a strong tendency to nest in the same parts of Bush Key in 1968 and 1970. As my plot and the ground immediately around it covered much less than 1 percent of the habitat suitable for Sooties on Bush Key, it seems unlikely that so many color-banded birds would return to this same area in 1970 by chance alone.

In early July 1971 I spent a few hours watching for color-banded birds on my plot and saw at least 13 different individuals. Many of these had lost one or more color bands. Of eight that were individually recognizable, seven probably had nested on the plot in 1968, again suggesting that the terns were returning to the same plot to nest.

Site tenacity implies individual attachment to a specific locale in the colony. Group adherence implies that subgroups exist within the colony and these subgroups stay together and individually recognize other members of the group. Austin (1951) describes such subgroups in Common Terns and they may well exist in Sooty Tern colonies. Young Sooties, if not allowed to return to their scrape, establish a spatial arrangement with respect to other chicks similar to the pattern that existed when they were at the home scrape (Burckhalter, 1969). This implies that they recognize other chicks around them and act as a group.

The fly-ups already described also suggest that subgroups exist in Sooty colonies. In these, adjacent birds react to the activities of one bird, seemingly as if they recognized one another.

Subgroups that stay together within the colony could also explain the clustered nesting of color-banded birds seen at the plot in 1970, but

this implies a fairly sizable group of perhaps several hundred birds functioning as a subgroup. Although I definitely think subgroups exist in Sooty colonies, site tenacity remains the more likely explanation for birds nesting in the same general part of the colony in successive years. If individuals repeatedly nest in the same part of the colony, they would of necessity contact the same birds year after year and then possibly form subgroups.

## DISCUSSION

Two broader aspects of Sooty Tern behavior are particularly important and warrant further discussion. First is the comparison of the behavioral repertoire of *fuscata* to that of other species of terns, especially those within the genus *Sterna*. This should clarify the affinities Sooties have with other terns. Fortunately several other terns have been studied carefully enough to provide a basis for comparison.

Equally important are the adaptations of *fuscata* that have allowed it to survive and thrive in a pelagic environment. By feeding in pelagic waters, Sooties differ considerably from most other terns and in many ways closely resemble pelagic species of birds in other orders such as the Procellariiformes.

## BEHAVIORAL COMPARISONS

Behavioral comparisons can be made with several other temperate *Sterna* terns, the White Tern (*Gygis alba*), the two *Anous*, several species of *Thalasseus*, the Black Tern (*Chlidonias niger*) and the Whiskered Tern (*C. hybrida*).

The high flights of the Common, Arctic, Roseate, and Sandwich Terns are all quite similar (Cullen, 1960a). The high flights of the Caspian Tern, Black Tern, and Whiskered Tern resemble those of the others, although in the latter two many birds may ascend together (Swift, 1960). The circling ascent and gliding descent of the Sooty Tern high flight are almost identical to those of the Common and Arctic Tern described by Cullen (1960a). In the high flight of the Brown Noddy the ascent is somewhat like the upward flutter of Sooties, but the birds descend in a circling glide rather than a long, essentially straight glide as the *Sterna* terns do (Moynihan, 1962; pers. obs.). The high flight of *Gygis* is similar to that of the dark Noddies (Moynihan, 1962).

The low flight is poorly developed in *fuscata* and not nearly so common as in other terns except *Gygis* (Dorward, 1963). Cullen (1960a) notes that the low flight has fewer special features and may have developed independently in each species. The rarity of the low flight by Sooties may be due to their different manner of carrying food. Cullen (1960a) notes

that food has little importance in advertising by unmated birds of both species of *Anous*, both of which carry food in the esophagus as Sooties do.

Perhaps carrying food in the esophagus allows Sooties to transport more food (Ashmole and Ashmole, 1967) than if they carried it in the bill. Also it may prevent food desiccation during the often lengthy return flight to the colony. The food is the major water source for the chicks, so moist food may be necessary for the chick's survival. Moist food should be easier to handle and swallow than dried-out food. Besides Sooties, *S. anaethetus* and both *Anous* carry fish in their esophagus.

The ground displays of Sooties are similar to those reported for other *Sterna* terns, all having some form of a parade display. In particular the parade of Sooties seems to resemble that of the Common Tern described by Palmer (1941) Incipient scrape-building activities are part of courtship in Sooties, just as they are in Common Terns.

The most conspicuous ground display of the dark Noddies is nodding, and generally their behavior is gull-like (Moynihan, 1962). Nodding emphasizes head movements, whereas the parade emphasizes the position of the wings and head, providing a clear contrast between the Noddies and the *Sterna* terns. The displays of *Gygis* are similar to those of the dark Noddies (Moynihan, 1962).

Comparisons of behavior help clarify the relationships of various terns. Moynihan (1959) used comparative behavior as a basis for classifying the Laridae and put all terns into three genera. *Larosterna* remains monotypic, *Anous* includes *Gygis* and *Procelsterna*, and the rest are placed in *Sterna*. I prefer the older terminology retaining numerous genera, but nonetheless agree with the group limits he has established on the basis of behavior. In Moynihan's classification, the typical black-capped terns include *fuscata*, *hirundo*, *paradisaea*, and others. He puts the large *Thalasseus* terns and the small *Sterna* terns like *albifrons* in separate groups within his large genus *Sterna* and also keeps the marsh terns (*Chlidonias*) together as a separate group within *Sterna*.

This grouping agrees well with my observations. The high flight of *fuscata* is almost identical to that of *hirundo* and *paradisaea*. The ground displays of *fuscata* are very similar to those of *hirundo*, and on behavioral grounds the two species clearly are closely related. In contrast the displays of *Gygis* and both species of *Anous*, three species that share the tropical oceans with Sooties, are clearly different from those of Sooties.

Moynihan (1959) points out, and I agree, that a most profitable area for future work is with the many Old World and tropical forms that are only slightly known. Two other tropical terns, *Sterna lunata* and *anaethetus*, resemble *fuscata* in their feeding habits and probably their breeding biology, although they may feed closer to the breeding colony than does *fuscata*. As yet these two are poorly known and further work on them certainly would be of interest.

### SOOTY TERNS AS A PELAGIC SPECIES

Of the 40 species of terns (Sterninae), most feed either on fresh-water marshes, lakes, and streams, or along marine coasts and estuaries. A few venture into offshore waters on continental shelves or near islands, especially in the nonbreeding season. Sooty Terns seem to be the most pelagic (beyond the continental shelf) of terns, although several other *Sterna*, both species of *Anous*, and *Gygis* feed in offshore and pelagic waters. Apparently by exploiting pelagic waters and breeding on isolated islands, Sooty Terns utilize a niche available to few other species. Several features of Sooty Terns deserve further comment in this regard.

One of the most puzzling facts about Sooty Terns is that they rapidly become waterlogged when placed on water (Watson and Lashley, 1915) and apparently seldom rest on water. As Sooties inhabit the open oceans during the nonbreeding season, birds from some colonies must fly continuously for 6 months or more. Virtually nothing is known of the physiological adaptations involved in flying for such long periods. For example, do they sleep on the wing as the Swift (*Apus apus*) apparently does (Lack, 1956), or do they go without any sleep at all? Perhaps Sooty Terns have some morphological adaptation that allows them to fly better than coastal terns, but as yet this remains another unstudied aspect of Sooty Tern biology.

Being able to feed without landing in the water certainly enhances the ability of a nonswimming bird to range far from land. Thus Sooties can exploit food in a large area far from land, reached by few other birds. Several factors restrict Sooty Tern food availability. Except for some areas where upwellings or convergences occur, tropical pelagic waters are poor in nutrients and the plankton that form the base of their food chain (Raymont, 1963). Sooties apparently are restricted to feeding on food items that occur at the very surface of the ocean, or in the air immediately above it. This food is driven to the surface mainly by large predacious fish (Ashmole and Ashmole, 1967: 58) and thus is not evenly distributed throughout the ocean.

The length of incubation shifts and brooding spells varies considerably between different Sooty Tern colonies. Adults usually shift at 1 or 2 day intervals on Bush Key whereas they vary from 2 hours to 3 days in the Seychelles (Ridley and Percy, 1958), and are as long as 6.5 days on Ascension Island (Ashmole, 1963), and 7 days on Christmas Island (Ashmole and Ashmole, 1967). The duration of the shift must depend somewhat on the time required to fly to the feeding ground, find enough food to last until the adult can feed again, and then return to the colony. The most reasonable explanation for the great variation between colonies in time spent foraging is that food is farther away or scarcer for some colonies than others.

More puzzling is the change in length of brooding spells once the

TABLE 7. COMPARATIVE BREEDING BIOLOGY OF SEVERAL SPECIES OF TERNS

Species	Feeding habitat	Usual Clutch size	Incubation period <sup>1</sup>	Fledging period <sup>1</sup>	Food carried exposed?	Reference
Black Tern	Marsh	2—3	20—22	20—24	Yes	Goodwin, 1960
Common Tern	Coastal	2—4	21—26	30	Yes	Palmer, 1941
Sooty Tern	Pelagic	1	29—30	55—60	No	This study
Least Tern	Coastal	2—4	19—22	28	Yes	Witherby et al., 1941; Hardy, 1957
Sandwich Tern	Coastal	1—2	20—24	35	Yes	Witherby et al., 1941
Brown Noddy	Offshore, pelagic	1	35—36	42 +	No	Thompson, 1903; Dorward and Ashmole, 1963
White Tern	Offshore, pelagic	1	36	60—95	Yes <sup>2</sup>	Dorward, 1963; Ashmole, 1968

<sup>1</sup> In days<sup>2</sup> Also carries food in esophagus

egg hatches and the chick must be fed. At Ascension Island adults change from 5.5-day-incubation shifts to feeding their chick about once a day (Ashmole, 1963), but detailed information on the rate of feeding is lacking. As the breeding cycle at that colony is nonannual (9.5 months), it seems unlikely that a regular change in food abundance could occur and thus account for the differences in foraging between incubation and fledging periods. On Bush Key adults change from 1- or 2-day incubation shifts to feeding the chick several times a day. As the breeding cycle there is annual, perhaps food is more plentiful, closer to the island, or the adults forage more diligently when chicks are present. The meager evidence available indicates that terns do not tend to capture smaller fish when they are feeding chicks as might be expected (Potthoff and Richards, 1970) but little is known about the food supply. However the many terns loafing on the beaches and soaring in flocks during the time when chicks are being fed suggest that food supply is not limiting the adults' activities even in that crucial period.

Table 7 gives some information on the breeding biology of several representative tern species. I have selected one species each from the genera *Chlidonias*, *Thalasseus*, and *Anous* and three from *Sterna*, picking species for which information is available and that seem to be representative of other similar species. This table is similar to one in Lack (1968: 262). Clutch size or other aspects of the breeding biology of a species may vary from colony to colony and from year to year within a colony, but this does not negate the comparisons to be made here. The purpose of the table is to try to compare some general features of the breeding biology of marsh and coastal feeding terns with those that feed offshore or pelagically.

On Bush Key, as at other Sooty Tern colonies, a scrape occasionally contains two eggs, but by far the usual clutch is one egg. Single egg clutches are common among marine birds (Lack, 1968) and seem to imply that something about the oceanic habitat limits their clutch size.

In contrast, coastal and freshwater feeding terns commonly lay more than one egg (Table 7). Besides *fuscata*, only *Anous*, *Gygis*, and a few other *Sterna* terns (e.g. *S. anaethetus* and *lunata*) have a usual clutch of one. A clutch of two or more presumably is the ancestral condition in Sooties and Brown Noddies, as they both have two brood patches. *Gygis* lays one egg and has only a single brood patch, but its unusual nesting habits may explain this (Dorward, 1963).

With the smaller clutch size, pelagic terns must have either a high nesting success, a long life span, or some combination of the two to maintain their populations. With a clutch of one, partial nesting success does not exist. Pairs either fledge an offspring or they fail. Among Sooties, a maximum of 50 percent may renest if the first attempt fails, and the percentage declines as the breeding season advances (Ridley and Percy, 1958; Ashmole, 1963).

The single egg of *fuscata* is incubated longer and the chick is cared

for longer than are those of inshore feeding terns (Table 7). As storms and a distant food supply may prevent Sooty Tern chicks from being fed at regular intervals, a lengthened period of development perhaps allows them to withstand occasional short periods of fasting (Lack, 1968). Chicks grow rapidly when food is available, but can survive long periods without food if the adults cannot find any for several days (Ashmole, 1963).

Feeding rates also differ between Sooties and coastal feeding terns. The latter generally forage close to their colony and, although they may raise more than one chick, they feed their young frequently. On the Farne Islands, Common, Arctic, and Sandwich Terns all feed each of their young about once an hour (Pearson, 1968) and Black Terns feed young as often as 15 times in an hour (Goodwin, 1960). As a result their young mature much faster than do young Sooties. The differences between Sooties and Noddies, both of which raise one chick per pair, have already been discussed. Noddies seem to forage closer to the colony, feed their young somewhat more frequently, and their young mature faster than those of the farther ranging Sooties (Table 7).

As has already been suggested, perhaps the longer pre fledging period of Sooty Terns produces relatively well-developed young that are better able to survive once they leave the island, even without a lengthened period of care by their parents, while shore tern young fledge rapidly but then depend on a subsequent period of care by their parents.

An important factor favoring the slow development of young Sooties is the scarcity of predators on their breeding islands. They can "afford" long incubation and fledging periods without drastically raising the risk of predation. Common and Least Terns nesting on or close to the mainland are constantly exposed to predation (Austin, 1948; Hardy, 1957) so it is probably advantageous for them to raise their young as quickly as possible. In turn rapid growth of their young is made possible by a food source close to the colony that permits more feeding trips in a day. Cat predation on Ascension Island shows vividly what can happen to seabirds, including Sooties, when a land predator is introduced (Stonehouse, 1962; Ashmole, 1963).

Sooty Terns defecate near their egg, do not always remove the empty egg shell, and nest in dense colonies. These habits seem related to the isolated and usually land-mammal-free islands where they nest. Sandwich Terns have similar habits, but frequently nest with gulls that help drive off intruders (Cullen, 1960b; Lind, 1963). In contrast, Arctic and Common Terns carry off the empty egg shell, defecate away from the nest, space their nests farther apart, and vigorously attack intruders, all of which should help reduce predation. Common and Arctic Terns also have much shorter incubation and fledging periods than Sooties, again reducing the time they are vulnerable to predation.

Sooty Terns probably do not first breed until 6 years old (Robertson, 1969). In contrast most Common Terns first breed when 3 or 4 years old and about 70 percent of their breeding population is made up of birds 6



years old or younger (Austin and Austin, 1956). Thus a cohort of Common Terns is probably past its peak in the breeding population before the equivalent cohort of Sooty Terns begins to breed. Deferred maturity occurs in many other seabirds, including many Larids (Lack, 1968). Robertson (1969) suggests that the transatlantic migration by juvenile Sooties from Bush Key, a colony relatively stable in numbers, keeps them from competing with older and presumably more efficient breeders for several years. The 3-year-old birds that visit Bush Key late in the breeding season have little chance of finding a suitable nest site and breeding successfully. By returning to the colony earlier in successive years, eventually they should be able to arrive early enough to find a suitable nest site and breed successfully. Thus deferred maturity keeps younger birds from competing with older, established breeders for nest sites, and also keeps the younger birds from undergoing the rigors of reproduction until they have a fairly high probability of success. The Fishers (1969) note a staggered arrival of age groups of Laysan Albatrosses, with the young birds not breeding for several years.

For deferred maturity to persist, individuals with such maturity must raise more offspring in the long run than if they first bred when younger. As one 32-year-old Sooty Tern is known to have bred on Bush Key (Robertson, pers. comm.), the adults there clearly have many breeding opportunities. Still Sooty Terns, by delaying breeding for several years and then by raising at most a single young per breeding season, have a lower maximum natality than other similar terns that feed close to their colony.

Lack (1968) proposes that birds raise as many offspring as possible with the usual clutch size being that that results in the most breeding adults in the next generation. Sooty Terns with a clutch size of one cannot raise more than one young per breeding season. Presumably the limiting factor is their distant and sometimes unreliable food supply.

Certainly the hypothesis fits the information from Ascension Island where an apparent failure of the food supply one season resulted in few chicks surviving (Ashmole, 1963). This and the long spells that Ascension adults spend foraging suggest that at most a pair could raise one chick. Other colonies that have been studied have not had such failures.

Except for the cats on Ascension Island, adult Sooty Terns suffer little predation and have a low annual adult mortality; perhaps around 12 to 18 percent at Bush Key (Austin, pers. comm.) versus 25 percent in adult Common Terns (Austin and Austin, 1956). The Austins' figures may have been influenced by band loss, as Grosskopf (1964) reports adult mortality in European *hirundo* as about 19 percent. Although the food supply may limit the number of young they can raise and hence determine the usual clutch size of Sooty Terns, perhaps deferred maturity is a function of the low predation on and high survivorship of the adults. High survivorship of adults could result in many birds competing for a limited

number of nest sites, but deferred maturity could reduce this competition as has already been discussed.

Some pelagic species can raise more than one young (see Harris, 1970), suggesting that food is not entirely limiting, but so far the problem has been following the survival of these "twins" until they return to breed.

Thus Sooty Terns differ from most other terns. Many of these differences derive from their adaptations to a pelagic environment. The basic behavioral patterns in pair formation and courtship show clearly that Sooties are closely related to typical *Sterna* terns such as *hirundo*.

I believe several behavioral differences between Sooties and most other species of *Sterna* are due to their different ways of carrying food. Sooties do not have a well-developed low flight display, a display in which other terns often carry a fish prominently in their bill. Other terns also may carry a fish openly in the bill during the high flight while Sooties do not, although they do have a well-developed high flight.

The high cost of obtaining food, compared to that of coastal feeding terns, perhaps explains why courtship feeding is relatively rare in Sooty Terns. A coastal feeding tern can easily replace the food it feeds to another bird in courtship. For a Sooty Tern, replacement might require a long flight. I have no information as to whether courtship feeding is important in providing food resources for the female prior to egg-laying. I had too few birds marked to obtain good information on whether she spends some time away from the colony prior to egg-laying, but it is possible that she does so and thus is not dependent on food from the male.

Comparison of the breeding biology of Sooties and coastal feeding terns shows other differences. The development of the Sooty Tern egg and chick is much slower than that of most other terns, perhaps so their young can survive lengthy periods when the parents are unable to find food. The high survivorship of adults and the distant food supply have led to their delayed maturity and small clutch size.

Thus in their breeding biology, with a long incubation and fledging period, deferred maturity, and a 1-egg-clutch, Sooty Terns resemble other pelagic birds such as the albatrosses, shearwaters, and tropicbirds more closely than most other terns.

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