

# EFFECT OF EXPERIMENTAL MANIPULATION OF VEGETATION DENSITY ON NEST-SITE SELECTION IN SOOTY TERNS<sup>1</sup>

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*Abstract.* We examined nest-site selection in Sooty Terns (*Sterna fuscata*) in two colonies of the Culebra Archipelago, Puerto Rico, using an experimental design to manipulate vegetation density. In 1986 Sooty Terns did not nest in six experimentally cleared plots (0% vegetation cover). In 1987 they did not use an additional cleared plot, but used the experimental plots from 1986 which had revegetated (25%–75% vegetation cover). Compared with random points, Sooty Terns selected nest sites with taller vegetation (with respect to total vegetation height, and height to canopy), with more cover directly above the nest, and that were farther from open areas. A worldwide comparison of habitat preferences and predation across islands where Sooty Terns nest revealed that on most islands Sooty Terns prefer to nest in open areas even when vegetation is available. The preference for nesting under vegetation at Culebra seems to be related to the degree of predation, and the presence of predator species which prey upon eggs, young, and adult Sooty Terns.

*Key words:* Habitat preference; nest-site selection; vegetation density; nest concealment; Sooty Tern; *Sterna fuscata*; Culebra; vegetation manipulation; predation.

## INTRODUCTION

The choice of a nest site is of prime importance to breeding birds because it directly affects the survival of offspring, and must therefore be under strong selective pressure (Hilden 1965, Smith 1974, Buckley and Buckley 1980, Burger 1987). Individuals placing nests in optimal microhabitats are more successful in fledging young than individuals choosing less suitable locations (Gochfeld 1978, Yahner 1983). Thus, birds that prefer habitats in which adverse factors are minimal, such as predation or inclement weather conditions, are selected for (Gibo et al. 1974, Bekoff et al. 1987).

Many marine birds regularly nest in large colonies on offshore islands which are free from terrestrial predators, but that offer little or no vegetation cover (Carter et al. 1984). In many inaccessible islands, the nesting birds are exposed to aerial predators which may cause varying degrees of damage to the breeding colony (Kruuk 1964, Lack 1968, Burger and Gochfeld 1981, Jehl and Mahoney 1987).

Vegetation may be important to some seabirds because it provides protection from predators and extreme weather conditions (Wray and Whitmore 1979, Burger and Gochfeld 1986).

Burger and Gochfeld (1981) showed that Kelp Gulls (*Larus dominicanus*) do not nest randomly with respect to the available habitat, but prefer to nest in flat, stable areas with some cover (rocks or vegetation). Nesting adults generally avoided heavily vegetated areas, areas devoid of vegetation, and areas with steep slopes; their habitat choices seemed to be related to predation and cannibalism pressure. Martin and Roper (1988) found that for the Audubon's Hermit Thrush (*Catharus guttatus auduboni*), nest concealment (vegetation density) was significantly greater at low predation nests than at high predation nests. They suggested that foliage density in the nest patch may impede nest discovery by inhibiting the transmission of chemical, auditory, or visual cues to potential predators. Whereas the importance of habitat characteristics on nest-site selection in birds has been investigated (Burger and Gochfeld 1986, Martin and Roper 1988), the preference for specific vegetation cover has not been examined experimentally.

One way to determine the importance of habitat characteristics to birds is to conduct experiments where habitat features are manipulated, and then monitor the responses of individuals to the manipulation (Wiens 1985, Gochfeld and Burger 1987). The Sooty Tern (*Sterna fuscata*) is a widely studied seabird that nests in remote islands usually on areas of exposed sand, coral rubble, or rocks with little or no vegetation cover

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(Sprunt 1948, Chapin 1954, Ashmole 1963, Harrington 1974, Feare 1976). In areas where vegetation has subsequently grown, the terns seem to avoid the vegetated parts and concentrate on the exposed soil (Watson 1908, Chapin 1954, Feare 1976). In the Culebra Archipelago, however, Sooty Terns nest under very dense vegetation cover. The objectives of our study were: (1) to describe qualitatively and quantitatively the nest sites selected by Sooty Terns in the Culebra Archipelago, and compare them to the available habitat, (2) to determine how single nest characteristics and combinations of characteristics play a role in the terns' choices of nest sites, and (3) to examine nest-site selection in Sooty Terns using an experimental design to manipulate vegetation density.

### STUDY AREA AND METHODS

Culebra is a hilly island 37 km east of Puerto Rico (18°19'N, 65°18'W) surrounded by 17 keys (Kepler and Kepler 1977). In the Culebra Archipelago, Sooty Terns nest on four offshore keys (Cayos Alcarraza, Molinos, Noroeste, and Yerba), and at the northwesternmost tip of Culebra Island itself (tip of Peninsula Flamenco). Two sites were selected: Cayo Yerba and the northwesternmost tip of Peninsula Flamenco. Cayo Yerba (11.6 ha) is a small tilted plain 2.35 km east of Culebra, and it is densely covered with sedge (*Cyperus planifolius*; Kepler and Kepler 1977). The tip of Peninsula Flamenco is a finger of land extending 305 m from the base of the main peninsula. It is covered with a mixture of plant species of which guinea grass (*Panicum maximum*), buttonwood (*Conocarpus erectus*), and sea grape (*Coccoloba uvifera*) are the main components. These two study sites were selected because (1) they were easily accessible, (2) larger numbers of terns nested there than elsewhere in Culebra, and (3) large areas of relatively homogeneous vegetation made them suitable for vegetation manipulation experiments.

Since open areas are scarce where Sooty Terns nest on Culebra, an experiment was designed to determine if the terns would prefer to nest in experimentally cleared areas if they were made available. In April 1986, before the arrival of the Sooty Terns, three experimental (devoid of vegetation) and three control (undisturbed) 4-m × 4-m plots were set up in each study site in areas approximately 32 m × 40 m. The plots were

monitored during the laying period in May and June (4 weeks) for the presence of nesting Sooty Terns. It was not possible to replicate the experiments due to the lack of suitable, homogeneous sites for experimental manipulation of the vegetation.

By 1987, the three experimental plots cleared in 1986 on Cayo Yerba had revegetated. Before the arrival of the terns, the vegetation in the three experimental plots was randomly removed to create plots with an estimated 25%, 50%, and 75% vegetation cover. An additional experimental plot and its control were added in which all vegetation was removed. Thus, in 1987, data were collected on nest-site characteristics from four experimental (0%, 25%, 50%, and 75% vegetation cover) and four control (100% vegetation cover) plots in Cayo Yerba. The plots in Peninsula Flamenco were not monitored in 1987 because of the great nest desertion and mortality of terns on that area in 1986.

Nest-site characteristics were measured between the peak of the laying and hatching periods in May and June 1987. The number of nests per plot was recorded, and for each nest the vegetation height, height to the canopy, percent vegetation cover directly above, orientation of nearest open path from nest, and distance to the nearest open path were measured. The orientation of the nearest open path from the nest was recorded with a Suunto MC-1 Mirror Compass. Percent cover directly above the nest was estimated visually from 1.5 m above each nest.

Twelve random points were located in each experimental and control plot using randomly selected x and y coordinates. The same habitat characteristics that were recorded for nests were recorded for the random points. By comparing the habitat characteristics of Sooty Tern nests in each experimental and control plot to random points, it is possible to determine which characteristics the terns prefer or avoid. If a characteristic varies similarly for nests and random points, then that characteristic is not preferred at that site (Burger and Gochfeld 1986).

Kruskal-Wallis tests with significance levels of  $P < 0.05$  were used to determine significant differences among means. Baschelet's (1965) parametric two-sample test applying the  $F$ -statistic was used to test for a difference in mean orientation between nests and random points, and between experimental and control plots.

TABLE 1. Placement of Sooty Tern nests in experimental (E) and control (C) plots in two areas of Culebra Archipelago.

Plot no.*	May 1986			May 1987	
	% Vegetation cover in plot	No. nests in plot	Nests at plot edge	% Vegetation cover in plot	No. nests in plot
Flamenco Peninsula					
01 (C)	100	4	0	—	—
02 (C)	100	6	0	—	—
03 (C)	100	1	0	—	—
04 (E)	0	0	0	—	—
05 (E)	0	0	4	—	—
06 (E)	0	0	0	—	—
Cayo Yerba					
07 (C)	100	14	0	100	16
08 (C)	100	16	0	100	8
09 (C)	100	7	0	100	11
14 (C)	—	—	—	100	5
10 (E)	0	0	0	25	26
11 (E)	0	0	0	75	19
12 (E)	0	0	0	50	13
13 (E)	—	—	—	0	0

\* Means and standard deviations for number of nests in control (C) and experimental (E) plots at Cayo Yerba in 1987 are  $11.65 \pm 4.04$ , and  $20.97 \pm 5.22$ , respectively ( $\chi^2 = 50.59$ ,  $P < 0.0001$ ).

## RESULTS

### NEST PLACEMENT

At the beginning and peak of the laying period in 1986, Sooty Terns did not nest in the three experimentally cleared plots on either study site, but nested within the control plots, and in areas adjacent to the experimental and control plots (Table 1). At the end of the laying period, three pairs of Sooty Terns nested 25–30 cm from the edge and one pair nested at the edge of an experimental plot in Peninsula Flamenco. Three of these nests had 100% vegetation cover directly above, while one nest had no vegetation cover.

No Sooty Terns nested in the experimental plots or at a distance less than 30 cm from the edge of the experimental plots in Cayo Yerba (Table 1).

In the 1987 breeding season Sooty Terns in Cayo Yerba did not use the additional experimental plot with 0% vegetation cover. However, they used the other experimental plots from 1986 that had revegetated (Table 1). When comparing the total number of nests in both experimental and control plots (98 nests), more nests were found in the experimental (63%) than in the control (37%) plots.

### NEST-SITE SELECTION

Nests in experimental and control plots differed significantly from random points in mean vegetation height, height to canopy, percent cover directly above, and distance to open path (Table 2). Nests and random points did not differ significantly in mean orientation to an open path. Sooty Terns selected nest sites with taller vegetation (with respect to total vegetation height, and height to canopy), with more cover over the nest, and that were farther from open areas than the random points.

Nests in experimental plots differed significantly from those in control plots in mean vegetation height, height to the canopy, percent cover directly above, distance to the nearest open path, and mean orientation to an open path (Table 3). Sooty Terns in control plots selected nest sites with taller vegetation, with more cover directly above the nest, and nest sites that were farther from an open path than those in the experimental plots. Although mean nest orientation to an open path was significantly different, the terns chose nest sites oriented south-southeast in both ex-

TABLE 2. Statistical differences between all nests and random points in experimental and control plots on Cayo Yerba, Puerto Rico, in 1987.<sup>a</sup>

Characteristic	Nests ( $n = 100$ )	Random points ( $n = 84$ )	$\chi^2$	$P$
Vegetation height (cm)	$71.23 \pm 20.87$	$60.83 \pm 37.94$	11.89	<0.05
Height to canopy (cm)	$29.46 \pm 9.23$	$26.09 \pm 16.69$	27.72	<0.0001
% Cover directly above	$83.65 \pm 30.04$	$62.24 \pm 44.53$	10.09	<0.05
Distance to open path (cm)	$48.24 \pm 33.14$	$43.07 \pm 40.32$	29.16	<0.0001
Orientation to open path <sup>b</sup>	$148.7^\circ \pm 111.2^\circ$ ( $n = 95$ )	$111.3^\circ \pm 99.6^\circ$ ( $n = 72$ )	3.84	ns

<sup>a</sup> Given are means with standard deviations, and  $\chi^2$  values for probability levels.

<sup>b</sup> Instead of  $\chi^2$  test we used Baschlet's (1965) parametric two-sample test for circular data, with significance level of  $P < 0.05$ , to test for a difference in mean orientation to the nearest open path.

TABLE 3. Statistical differences between habitat characteristics for nests in experimental and control plots on Cayo Yerba, Puerto Rico, in 1987.<sup>a</sup>

Characteristic	Experimental plots (n = 60)	Control plots (n = 34)	$\chi^2$	P
Vegetation height (cm)	67.22 ± 21.64	77.25 ± 18.33	11.89	<0.001
Height to canopy (cm)	26.22 ± 8.25	34.33 ± 8.55	27.72	<0.0001
% Cover directly above	76.42 ± 34.09	94.50 ± 18.22	10.09	<0.001
Distance to open path (cm)	33.87 ± 21.02	69.80 ± 36.39	29.16	<0.0001
Orientation to open path <sup>b</sup>	153.5° ± 104.7° (n = 56)	141.9° ± 121.1° (n = 39)	4.67	<0.05

<sup>a</sup> Given are means with standard deviations, and  $\chi^2$  values for probability levels.

<sup>b</sup> Instead of  $\chi^2$  test, we used Baschelet's (1965) parametric two-sample test for circular data to test for a difference in mean orientation to the nearest open path.

perimental and control plots ( $S = 180^\circ$ ,  $SE = 135^\circ$ ).

Mean percent cover directly above was significantly different between nests and random points for both experimental and control plots (Table 4). The Sooty Terns selected nest sites that provided the greatest percent cover directly over the nest. Mean vegetation height, and height to the canopy were significantly different between nests and random points for the experimental plots. Nests and random points in experimental plots did not differ significantly in mean distance and orientation to the nearest open path (Table 4). In the control plots, nests and random points differed significantly only in percent cover directly above, and distance to the nearest open path (Table 4). Again, the terns selected nest sites with more percent cover directly above the nest, and that were farther from an open path than expected by chance alone.

## DISCUSSION

### HABITAT PREFERENCE

Nest-site selection is a function of the characteristics within the immediate vicinity of the nest (e.g., concealment, overhead cover, orientation), as well as characteristics of the habitat patch surrounding the nest (Burger and Gochfeld 1988a, Martin and Roper 1988). Birds select nest sites within certain specific habitats, responding to a complex pattern of stimuli rather than to simple variables (McCrimmon 1978, Brennan et al. 1986, Burger and Gochfeld 1987a). The ability of birds to identify characteristics of the nest site that increase reproductive success would clearly be adaptive (Heagy and Cooke 1979, Burger and Gochfeld 1988b).

Sooty Terns throughout the tropics usually nest on areas of bare ground with no vegetation cover (Ashmole 1963). In the Dry Tortugas, Sooty Terns

ordinarily avoid areas with dense shrubbery or heavy herbaceous ground cover (Robertson 1964). Brown (1976) found that on Manana Island, Hawaii, high grasses excluded Sooty Terns and Brown Noddies, *Anous stolidus*, from nesting in the central crater and parts of the western slope of the island in 1972. Sooty Terns nested extensively in 1973 when, following a dry winter, the grass was much shorter than in 1972.

The Sooty Tern colony in Bird Island, Seychelles, became restricted to the northwest corner of the island when coconuts (*Cocos nucifera* L.) were planted over most of the island (Feare 1976). In 1967 the area available for the Sooty Terns was increased by clearing part of the coconut plantation, and the terns rapidly occupied the open space.

In view of the differences between the nesting habits of Sooty Terns at Culebra Archipelago compared to other islands in the tropics (Burger and Gochfeld 1986), we experimentally manipulated the vegetation to examine nest placement and nest-site selection on Culebra. Since on Culebra open areas are scarce, we expected that Sooty Terns would nest in the experimentally cleared areas. Such has been the case for Sooty Tern colonies in the Dry Tortugas (Robertson, pers. comm.), the Seychelles (Feare 1976), and Jamaica (Haynes-Sutton, pers. comm.) where the terns occupied open areas after the vegetation had been removed. However, in this study Sooty Terns did not nest in three experimentally cleared areas (0% vegetation cover). Only at the end of the laying period, and after some vegetation had colonized part of the plots, did a few terns nest at the edge of one experimental plot in the Flamenco colony. No terns nested near the edge of the experimental plots in Cayo Yerba. This avoidance of open areas suggests that Sooty Terns on Culebra may derive an antipredator or ther-

mal advantage by nesting under dense vegetation cover.

PREDATION

Predation pressure may not be exerted equally throughout an area but vary from habitat to habitat (Martin 1987). Sooty Terns at Culebra may prefer vegetation cover if they experience higher predation rates than Sooty Terns elsewhere nesting in the open. The type and intensity of predation on Sooty Terns varies among colonies throughout the world. In most colonies studied, Sooty Terns have very few predators (Table 5). Some authors suggest that predation is negligible because of the low number of individuals of the predator species, or because only a few individual predators of a particular species prey upon Sooty Terns (Serventy 1952, Chapin 1954, Robertson 1962, Harrington 1974, Kepler 1978). However, they mention that unattended, exposed eggs or chicks are easily preyed upon, and once the chicks are able to move around they seek shelter under rocks or vegetation.

Despite the availability of vegetation cover in most of the colonies examined (Table 5), Sooty Terns prefer nesting on bare ground. Three colonies have little or no vegetation (Sand, Ascension, and Sahul Shelf islands). However, in the Culebra, La Orchila, Little Tobago, and Pelsaert Island colonies, most Sooty Terns selected nest sites under vegetation. In most colonies where the terns nest in open areas, there are only four or fewer predator species, and most only prey upon eggs or very young tern chicks (except cats in two colonies, and the isolated case of a Common Barn-Owl, *Tyto alba*, on Manana Island).

Three of those colonies where Sooty Terns select vegetated areas for nesting (Culebra, La Orchila, and Pelsaert islands) share four predator types in common: a gull species, one or two raptor species, cats, and humans (Table 5). The latter three predator types not only take eggs and young, but also adult terns. These predators can potentially act as a selective force to eliminate terns that nest in exposed areas. However, the hunting success of avian predators can be reduced or eliminated by the presence of vegetation cover over the nest (Saliva, unpubl. data), therefore only those terns nesting under protective vegetation would survive.

On Little Tobago, Sooty Tern nests were scattered under tangled vegetation or in rock crevices (Morris 1984). Like Culebra, Little Tobago does

TABLE 4. Statistical differences between experimental and control plots, comparing nests vs. random points on Cayo Yerba, Puerto Rico, in 1987.<sup>a</sup>

Characteristic	Experimental plots			Control plots			χ <sup>2</sup>	P
	Nests (n = 39)	Random points (n = 48)		Nests (n = 39)	Random points (n = 48)			
Vegetation height (cm)	67.22 ± 21.64	44.90 ± 37.86	5.76	77.25 ± 18.33	76.77 ± 30.93	2.03	ns	
Height to canopy (cm)	26.22 ± 8.25	17.08 ± 14.29	8.18	34.33 ± 8.55	35.10 ± 13.90	2.73	ns	
% Cover directly above	76.42 ± 34.09	52.81 ± 47.40	6.30	94.50 ± 18.22	71.67 ± 39.74	8.24	<0.05	
Distance to open path (cm)	33.87 ± 21.02	32.40 ± 34.07	0.79	69.80 ± 36.39	53.75 ± 43.51	5.72	<0.05	
Orientation to open path <sup>b</sup>	153.5° ± 104.7° (n = 56)	97.8° ± 97.0° (n = 29)	2.83	141.9° ± 121.1° (n = 39)	120.3° ± 101.4° (n = 43)	0.48		

<sup>a</sup> Given are means with standard deviations, and χ<sup>2</sup> values for probability levels.

<sup>b</sup> Instead of χ<sup>2</sup> test, we used Baschelet's (1965) parametric two-sample test for circular data, with significance level of P < 0.05, to test for a difference in mean orientation to the nearest open path.

TABLE 5. Predator species and nesting habitats of Sooty Terns at different colonies.

Reference	Colony location	Nest substrate	Cover available	Preferred habitat	Predator species
Flint 1984	Tern Island (24°N, 166°W)	rubble	yes	unvegetated	<i>Fregata minor</i> <i>Arenaria interpres</i>
Hadden 1941, Howell and Bartholomew 1962	Midway Island (28°N, 177°W)	sand and rubble	yes	unvegetated	<i>Fregata minor</i>
Kepler 1978	Monito Island (18°N, 67°W)	soil and rock	yes	unvegetated	<i>Larus atricilla</i> <i>Fregata magnificens</i> <i>Rattus rattus</i>
Saliva (pers. observ.)	Mona Island (18°N, 67°W)	soil and rock	yes	unvegetated	<i>Larus atricilla</i> <i>Fregata magnificens</i> <i>Rattus rattus</i>
Harrington 1974	Sand Island (16°N, 169°W)	sand and rubble	no	unvegetated	<i>Fregata minor</i>
Chapin 1954, Ashmole 1963	Ascension Island (8°S, 14°W)	sand and rock	no	unvegetated	<i>Fregata aquila</i> <i>Felis catus</i> <i>Homo sapiens</i>
Serventy 1952	Sahul Shelf (12°S, 123°E)	sand	no	unvegetated	<i>Larus novaehollandiae</i> <i>Fregata ariel</i> <i>Arenaria interpres</i>
Schreiber and Ashmole 1970	Christmas Island (2°N, 157°W)	sand	yes	unvegetated	<i>Fregata minor</i> <i>Felis catus</i> <i>Homo sapiens</i>
Vesey-Fitzgerald 1941, Feare 1973	Bird Island (3°S, 55°E)	sand	yes	unvegetated	<i>Arenaria interpres</i> <i>Bubulcus ibis</i> <i>Rattus rattus</i> crab species
Brown 1973, Burger and Gochfeld 1986	Manana Island (20°N, 155°W)	sand, soil, and rock	yes	unvegetated	<i>Arenaria interpres</i> <i>Nycticorax nycticorax</i> <i>Tyto alba</i> <i>Oryctolagus cuniculus</i> <i>Ocypode ceratophthalmus</i>
Sprunt 1948, Robertson 1964, Dinsmore 1972, White et al. 1976	Dry Tortugas (25°N, 83°W)	sand	yes	unvegetated	<i>Fregata magnificens</i> <i>Bubulcus ibis</i> <i>Larus atricilla</i> <i>Arenaria interpres</i> <i>Falco peregrinus</i> <i>Ardea occidentalis</i> <i>Rattus norvegicus</i> <i>Ocypoda arenaria</i> <i>Cenobita diogones</i> <i>Homo sapiens</i>
van Halewijn 1971	La Orchila Island (12°N, 66°W)	?	yes	unvegetated	<i>Larus atricilla</i> <i>Falco peregrinus</i> <i>Felis catus</i> <i>Homo sapiens</i>
Morris 1984	Little Tobago (11°N, 60°W)	soil	yes	vegetated	<i>Fregata magnificens</i> <i>Larus atricilla</i> <i>Coenobita</i> spp.
Serventy and Whittell 1976, Fuller and Burbidge 1981, Lane 1986	Pelsaert Island (28°S, 113°E)	sand	yes	vegetated	<i>Arenaria interpres</i> <i>Larus novaehollandiae</i> <i>Larus pacificus</i> <i>Haliaeetus leucogaster</i> <i>Rallus philippensis</i> <i>Porzana tabuensis</i> <i>Rattus rattus</i> <i>Felis catus</i> <i>Egernia kingii</i> <i>Homo sapiens</i>

TABLE 5. Continued.

Reference	Colony location	Nest substrate	Cover available	Preferred habitat	Predator species
Saliva and Burger (this study)	Culebra Island (18°N, 65°W)	soil	yes	vegetated	<i>Fregata magnificens</i> <i>Larus atricilla</i> <i>Arenaria interpres</i> <i>Bubulcus ibis</i> <i>Haematopus palliatus</i> <i>Nycticorax violaceus</i> <i>Buteo jamaicensis</i> <i>Falco peregrinus</i> <i>Asio flammeus</i> <i>Rattus rattus</i> <i>Felis catus</i> <i>Gecarcinus ruricola</i> <i>Coenobita</i> spp. <i>Solenopsis</i> spp. <i>Homo sapiens</i>

not have available open ground. However, on this island there are no predators of adult terns (except possibly humans) that would select against terns nesting in open patches. Although Morris (1984) reported low reproductive success at this Sooty Tern colony, he could not determine the actual fate of eggs and chicks following presumed desertion by adults. The age of this Sooty Tern colony is unknown, and neither if open patches were available in the past (Morris, pers. comm.). We can only speculate that this Sooty Tern colony could be a subset of the Culebra colony, given its relative proximity to Culebra, and thus the similarity on the terns' choices of nest sites.

Nonetheless, there are always exceptions. In the Dry Tortugas Sooty Tern colony, despite the presence of 10 predator species (including humans, a gull, and a raptor species), the terns prefer to nest in open areas (Table 5). In the Dry Tortugas colony the chief predator of adult Sooty Terns is the Peregrine Falcon, *Falco peregrinus* (Dinsmore 1972). Peregrine Falcons, however, are casual migrants that do not stay in the colony throughout the tern's entire breeding season (Robertson, pers. comm.). Therefore, they would not be expected to exert strong selective pressure on the terns for nesting under vegetation.

Unlike the Dry Tortugas, the raptors on Culebra and Pelsaert islands are permanent breeding residents (except Peregrine Falcons on Culebra Island). The effect of White-breasted Sea Eagles (*Haliaeetus leucogaster*) on the Pelsaert Island Sooty Tern colony is not clear (Lane, pers. comm.). On Culebra Island, however, Red-tailed Hawks (*Buteo jamaicensis*) prey upon Sooty

Terns throughout the tern's entire breeding season, and they only take terns that are roosting on the vegetation or in open patches (Saliva, pers. observ.). Therefore, Sooty Terns could minimize avian predation by nesting under the shelter of thick vegetation.

Several authors have suggested that open areas close to the nest allow birds to detect intruders and predators, but preserve an adult's ability to flee rapidly (Yahner 1983, Burger and Gochfeld 1986, Jehl and Mahoney 1987). In our study Sooty Terns selected nest sites farther from an open path in the control plots (Table 3). In Culebra, nesting close to an open path could increase the chances of avian predation. Red-tailed Hawks, Laughing Gulls (*Larus atricilla*), and Cattle Egrets (*Bubulcus ibis*) prey upon eggs, young, or adult terns that are within 60 cm of open areas (Saliva, unpubl. data).

#### MICROHABITAT SELECTION

Walsberg (1981) observed that the Warbling Vireo (*Vireo gilvus*) locates its nest with regard to the vegetation/sky mosaic produced by the plant canopy so as to create a favorable radiative environment. This favorable environment was not solely produced by the tree or shrub in which the nest was placed, but also by any other overhead vegetation within view of the nest. Besides making the nest less conspicuous to predators, such placement shelters the nest from wind, excess nocturnal radiation loss, or excess diurnal heat gain from solar radiation (Walsberg 1985). Thus, we predicted that the Sooty Terns would nest under taller and denser vegetation that would

provide easy movement to and from the nest, and enough cover to avoid heat stress, adverse climate (e.g., heavy rain), and predators. Sooty Terns at Cayo Yerba selected nest sites where the percent vegetation directly above the nest was higher than in the random points (Table 2). As suggested by Burger and Gochfeld (1986), this preference may relate to maximizing cover for protection from predators and inclement weather.

In this study, Sooty Terns in the experimental plots showed a marked preference for nesting where the orientation of the closest open path from the nest was south to southeast. Since the predominant wind blows over Cayo Yerba from the east or southeast, the terns chose a nest site where a path for easier departure and arrival was located (it is easier for the terns to take off and land facing the predominant wind direction). A thermoregulatory advantage may also be conferred by orienting the nest in the predominant wind direction. Orientation into the wind may increase convection, thus removing the excess heat from the nest or enhance the evaporative cooling of the young (Ricklefs and Hainsworth 1968, 1969; Austin 1974, 1976; Burger and Gochfeld 1987b).

In the control plots the orientation to the nearest open path was not significantly different between nests and random points, apparently because the control plots had very few sparse open paths, and more than 95% vegetation cover. Given that very little effective wind can penetrate the thick canopy, the terns would not gain any particular thermoregulatory advantage by orienting their nests towards the wind.

When the microhabitat around the nest is unfavorable (e.g., lethal temperatures, incident radiation, or exposure to predators), parent Sooty Terns may become inattentive, exposing eggs or nestlings to heat stress or predation, and thus eventually decreasing their reproductive success. In such cases, only those terns nesting in optimal microhabitats would nest and fledge young successfully. Sooty Terns at Culebra choose nest sites under tall vegetation relatively far from open areas, and which offer the highest percent vegetation cover directly over the nest that is available on the plots. Our study suggests that the Sooty Terns at Culebra select nest sites which provide: (1) nest concealment from predators under dense vegetation cover, (2) greater distance from an open path to potential avian predators,

and (3) protection from heat stress and extreme weather conditions.

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#### LITERATURE CITED

- ASHMOLE, N. P. 1963. The biology of the Wideawake or Sooty Tern (*Sterna fuscata*) on Ascension Island. *Ibis* 103b:297-364.
- AUSTIN, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. *Condor* 76: 216-217.
- AUSTIN, G. T. 1976. Behavioral adaptations of the Verdin to the desert. *Auk* 93:245-262.
- BASCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. The American Institute of Biological Sciences, Washington, DC.
- BEKOFF, M., A. C. SCOTT, AND D. A. CONNER. 1987. Nonrandom nest-site selection in Evening Grosbeaks. *Condor* 89:819-829.
- BRENNAN, L. A., W. M. BLOCK, AND R. J. GUTIÉRREZ. 1986. Habitat use by Mountain Quail in Northern California. *Condor* 89:66-74.
- BROWN, W. Y. 1973. The breeding biology of Sooty Terns and Brown Noddies on Manana or Rabbit Island, Oahu, Hawaii. Ph.D. diss. Univ. of Hawaii.
- BROWN, W. Y. 1976. The breeding of Sooty Terns and Brown Noddies on Manana Island, Hawaii. *Condor* 76:61-66.
- BUCKLEY, F. G., AND P. A. BUCKLEY. 1980. Habitat selection in marine birds, p. 69-112. *In* J. Burger, B. L. Olla, and H. E. Winn [eds.], Behavior of marine animals. Current perspectives in research. Vol. 4. Plenum Press, New York.
- BURGER, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. *Condor* 89:811-818.
- BURGER, J., AND M. GOCHFELD. 1981. Colony and habitat selection of six Kelp Gull *Larus dominicanus* colonies in South Africa. *Ibis* 123:298-310.
- BURGER, J., AND M. GOCHFELD. 1986. Nest site selection in Sooty Terns (*Sterna fuscata*) in Puerto Rico and Hawaii. *Colonial Waterbirds* 9:31-45.
- BURGER, J., AND M. GOCHFELD. 1987a. Nest-site selection by Mew Gulls (*Larus canus*): a comparison



- of marsh and dry-land colonies. *Wilson Bull.* 99: 673-687.
- BURGER, J., AND M. GOCHFELD. 1987b. Colony and nest-site selection behaviour in Silver Gulls *Larus novaehollandiae* in Queensland, Australia. *Bird Behav.* 7:1-21.
- BURGER, J., AND M. GOCHFELD. 1988a. Nest-site selection and temporal patterns in habitat use of Roseate and Common terns. *Auk* 105:433-438.
- BURGER, J., AND M. GOCHFELD. 1988b. Habitat selection in Mew Gulls: small colonies and site plasticity. *Wilson Bull.* 100:395-410.
- CARTER, H. R., K. A. HOBSON, AND S. G. SEALY. 1984. Colony site selection by Pelagic Cormorants (*Phalacrocorax pelagicus*) in Barkley Sound, British Columbia. *Colonial Waterbirds* 7:25-34.
- CHAPIN, J. P. 1954. The calendar of Wideawake Fair. *Auk* 71:1-15.
- DINSMORE, J. J. 1972. Sooty Tern behavior. *Bull. Fl. State Mus. Biol. Sci.* 16:129-179.
- FEARE, C. J. 1973. Research on Sooty Terns in Seychelles. *Biol. Conserv.* 5:236-238.
- FEARE, C. J. 1976. The breeding of the Sooty Tern *Sterna fuscata* in the Seychelles and the effect of experimental removal of its eggs. *J. Zool. (Lond.)* 179:317-360.
- FLINT, E. N. 1984. Energetics and social behavior of the Sooty Tern (*Sterna fuscata*) in the Central Pacific. Ph.D. diss. Univ. of California, Los Angeles.
- FULLER, P. J., AND A. A. BURBIDGE. 1981. The birds of Pelsaert Island, Western Australia. Report No. 44. Department of Fisheries and Wildlife, Western Australia.
- GIBO, D. L., R. STEPHENS, A. CULPEPER, AND H. DEW. 1974. Nest-site preferences and nesting success of Starling *Sturnus vulgaris* L. in marginal and favorable habitats in Mississauga, Ontario, Canada. *Am. Midl. Nat.* 95:493-499.
- GOCHFELD, M. 1978. Colony and nest site selection by Black Skimmers. *Proc. First Conference of the Colonial Waterbird Group* 1:78-90.
- GOCHFELD, M., AND J. BURGER. 1987. Nest-site selection: a comparison of Roseate and Common terns (*Sterna dougallii* and *S. hirundo*) in a Long Island, New York colony. *Bird Behav.* 7:58-66.
- HADDEN, F. C. 1941. Midway Islands. *Hawaii. Plant. Rec.* 45:175-222.
- HARRINGTON, B. A. 1974. Colony visitation behavior and breeding ages of Sooty Terns *Sterna fuscata*. *Bird-Banding* 45:115-144.
- HEAGY, M. I., AND F. COOKE. 1979. Vegetation characteristics of Snow Geese nest sites. *Can. J. Bot.* 57:1502-1504.
- HILDEN, O. 1965. Habitat selection in birds: a review. *Ann. Zool. Fenn.* 2:53-75.
- HOWELL, T. R., AND G. A. BARTHOLOMEW. 1962. Temperature regulation in the Sooty Tern *Sterna fuscata*. *Ibis* 104:98-105.
- JEHL, J. R., JR., AND S. A. MAHONEY. 1987. The roles of thermal environment and predation in habitat choice in the California Gull. *Condor* 89:850-862.
- KEPLER, C. B. 1978. The breeding ecology of sea birds on Monito Island, Puerto Rico. *Condor* 80:72-87.
- KEPLER, C. B., AND A. K. KEPLER. 1977. The seabirds of Culebra and its adjacent islands, Puerto Rico. *Living Bird* 16:21-50.
- KRUUK, H. 1964. Predators and anti-predator behavior of the Black-headed Gull (*Larus ridibundus* L.). *Behaviour Suppl.* 11:1-129.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LANE, S. G. 1986. Nesting behaviour of Sooty Terns *Sterna fuscata* on Pelsaert Island, Western Australia. *Corella* 10:28-29.
- MARTIN, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. *Condor* 89:925-928.
- MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90:51-57.
- MCCRIMMON, D. A., JR. 1978. Nest site characteristics among five species of herons on the North Carolina coast. *Auk* 95:267-280.
- MORRIS, R. D. 1984. Breeding chronology and reproductive success of seabirds on Little Tobago, Trinidad, 1975-1976. *Colonial Waterbirds* 7:1-9.
- RICKLEFS, R. E., AND F. R. HAINSWORTH. 1968. Temperature dependent behavior of the Cactus Wren. *Ecology* 49:227-233.
- RICKLEFS, R. E., AND F. R. HAINSWORTH. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. *Condor* 71:32-37.
- ROBERTSON, W. B., JR. 1962. Florida region. *Audubon Field Notes* 16:468-473.
- ROBERTSON, W. B., JR. 1964. The terns of the Dry Tortugas. *Bull. Fl. State Mus. Biol. Sci.* 8:1-95.
- SCHREIBER, R. W., AND N. P. ASHMOLE. 1970. Seabird breeding seasons on Christmas Island, Pacific Ocean. *Ibis* 112:363-394.
- SERVENTY, D. L. 1952. The bird islands of the Sahul Shelf with remarks on the nesting seasons of western Australian sea-birds. *Emu* 52:33-59.
- SERVENTY, D. L., AND H. M. WHITTILL. 1976. Birds of Western Australia. 5th ed. Univ. of Western Australia Press, Perth.
- SMITH, S. M. 1974. Nest-site selection in Black-capped Chickadees. *Condor* 76:178-179.
- SPRUNT, A., JR. 1948. The tern colonies of the Dry Tortugas Keys. *Auk* 65:1-19.
- VAN HALEWIJN, R. 1971. Report on marine ornithology. C.I.C.A.R. p. 20.
- VESEY-FITZGERALD, D. 1941. Further contributions to the ornithology of the Seychelles Islands. *Ibis* 5:518-531.
- WALSBERG, G. E. 1981. Nest-site selection and the radiative environment of the Warbling Vireo. *Condor* 83:86-88.
- WALSBERG, G. E. 1985. Physiological consequences of microhabitat selection, p. 389-413. *In* M. L. Cody [ed.], *Habitat selection in birds*. Academic Press, New York.
- WATSON, J. B. 1908. The behavior of Noddy and Sooty Terns. *Papers from the Tortugas Lab* 2:187-255.
- WHITE, S. C., W. B. ROBERTSON, JR., AND R. E. RICKLEFS. 1976. The effect of hurricane Agnes on growth and survival of tern chicks in Florida. *Bird-Banding* 47:54-71.

- WIENS, J. A. 1985. Habitat selection in variable environments: shrub-steppe birds, p. 227-251. *In* M. L. Cody [ed.], *Habitat selection in birds*. Academic Press, New York.
- WRAY, T., II, AND R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. *Auk* 96:802-805.
- YAHNER, R. H. 1983. Site-related nesting success of Mourning Doves and American Robins in Shelterbelts. *Wilson Bull.* 95:573-580.