

Sooty tern nesting success as a function of nest location, density and vegetation type in a neotropical atoll

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RESUMO. Sucesso reprodutivo de *Sterna fuscata* em função da localização do ninho, densidade e tipo de vegetação em um atol neotropical. A densidade de ninhos e o sucesso reprodutivo são usados como indicadores da preferência de habitat por animais. No entanto, o tratamento isolado desses fatores pode ser incorreto. Estudamos seleção de habitat no Trinta-réis de Manto Negro (*Sterna fuscata*) em um atol composto pelas Ilhas do Farol e do Cemitério, no Brasil. As ilhas foram usadas separadamente para avaliar a escolha de habitat através da análise de densidade de ninhos, sucesso reprodutivo, local de nidificação e tipos de vegetação onde ninhos foram construídos. As diferenças de densidade de ninhos não se relacionaram com o sucesso de nidificação. Na Ilha do Farol, a densidade de ninhos mostrou-se semelhante em duas vegetações (*Cyperus ligularis* e *Portulaca oleracea*), mas foi mais baixa em uma terceira vegetação (*Iresine portulacoides*), apesar da grande abundância desta última. O sucesso de nidificação, no entanto, foi significativamente maior em *C. ligularis*, indicando que essa vegetação é vantajosa para a reprodução da espécie. Na Ilha do Cemitério, onde predomina um tipo de vegetação, a densidade de ninhos foi mais alta na periferia do que no centro da colônia. No entanto, o sucesso de nidificação foi equivalente nessas duas localidades e sem relação com a cobertura vegetal. Aqui argumentamos que a avaliação de qualidade de habitat pode ser imprecisa se baseada sobre indicadores isolados; efeitos inter-relacionados de diversos parâmetros reprodutivos associados a outras características, tais como tipo de vegetação, podem ser mais úteis. Outros fatores também devem ser considerados. Nesse estudo, por exemplo, a distribuição de predadores nas ilhas pode ter afetado a escolha de habitat para nidificação do Trinta-Réis-de-Manto-Negro.

PALAVRAS-CHAVE: seleção de habitat, sucesso de nidificação, sucesso reprodutivo, *Sterna fuscata*, Trinta-Réis-de-Manto-Negro

ABSTRACT. Nest density and reproductive success are used as indicators of habitat preference by animals. However, isolated treatment of these factors may be misleading. We studied habitat selection by Sooty Terns (*Sterna fuscata*) in an atoll in Brazil, composed of Farol and Cemitério Islands. The islands were used separately to assess habitat choice, by analyzing nest density, nesting success, nesting locations and types of vegetation used for nesting. Differences in nest density were unrelated to nesting success. On Farol Island, nest density was similar in two vegetations (*Cyperus ligularis* and *Portulaca oleracea*), but higher in these than in a third vegetation (*Iresine portulacoides*), despite the latter's high abundance. Nesting success, however, was significantly higher on *C. ligularis*, indicating that this vegetation is advantageous for reproduction. On Cemitério Island, covered largely with one vegetation type, nest density was higher at the periphery of the colony than at the center. Nesting success was similar at these two localities, and unrelated to vegetation coverage. We argue that the assessment of habitat quality may be inaccurate if based upon isolated indicators; inter-related effects of several reproductive parameters in association with other characteristics, such as vegetation type, are more useful. Other factors should also be considered. In this study, for instance, the differential distribution of predators in the islands may have affected nesting habitat choice by the Sooty Terns.

KEY WORDS: habitat choice, nesting success, reproductive success, *Sterna fuscata*, Sooty Tern

One fundamental aspect associated with reproduction concerns habitat choice, since nesting site characteristics may directly affect the survival of nestlings (Cody 1985, Saliva and Burger 1989, Ens et al. 1992). Habitat choice involves a decision-making process that includes the choice of the habitat within a finite area, followed by territory acquisition and specific nest site selection (Burger 1985).

Several approaches have been applied in the investigation of avian-habitat associations, particularly the assessment of habitat quality. Many factors contribute to what may be considered habitat quality. Often applied, but seldom questioned, is the assumption that the density of a species in a habitat is directly correlated with the quality of the habitat (Vickery et al. 1992). This is due to the notion that the increased number of individuals reflects the larger amount of resources necessary for the species in that locality.

Fretwell and Lucas (1970) suggest that in the most advantageous locations a density limitation occurs since the quality of these areas will decrease as density increases. Consequently, other initially less advantageous areas would acquire the same qualitative potential, given the smaller number of competitors. Another consideration is that density may not simply reflect a better resource base, but result from less discernible ecological contingencies, such as timing of arrival of individuals at a colony, social factors, and environmental characteristics (substrate, vegetation, slope of the ground, etc.) (Wiens 1976, Burger 1986, Vermeer et al. 1992, Sutherland 1996). The specific location of a nest within a colony is also a factor that may be indicative of habitat quality. The "selfish herd" hypothesis (Hamilton 1971) proposes that centrally-located individuals may be at an advantage because they will suffer less predation than those located at the borders of the colony.

Thus, it would be erroneous to make assumptions about habitat selection and quality based only upon nest density (Van Horne 1983, Vickery et al. 1992). Several factors, though often considered independently, may have inter-related effects. For instance, vegetation type may affect the density of nests in a given area, which may, in turn, bias nesting success. It appears that not only are several factors important in determining habitat quality, but their inter-related effects may play a substantial role.

Sooty Terns (*Sterna fuscata*) reproduce in large colonies in the tropics. However, extensive reductions in colony and breeding numbers have occurred due to human exploitation and habitat modification (Feare et al. 1997). Typically, Sooty Terns nest in large colonies on oceanic islands; a single egg is laid in the nest, which is a simple scraped depression in the substrate, often composed of coral, exposed rocks, sand or low vegetation (Dinsmore 1971, Feare et al. 1997). Studies of Sooty Terns have examined habitat selection as a function of vegetation type and/or reproductive success (Ashmole 1963, Robertson 1969, Dinsmore 1971, Feare 1976, Morris 1984), or based solely upon nest density (Burger and Gochfeld 1988, Feare et al. 1997).

The objective of this study was to elucidate nest site preference of Sooty Terns in two islands located in the Rocas Atoll of northeastern Brazil by analyzing the inter-related effects of habitat and reproductive characteristics: nest density, nesting success, vegetation type, and nest location within the colony. In the Farol Island colony, analyses were based on: (1) nest density and nesting success within different vegetation types; (2) nest density and its association with nesting success; and (3) percentage coverage of each vegetation type. In the other colony, located on Cemitério Island, we analyzed: (1) nest density and nesting success relative to location (periphery vs. center); (2) nest density and its association with nesting success; and (3) percentage coverage of each vegetation type. Because this latter island is covered almost exclusively with one type of vegetation, variability due to this factor was practically eliminated.

MATERIALS AND METHODS

Study site. In Brazil the Sooty Tern reproduces in northeastern regions, with its major nesting area located at Rocas Atoll (03°45' to 03°56' S and 33°37' to 33°56' W). In 1982 there were approximately 115,000 breeding adults on the two islands of the atoll (Antas 1991). This study took place during two breeding cycles in 1997, one initiated in February and the other in September, on colonies located on Farol Island (approximately 34.6 ha) and Cemitério Island (approximately 31.5 ha). We did not ring adult birds during the study, and thus it is unclear whether the birds in the two reproductive cycles represent different groups or the same group of re-nesting birds.

The vegetation of the islands is mostly herbaceous, and consists chiefly of *Portulaca oleracea* (Portulacaceae), *Cype-*

rus ligularis (Cyperaceae) and *Iresine portulacoides* (Amaranthaceae). On Cemitério Island the vegetation is composed almost exclusively of *C. ligularis*. Timing of hatching relative to vegetation type was assessed on Farol Island, since it exhibits the more diverse vegetation. It was assessed relative to location (periphery vs. center) on Cemitério Island, where vegetation is mostly of one type and could not be an influencing factor. Due to time constraints we applied this assessment only in the September breeding cycle, which was divided into six-day periods, in which we monitored daily the number of hatchings that took place. Timing of hatching was used to estimate the timing of occupation of each type of vegetation during the laying period.

Nesting success relative to vegetation and nest density. We monitored nests on Farol Island to assess nesting success relative to the type of vegetation used by the birds. We defined nesting success in terms of both hatching rate as well as the survival of chicks until the tenth day. Only the three vegetation types indicated above are used for nesting on this island. To choose nests for monitoring, we established transects (50 cm wide) along the east-west axis of the island at 40 m intervals. In one section of the island the intervals were of 20 m, due to the low density of nests found in *I. portulacoides*. We selected the first 50 nests found within each vegetation type for monitoring (we considered the vegetation selected by individuals as that closest to the nest). Due to the loss of a few nest markers, at the end of the census period sample sizes varied from 41 to 46 nests in the vegetation types. The single egg at each nest was marked with an identification number using a non-toxic marker.

We monitored nests on alternate days, and characterized them as: (1) depredated when egg predation was obvious (egg shell remains were found) or when the egg disappeared (no egg shell remains found); (2) hatched; (3) presence or absence of nestling; and (4) nest deserted, when at the end of the incubation period the egg did not hatch and parents deserted. Because in the first 10 days of life chicks remain very close to their location of hatching, absence is a good indicator of mortality. Thus, we considered nestlings as dead if they were not seen on two consecutive nest checks. A small possibility exists that, due to human disturbance, some adults may have relocated chicks. However, we consider this unlikely for the majority of cases, because our observations suggest that chicks that left their nest areas were attacked by other nesting adults. Thus, the survival and feeding of chicks away from their nests would apply only to a negligible number of cases.

Nestlings were marked with a single, plastic colored ring on their second or third day post hatching. Feare (1976) verified that nestling mortality in this species in the Seychelles Islands is greatest during the ten-day period post hatching. Results concerning nesting success are shown as rates and probabilities of survival according to Mayfield's (1961, 1975) method.

To assess how nest density affected nesting success, on Farol Island we counted nests found within a 2 m radius of

each of the 50 nests marked in each vegetation type. Fewer nests were used in analyses due to the loss of some markers. These measures were performed in the February and September breeding cycles. In February we also measured the distance to the nearest neighbor for each of the marked nests.

We determined the percentage coverage for each vegetation type on Farol Island, relating this to the number of nests present in each vegetation type. We established 99 transects, spaced 10 m apart, along the east-west axis of the island. Along each transect a tape-measure was used to record the extension of each vegetation coverage, which included the three vegetation types above as well as grass and sand. Nests were counted in each vegetation type.

Nesting success relative to location and nest density. At Cemitério Island we evaluated nesting success relative to location of the nests, which were distributed from the periphery to the center of the island. The colony occupied about the whole island. The periphery was considered to be a 30 m-wide strip along the water. We randomly established eight 50 m² squares along the periphery of the island and three squares in the center (two with 200 m² and one with 400 m²). On hundred nests were marked randomly within each square at each location (periphery versus center). Each nest was monitored in the same way as described above.

To evaluate nest density in the two areas, center and periphery, two methods were used. The first method was used to determine the density distribution patterns within the island, moving from the periphery toward the center. This allowed an appraisal of gradual changes along a distance gradient from the island's edge. For this method we established two 5 m wide transects along the north-south and east-west axes of the island, divided each transect into 25 m² squares and counted nests in each one, thus obtaining a measure of density in each square. To analyze the density along these distance gradients, the island was divided into four concentric ellipses. The outermost ellipse was classified as 'A', followed by ellipses 'B' through 'D', the last at the very center of the island. We evaluated the different densities of nests in each category by using the mean density values recorded for the squares within each elliptically bounded area. We also measured percentage of vegetation coverage to establish whether there was a pattern of association between vegetation coverage and nest density. Measures were carried out within the same 25 m² squares in each of the two transects cited above. A tape-measure was placed along the diagonals of each square and the extent of sand and *C. ligularis* (the only vegetation on this island) were measured.

The second method was used to compare density values between the outermost area of the island and the central portion, and to associate each nest's success with the neighboring density of nests. In this second methodology, we counted the number of nests within a 2 m radius for each of the 200 nests marked at the periphery and at the center. These nests were used to assess nesting success, allowing the comparison of average density around successful and unsuccessful nests.

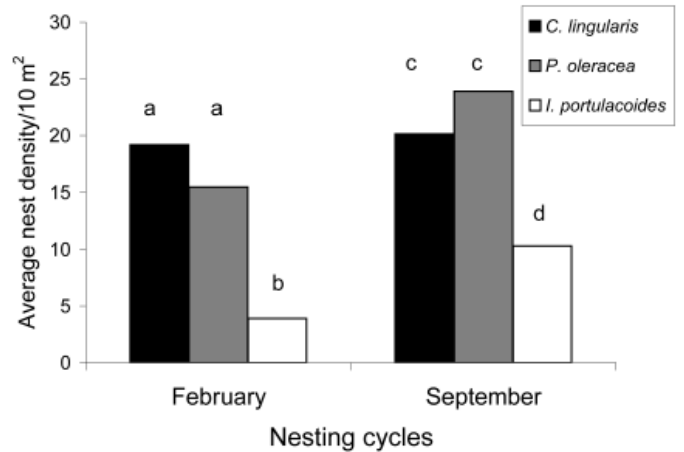


Figure 1. Average nest density in the three vegetation types found in Farol Island. The different letters above each bar indicate significant differences ($P < 0.001$) in nest density between specific vegetation types.

Fewer nests were used in the analyses due to the loss of some markers.

Timing of hatching (Farol and Cemitério Islands). If habitats in a colony differ in quality, reproductive individuals should attempt to first occupy the area that offers the greatest advantages. In this light, our expectations were that in the areas occupied first, eggs should be first to hatch. To indirectly verify whether there was laying synchrony among the three vegetation types in Farol Island, we compared the number of hatchings that occurred within each of five consecutive periods (each period = 6 days) in the September cycle, in each of the vegetation types.

Statistical analyses. We used SYSTAT 7.0 (SPSS 1997) software for all analyses. We used ANOVA and Tukey HSD tests to examine differences in nest density between each of the vegetation types. Chi-square tests were used to assess the differences in the absolute number of nests among vegetation types, for survival rates of nestlings in different vegetation and colony localities (periphery vs. center), and in considering hatching rates among the three vegetation types and among localities. We used a Student's two-tailed *t*-test (when data were distributed normally) to examine the difference in nest density between peripheral and central locations in the islands. When the data were not normally distributed, for example when comparing timing of hatching in peripheral versus central locations, we used the non-parametric Mann-Whitney *U*-test or the Kruskal-Wallis *H*-test. All data are presented as means \pm SD.

RESULTS

Nest density relative to vegetation types (Farol Island). There was a significant difference in nest density among vegetation types used for nesting (February: $F_{2,72} = 20.15$, $P < 0.001$; and September: $F_{2,142} = 48.12$, $P < 0.001$; Fig. 1). A Tukey HSD test was applied to identify the differences in nest density among vegetation types, and indicated that densities

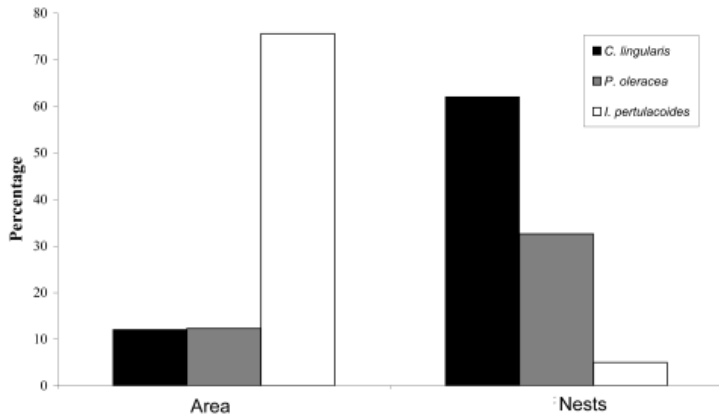


Figure 2. Percentage of area covered with each vegetation type and percentage of nests found in each vegetation type in Farol Island (15 to 17 February 1997).

were the same in *C. ligularis* and *P. oleracea* (February: $P = 0.22$; September: $P = 0.25$), and that nest density in *I. portulacoides* was significantly lower than in the other two (February and September: $P < 0.001$ for both comparisons).

In February the average inter-nest distance found in *I. portulacoides* was 152.1 ± 112.2 cm ($N = 19$). In *P. oleracea* and *C. ligularis* distances were 95.5 ± 71.0 cm ($N = 29$) and 63.5 ± 26.2 cm ($N = 32$), respectively. A significant difference was found among the distance values in the three vegetation types ($H = 9.75$, $N = 80$, $P < 0.01$).

On Farol Island 49.2% of the area was covered by *I. portulacoides*, 31.4% by sand, 8.0% by *P. oleracea*, 7.9% by *C. ligularis* and 3.6% by grass. Excluding sand and grass, which were not used for nesting, the three main vegetation types that occupied the area of the island were (Fig. 2): *C. ligularis* (12.2%), *P. oleracea* (12.3%) and *I. portulacoides* (75.6%). In the February cycle, the greatest number of nests (2,023) was found in *C. ligularis*, suggesting that this is possibly the most advantageous area for nesting. In *P. oleracea* 1,060 nests were

counted, while only a few Sooty Terns used *I. portulacoides* (166). The number of nests found in each vegetation type is significantly different from expected if nests occurred in equal proportions ($X^2_2 = 1592.8$, $P < 0.001$; Fig. 2). If we exclude the vegetation category with the smallest number of nests (*I. portulacoides*) from this analysis, and compare the number of nests found in the two vegetation types that occurred in almost equal proportions, we find that the number of nests in each vegetation still differed from the expected equal proportions ($X^2_1 = 300.8$, $P < 0.001$).

Nest density relative to peripheral versus central locations (Cemitério Island). To assess the patterns of nest density relative to specific locality, in the September reproductive cycle we monitored density from the periphery to the center, using the concentric ellipses A-D (A = periphery; D = center). Density values during this cycle were measured one month apart (28 September and 28 October). These nest density values differed among ellipses in both periods (September: $F_{3,70} = 6.16$, $P < 0.001$; October: $F_{3,70} = 11.21$, $P < 0.001$), with nest density gradually declining from the periphery (A) towards the center (D) of the island (Table 1). We found no variation in vegetation cover among the four categories (A to D): ($F_{3,69} = 2.05$, $P = 0.12$), which indicates that nest density was not associated with vegetation coverage in this island.

In the second methodology used, we found that the nest density of the periphery was significantly greater than that at center for both February ($t_{77} = 8.43$, $P < 0.001$) and September ($t_{194} = 11.43$, $P < 0.001$). Average nest density at the periphery was 8.5 ± 4.0 nests/10m² ($N = 58$) in February, and 6.8 ± 2.9 nests/10 m² ($N = 100$) in September. At the center of the island these values were 1.0 ± 0.8 nests/10 m² ($N = 21$) in February and 2.9 ± 1.6 nests/10m² ($N = 96$) in September.

Nesting success relative to vegetation types (Farol Island). The type of vegetation used for nesting on Farol Island was strongly associated with the nesting success of the terns. Not only did hatching rate differ among the three vegetation types

Table 1. Values for P (Tukey HSD Test for unequal sample sizes) when comparing nest densities among classes A to D (from the periphery to enter) of Cemitério Island, and average nest density for each class, given for two sampling periods (September and October 1997).

	A	B	C	D	Average nest density / 25 m ²
28 Sept 97					
A	—	0.605	0.051	0.001	17.38
B	—	—	0.511	0.040	14.05
C	—	—	—	0.549	10.55
D	—	—	—	—	7.10
28 Oct 97					
A	—	0.442	0.000	0.000	29.00
B	—	—	0.010	0.014	25.05
C	—	—	—	0.999	16.61
D	—	—	—	—	16.90

(*C. ligularis*: $N = 40/48$ (81.6%); *P. oleracea*: $N = 27/46$ (57.4%); and *I. portulacoides*: $N = 23/46$ (50%); $X^2_2 = 12.54$, $P < 0.005$), but when considering nestlings that reached 10 days of age, there was also a significantly higher success for the terns in *C. ligularis* ($N = 26/40$ [65.9%]) than for those nesting in either *P. oleracea* ($N = 0/27$ [0%]) or in *I. portulacoides* ($N = 9/23$ [39.0%]; $X^2_2 = 32.42$, $P < 0.001$; Fig. 3).

According to Mayfield's method, which was used to reinforce the results, the probability of survival to hatching in *C. ligularis* was 0.78, and 0.50 to 10 days of age. In the other two vegetation types there was a greatly reduced nestling survival. In *I. portulacoides*, the probability of hatching was 0.43 and 0.16 to 10 days of age. Nests in *P. oleracea* presented the lowest rate of nesting success: hatching probability was 0.52, with a survival rate to 10 days of age of only 0.02.

Nesting success relative to peripheral versus central locations (Cemitério Island). The hatching rates found for the periphery ($N = 76/98$ [77.6%]) and for the center ($N = 71/100$ [71.0%]) of Cemitério Island were similar ($X^2_1 = 0.74$, $P > 0.05$). The survival rate from hatching to 10 days of age for the two areas, 81.8% and 78.8%, respectively, was also similar (periphery: $N = 62/76$; and center: $N = 56/71$; $X^2_1 = 0.18$, $P > 0.05$). We found hatching probabilities (Mayfield) of 0.73 and 0.67 for the periphery and center of the island, respectively, and survival probabilities from incubation to 10 days of age of 0.58 and 0.53, respectively.

Nesting success relative to nest density (Cemitério and Farol Islands). To verify whether nesting success could be associated with a greater nest density around focal nests, we compared the average nest density, measured within a 2 m radius of successful nests with the average density around those that were unsuccessful. On Cemitério Island we did not find any difference between these two categories ($F_{1,175} = 0.74$, $P = 0.39$). On Farol Island density also appeared unrelated to the hatching probability in the three vegetation categories, as shown by the independent analysis for each vegetation type (*C. ligularis*: $F_{1,44} = 0.27$, $P = 0.61$; *P. oleracea*: $F_{1,42} = 0.82$, $P = 0.37$; *I. portulacoides*: $F_{1,39} = 0.15$, $P = 0.70$).

Timing of hatching (Farol and Cemitério Islands). The indirect assessment of laying synchrony among the three vegetation types in Farol Island, using a comparison of the number of hatchings that occurred within each of five consecutive 6-day periods in the September cycle in each of the vegetation types, yielded no significant difference between periods ($H = 0.06$, $N = 15$, $P = 0.97$). Nevertheless, about 50% of hatchings that occurred in *C. ligularis* were restricted to the last period, a pattern that was the opposite of that found for *I. portulacoides* and *P. oleracea* (30% and 17% hatchings in last period, respectively). The same analysis, relative to periphery versus center in Cemitério Island, indicates that in the two localities hatching rates were similar through time periods ($U = 11.0$, $N = 10$, $P = 0.75$).

Nest predators (Farol Island). There are several species in the island that commonly consume eggs, the chief predator

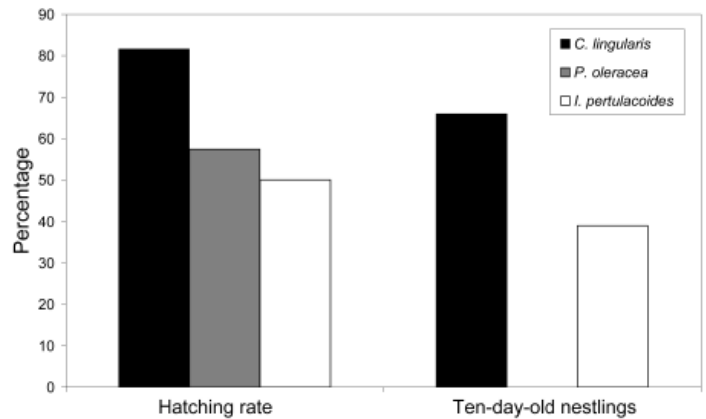


Figure 3. Sooty Tern nesting success, as indicated by hatching rate (number of hatched eggs) and number of nestlings surviving to 10 days, in the three vegetation types in Farol Island (September 1997).

being the terrestrial crab *Geocarcinus lagostoma*. The crabs were very numerous on both islands and their depredation of eggs occurred mostly at night. Eggs were consumed either at the nest site or were dragged away from the nest. We also found evidence of chick predation (partially digested tern chicks in regurgitations on several occasions) by the Masked Booby *Sula dactylatra*. The only mammal found in the islands is the mouse *Mus musculus*, and there are no reptiles of large size. Predation and nest desertion were lowest in *C. ligularis* vegetation (Table 2). Although our evidence is highly circumstantial, we suspect that the predation of nestlings by boobies may be high in the studied colony. Eleven of the nests studied in *I. portulacoides* were monitored in an isolated part of the island, which was not frequently used by boobies. The survival of nestlings in this area was much higher than for the rest of nests located in the same vegetation type ($X^2_1 = 6.64$, $P < 0.01$). Of the six nestlings that hatched in this area, five reached 10 days of age (83.3%) while of the 17 eggs that hatched in other areas of *I. portulacoides*, where boobies were frequently found, only four attained 10 days of age (23.5%).

DISCUSSION

Impact of vegetation type on reproduction. In this study, the difference in nest density found in each habitat had no association with nesting success. In Farol Island, in both the February and September reproductive periods, the nest density found in *C. ligularis* and in *P. oleracea* was similar. We found, however, that nesting success was much higher in the former vegetation, similarly to what was found by Vickery et al. (1992). If nest density alone was considered the measure of habitat quality, then *C. ligularis* and *P. oleracea* would be the best habitats. However, when nesting success is also considered, *C. ligularis* should be preferred.

What factors influence nest density in the three habitats? If vegetation structure is the major factor, then birds should

Table 2. Percentage of nests lost through egg predation and desertion in Farol and Cemitério Islands, by location (periphery and center) and vegetation types.

	Cemitério Island		Farol Island		
	Periphery	Center	<i>C. ligularis</i>	<i>P. oleracea</i>	<i>I. portulacoides</i>
Depredated eggs (%)	15.3	18	14.3	38.3	39.1
Deserted nests (%)	7.1	11	4.1	4.3	10.0

select the preferred vegetation type, whenever it is available. Feare et al. (1997) found in the Seychelles Islands that terns nest in *P. oleracea* at a density five times greater than in *C. ligularis*, and conclude that this species prefers this type of habitat. In contrast, we found that in Farol Island the density of nests in these two vegetation types was similar for two consecutive reproductive cycles, denoting that this may be a frequent distribution pattern for the island.

The high number of nests found in *C. ligularis* and in *P. oleracea* is not explained by the absence of other vegetation types on the island. By the end of the laying period we observed that much of the *I. portulacoides* vegetation remained empty of nesting birds, which indicates that space is not a limiting factor for this species in the atoll. The similar nest densities found in *C. ligularis* and *P. oleracea* vegetations could be explained by the sequential occupation of each area, by a possible optimal distance between nests, by the quality of individuals in each area, and even by elements involving individual reproductive strategies.

We used timing of hatching to analyze the sequence of occupation of each of the three vegetation types used for nesting. The expectation was that the preferred habitat should have been occupied first. The statistical tests show that hatching, and thus indirectly laying, occurred within similar periods. However, results revealed that in the *I. portulacoides* vegetation the number of hatchings was more evenly spread out than in the *C. ligularis* vegetation. In the latter, only 10.5% of hatchings occurred within the first three periods, as compared to 45.8% in *I. portulacoides*. Thus, we conclude that the occupation of *C. ligularis* occurred later than in *I. portulacoides*. This is perplexing, in face of the greater reproductive advantages offered by the *C. ligularis* vegetation. We suggest that these contradictory results may be explained by a difference in the incubation period among the three vegetation types. *Cyperus ligularis* offers greater shading for nests, when compared to the other two vegetations. Thus, the incubation period in this vegetation may be slightly longer, since temperature is one of the factors that determines incubation length.

Impact of peripheral versus central location on reproduction. Nesting success in Cemitério Island was not associated with nest density. The nest density found at the periphery was significantly higher than that found for the central area, but nesting success was similar in the two localities. Since one of

the factors that may influence nest density is vegetation cover, we evaluated a possible difference in this variable in the central and peripheral areas. We found no variation in vegetation cover, thus rejecting this as a possible factor to explain the difference in nest density.

A possible hypothesis to explain differential nest densities among nesting areas is that the preferred area is occupied by higher quality adults that exclude others (as in Coulson 1968). Lower-quality individuals would be forced to cluster in sub-optimal areas. Hence, if the central area is more advantageous, then there will be a greater density in the periphery; likewise, if the periphery is better, then there will be a greater density in the central area. The distribution of individuals in Cemitério Island could be explained by the former. However, because territory defense involves energetic costs, one supposes that there should be some benefits available in the central area to justify its defense, e.g. resources, mating opportunities or defense against predators. However, none of these benefits were measured in this study.

Impact of predation on reproduction. Results in this study strongly suggest that alternative factors should be considered when examining habitat choice questions. For example, nest predation may be responsible for the majority of nest losses (Ricklefs 1969), thus habitat choice could be a function of a reduced probability of predation in some habitats (Martin 1993). The presence of predators could stimulate individuals to search for areas where they are absent or are found in reduced numbers.

Studies about nesting-site choice that take predation risk into account have been conducted with Roseate Terns (*Sterna dougallii*; Burger and Gochfeld 1988) and Sooty Terns (Saliva and Burger 1989). In the latter study the authors found that individuals select habitats with a specific proportion of plant coverage and avoid nesting in very open spaces. When comparing their findings with studies conducted in other localities, they verified that different choices occur in other colonies, and concluded that these differences are based upon the types of predators that occur in these areas.

Hamilton (1971) suggested that individuals should preferentially choose central areas of a colony for nesting, because of a presumed lower predation pressure. Some studies have shown that nest predation at the periphery is really the determining factor leading to a lower reproductive success (Pat-

terson 1965, Tenaza 1971, Feare 1976, Hoogland and Sherman 1976). However, the opposite trend has been observed in Least Terns (*Sterna antillarum*; Brunton 1997). Since different predators use strikingly different approaches to a colony, as well as prey capturing strategies, this may determine the relative nesting success values of peripheral versus central nesting.

In the present study, predation was the most influential factor contributing to egg loss in the colony of Cemitério Island. The main egg predator on the island is the terrestrial crab. With the exception of one rocky outcrop in the northern part of the island, where there was a large aggregation of crabs, they were apparently distributed evenly throughout the island. Given this uniform distribution, we found similar predation rates in the central versus peripheral areas of the colony. Thus, if there is a preference for a given locality in the colony, it is unlikely to be based on the probability of egg predation.

The Masked Booby may be one, and perhaps the main, avian predator of Sooty Tern nestlings. If so, chick survival would probably be reduced due to the thousands of these birds that occur in Farol Island. These birds reproduce in the atoll from around April until August (Antas 1991) and thousands feed in the area at other times of the year. Boobies were confined mostly to the *P. oleracea* and *I. portulacoides* vegetations, similarly to previous observations in the area (Andrade 1998). Nest site preference by Sooty Terns in Farol Island may be influenced by the presence of boobies in two of the vegetation types available. The hypothesis that the presence of boobies may affect habitat choice is consistent with our results: areas within the same vegetation but with different concentrations of boobies had different nesting success rates.

Conclusions. Our results provide a strong argument that vegetation type and nest site location are key components associated with habitat quality for the Sooty Tern. It is important to point out that our study site exhibited two crucial habitat variables that should be considered. Sooty Terns were faced with a very limited choice of vegetation types for nesting, in addition to the presence of predators. These selective factors may differ from those faced by birds nesting in other locations. For example, in the Seychelles Islands Sooty Terns use various types of habitats, ranging from open areas with low vegetation to the ground underneath closed canopy in woodland (Feare et al. 1997). In Hawaii, nesting of Sooty Terns occurred on bare sand, grass and rock while in Puerto Rico they nested in dense vegetation (Burger and Gochfeld 1986). These studies, however, gave no indication of nesting success relative to choice of habitat. In our study, nest density was different among the three vegetation types found on Farol Island, this being due to the low level of occupation for *I. portulacoides*, despite its availability. However, nesting in one type of vegetation, *C. ligularis*, conferred a higher nesting success. Additionally, it is important to consider that the characteristics of vegetation at hatching may differ from those at nest site selection and laying. This may especially be the case for *Portulaca*, which changes through the season due to

trampling by the birds and drying. Thus, seasonal variation in vegetation is a factor that should be considered in further studies. We found that, although nest density decreased with distance from the periphery of the colony, this was not associated either with vegetation cover or the pattern of nesting success. The costs in reproductive investment by parents in these localities may relate to microhabitat differences (e.g. temperature, flight costs, etc.). For instance, we observed that the structure of *C. ligularis* offers the most shade, in comparison to the other two vegetation types. Sooty Tern nestlings do not have good thermo-regulatory capacity and, without shade from vegetation and parents, suffer a dangerous increase in body temperature. Sooty Tern parents are increasingly absent after nestlings hatch (Dinsmore 1971; Feare 1976), and chicks seek shade within the vegetation (Saliva and Burger 1989). We also suggest that the chief predators of Sooty Tern eggs and chicks in this atoll, terrestrial crabs and Masked Boobies, and their differential distribution patterns on the islands, may strongly influence habitat choice for nesting purposes.

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