PRE- AND POST-EL NIÑO SOUTHERN OSCILLATION COMPARISON OF NEST SITES FOR RED-TAILED TROPICBIRDS BREEDING IN THE CENTRAL PACIFIC OCEAN[1]

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Abstract. Red-tailed Tropicbirds (*Phaethon rubricauda*) breeding on Christmas Island, Central Pacific Ocean, exhibited stable preferences for nest sites over time, such that vegetative characteristics associated with active nests were similar in 1980 and 1984. Before the El Niño Southern Oscillation (ENSO, 1980) the vegetative structure of randomly placed points differed from that of actual nests. After the ENSO (1984) the vegetative structure at randomly placed points resembled that of actual nests, suggesting that the overall availability of preferred sites may have increased. Records of the thermal environment surrounding actual nests and other points within the same shrub suggest that shifts in vegetative structure of nesting habitat created a favorable thermal environment for tropicbird chicks. This post-ENSO shift in habitat structure was accompanied by an increase in the number of active nests at the Y-site colony relative to pre-ENSO breeding seasons. These data support the hypothesis that suitable nest sites may limit short-term reproductive opportunities of tropicbirds, hence influence the rate of population growth and time course of recovery from catastrophic events such as ENSO.

Key words: Red-tailed Tropicbird; Phaethon rubricauda; El Niño Southern Oscillation; nest-site selection; breeding constraints; Christmas Island.

INTRODUCTION

An axiom of ecology is that factors of habitat (e.g., food, refugia from predators, and breeding sites) are important in limiting a species' breeding opportunities and distribution (Grinnell 1928, Miller 1942). Energy constraints and predation affect reproductive success (Lack 1948, Perrins 1977, Ricklefs 1977), and by implication, influence the distribution of many species of birds (Lack 1954, Rosenzweig 1985). However, documenting whether availability of breeding sites affects either breeding opportunity or success has remained more elusive.

Univariate correlations of the location of nests with vegetation structure have done much to characterize species-specific utilization patterns, but such descriptive studies do not address whether species show preferences relative to available habitat features and whether availability might limit breeding. Studies emphasizing hypothesis testing are increasing, however. For example, Burger and Gochfeld's (1981) uni-

variate study showed that vegetative features associated with nest sites differed from available vegetative features associated with nearby, arbitrarily selected, points. The nonrandom selection (and by implication, preference) of nest sites based upon multiple variables has been documented for a variety of species (MacKenzie and Sealy 1981, Clark et al. 1983, Petersen and Best 1985, Bekoff et al. 1987, Sutherland and Maher 1987, Martin and Roper 1988). These multivariate approaches have shown how preferences for vegetative characters exclude much of a habitat from consideration for nest placement, despite the superficial uniformity of the habitat. Such studies indicate that the types of sites used by some birds may not be commonly available. The question remains whether availability of preferred sites limits breeding success or opportunities.

We previously reported on the pattern of habitat and nest-site selection by Red-tailed Tropicbirds (*Phaethon rubricauda*) nesting on Christmas Island, Republic of Kiribati, 2°N 157°W, during July of 1980 (Clark et al. 1983). Briefly, Clark et al. (1983) found that scaevola (*Scaevola taccada*)/turnefortia (*Messerschmidia argetea*)

habitats supporting nesting colonies of tropic-birds were quantitatively distinct from superfi-cially similar habitats in several vegetative char-acters. Furthermore, comparison of vegetative characteristics of actual nests with those asso-ciated with randomly placed points within col-ony sites showed that several variables closely associated with actual nest sites were not com-mon attributes of vegetation found within the colony site. Together these results were consis-tent with the possibility that suitable nest sites might be a resource limiting reproductive op-portunities for tropicbirds. However, in the ab-sence of experimental data Clark et al. (1983) could not determine whether potential nest sites were sufficiently uncommon to prevent addi-tional birds from nesting in the colony, or oth-erwise force late arriving pairs to use suboptimal nest sites such that their probability of repro-ductive success was lowered.

During 1982–1983 an El Niño-Southern Os-cillation (ENSO) occurred (Rasmusson and Wal-lace 1983). The immediate effect of this ocean-ographic–meteorological event was to cause massive disruption of the reproductive cycle of tropicbirds and other seabirds, as well as high mortality to chicks and adults (Schreiber and Schreiber 1984). The ENSO also caused an ap-parent change in the structure of the scaevola/turnefortia habitat on Christmas Island, in effect creating a natural longitudinal habitat manipu-lation experiment. We returned to Christmas Is-land in 1984 to capitalize on this natural exper-iment in habitat manipulation to (1) quantify potential changes in availability and utilization of nest-site resources, and (2) relate such changes to the breeding status of the local population of tropicbirds.

METHODS

HABITAT AND STUDY SITE

Data characterizing nest sites for the pre-ENSO period (1980) were derived from Clark et al. (1983). Data characterizing nest sites after the ENSO were gathered at the same colony site as the 1980 study (Y-site). Tropicbirds have bred at Y-site since at least 1967 (Schreiber, unpubl.).

We visited nests throughout July, the peak pe-riod of hatching for tropicbirds breeding on Christmas Island (Schreiber and Ashmole 1970). All active nests (AN) within the Y-site area were censused and marked, as they have been since 1980. Nests were typically located under small scattered shrubs (0.5–3.5 m high) within the scae-vola/turnefortia habitat.

We also established a null data set composed of randomly placed points (RP). Shrubs contain-ing RP were located by randomly selecting a compass bearing and randomly selecting shrubs encountered along that bearing. Additional shrubs containing RP were selected by repeating the above procedure. Once a shrub was marked, the RP was located by randomly assigning the null nest site to a 45° octant (with the main trunk of the shrub as the origin), and randomly assigning the null nest site a position from the outer edge of the shrub. Shrub radius ranged from 1–4 m.

For each nest site, actual or random, we mea-sured the following variables: (1) Species, the species of tree under which the nest occurred. (2) Height, the maximum height (m) of the shrub. (3) Stems, the number of stems intersecting an 0.5-m^3 'nest space,' centered at the nest site. (4) Edge, the shortest linear distance (m) from the edge of the shrub to the center of the nest site. (5) Center, the shortest linear distance (m) from the main trunk of the shrub to the center of the nest site. (6) Cover (east), the extent of vegetative cover on the outer surface of the shrub, along the arc described by the two octants centered around 90°, 0.6 m in height, and estimated to the nearest 20%. (7) Nearest shrub (Nshrub), the nearest dis-tance (m) between the edge of a shrub containing AN or RP and the edge of a second shrub. (8) Neighbor (Neigh), the nearest distance (m) be-tween two nest sites or RP. (9) Orientation, the compass position of the nest site within the shrub. The trunk of the shrub was the center of origin, and each nest was located in an octant of 45° (0–45°, 46–90°, etc.) with respect to magnetic north.

THERMAL ENVIRONMENT

We monitored black-body (T_B) and ambient (T_a) temperatures at two nest sites on 10 and 12 July 1984. At the first nest (A) we placed water-filled, 2-dram glass vials, painted flat black, on the ground at the actual nest site, and along the solar path on either side of the nest. We also monitored T_B and T_a at a second active nest (B). Within the shrub containing nest (B), we monitored T_B at four locations used by tropicbirds as nest sites in previous years. At Y-site, nests are perma-nently marked with numbered tags and area readily identifiable by depressions that persist over many years.

The black-body temperature is an index of temperature which integrates heat transfer due to conduction, convection, and radiation. As measured in this study the black-body temperature recorded at ground level represented a crude index of heat load that a tropicbird, or its chick, faced during the day. Despite the fact that the vials had different spectral properties than tropicbird feathers, the integrative index was a better representation of heat load than air temperature alone (Gates 1980). Temperatures were monitored via a Chromal-Alumel thermocouple placed within each vial. Ambient temperature was monitored by placing a thermocouple 0.5 m above ground, but within the understory of the shrub. The thermocouple was shielded from direct exposure to the sky and ground to minimize radiative influences. All thermocouples were attached to a multiplexing unit, cold junction compensator, and linear chart recorder (Omega Engineering) for a continuous record of temperatures. Thermocouples were calibrated in a water bath against a mercury thermometer whose calibration is traceable to the National Bureau of Standards, U.S.A.

ANALYSES

We used discriminant function analysis to test hypotheses about nest-site preferences and habitat structure. Initially, we compared actual nests to randomly placed points in 1984 (AN84 vs. RP84) to determine whether tropicbirds used nest sites nonrandomly (cf. Clark et al. 1983). The comparison of actual nests from 1980 and 1984 (AN80 vs. AN84) tested the hypothesis that preferences for nest sites did not change as a consequence of the ENSO. Finally, we compared randomly placed points from 1980 and 1984 to test the hypothesis that the overall habitat structure did not change as a consequence of the ENSO (RP80 vs. RP84).

For each hypothesis tested, all appropriate z-transformed variables were entered directly into the analysis to correct for differences in measurement scale among variables. All variables were considered in the AN84/RP84 comparison. Only four variables pertaining to vegetation structure were considered for the RP80/RP84 analysis. Variables pertaining to nest-site placement were not considered because these were determined by us in both cases. We used a prior probability proportional to sample size for all classifications. Sample sizes were AN80 = 31, RP80 = 31, AN84 = 77, and RP84 = 72.

Univariate comparisons of nest-site measurements were carried out using t-tests between groups. In cases where group variances were unequal, an approximate t-statistic and Satterthwaite's approximation for the degrees of freedom were used as tests for differences between group means (SAS 1985).

Patterns of AN and RP dispersion were tested using Kolmogorov-Smirnov tests. Z-transforms of the variables: stem, cover, and height were used to compute dissimilarity scores based upon Euclidean distances between pairs of nests. Scores for nearest-neighbor pairs were used in correlation analysis with nearest-neighbor distances to test hypotheses regarding the dispersion pattern of vegetation resources used for nest sites. This information was useful in interpreting whether clumped resources or sociality were important in explaining the dispersion pattern of nests.

RESULTS

NONRANDOM NEST-SITE SELECTION:
AN84 VS. RP84

Discriminant analysis separated randomly placed points from actual nest sites (Table 1, Fig. 1). Actual nest sites tended to be shielded by more peripheral vegetative cover than the random points. Moreover, the distances between nest sites were shorter than interpoint distances for randomly placed points (Table 2). This clumping of nest sites may reflect social attraction among breeding tropicbirds and/or a clumped distribution of suitable nesting shrubs (see below).

The overall efficiency of classification for the discriminant analysis was 77.2%, whereas the frequency of correct classification prior to the ENSO in 1980 was 79.1% (x^2 = 1.65, df = 1, P < 0.25). This pattern suggests that nonrandom nest-site selection continued even after the ENSO. The extent of peripheral cover available from the nest-site shrub was the most important variable in discriminating between actual nests and random points in both years (Table 3, Clark et al. 1983).

CHANGES IN NEST-SITE CHARACTERISTICS:
AN80 VS. AN84

Discriminant analysis was not able to adequately distinguish between the actual nest sites used by tropicbirds at Y-site before and after the 1982–

TABLE 1. Summary of discriminant analyses for each of the pairwise group comparisons.

	AN84 vs. RP84	AN80 vs. AN84	RP80 vs. RP84
Eigenvalue[a]	0.475	0.106	0.500
Canonical correlation[b]	0.567	0.310	0.576
Wilk's lambda[c]	0.678	0.904	0.668
χ^2	55.74	10.45	39.95
df	7	5	4
P	<0.001	0.063	<0.001

[a] Large values are associated with functions with good discriminatory ability.
[b] A measure of association between discriminant scores and groups.
[c] The proportion of total variance in discriminant scores not explained by differences among groups, i.e., small values indicate good discriminating potential of the variables.

1983 ENSO (Table 1). The broad overlap in discriminant scores (Fig. 2) indicates that despite the occurrence of ENSO, tropicbirds exhibited stable nest-site preferences over time.

CHANGES IN HABITAT STRUCTURE: RP80 VS. RP84

Discriminant analysis separated characters associated with random points between pre- and post-ENSO breeding seasons (Table 1, Fig. 3) based primarily upon the height of shrubs and the number of stems occurring at the sampling point (Table 3). Shrubs were taller, had denser canopies, and had clearer understories after the ENSO (Table 2). The decreased number of stems within sampling spaces observed after the ENSO represented an overall habitat shift for this character toward a range preferred by nesting tropicbirds, perhaps increasing the amount of suitable breeding habitat to the birds.

The ENSO visibly affected the structure of the vegetation. During the 1982–1983 ENSO, the
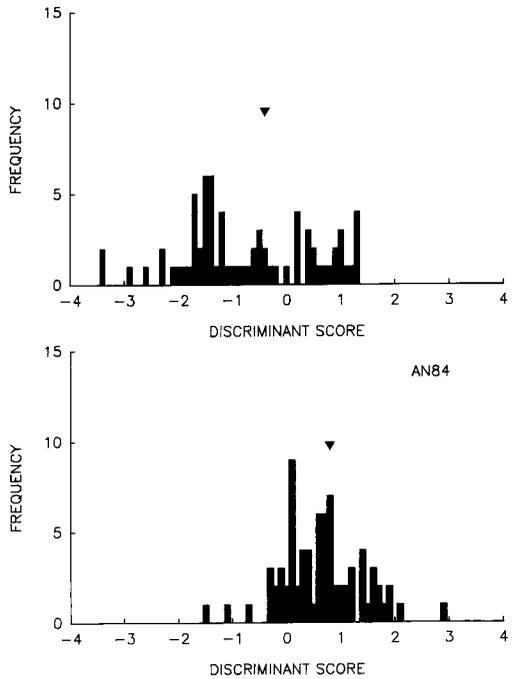
FIGURE 1. The frequency distribution of scores for the discriminant function from the analysis AN84 vs. RP84 (see Methods for definitions). The arrows indicate group centroids. The discriminant axis is interpreted as a cover-edge/nearest-neighbor axis. Actual nest sites were protected by more peripheral vegetative cover, were further from the edge of the perimeter of the nest shrub, and were closer to another nest site than the random points.

island received over 100 mm of rain per month; 600 mm fell within a 4-month period. The 47-year mean rainfall was less than 50 mm per year (Schreiber and Schreiber 1984). Rapid leaf growth occurred during the period of flooding creating

TABLE 2. Summary statistics of nest-site characteristics.

	AN80		AN84			RP80		RP84		
	x̄	SE	x̄	SE	P[a]	x̄	SE	x̄	SE	P[b]
Height	2.07	0.15	2.03	0.17	0.887	9.2	0.16	13.9	0.14	0.053
Stems	3.0	0.4	2.1	0.2	0.039[c]	11.5	2.2	2.4	0.3	0.001[c]
Edge	1.11	0.17	1.0	0.12	0.565	1.92	0.27	0.58	0.07	0.001[c]
Center			0.66	0.1				0.57	0.12	
Nshrub	2.33	0.45	1.95	0.41	0.455	1.94	0.55	1.23	0.42	0.278
Neigh			5.66	0.66				10.3	1.62	
Cover	73.8	4.9	84.4	2.1		47.6	7.3	52.1	4.8	

[a] The probability of the t-test for a comparison of AN80 and AN84.
[b] The probability of the t-test for a comparison of RP80 and RP84.
[c] Indicates that the variances were unequal and that probabilities were estimates of the t-statistic and Satterthwaite's approximation of df.
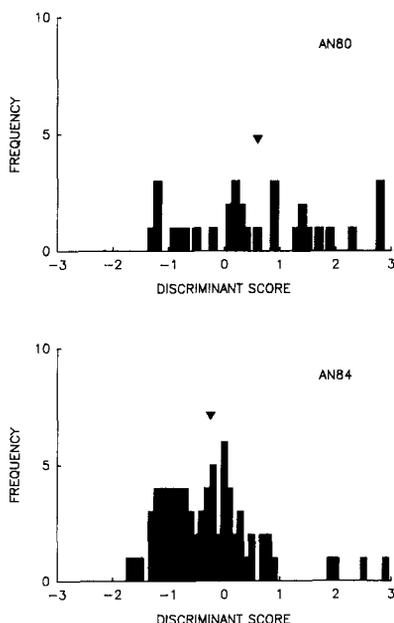
FIGURE 2. Frequency distribution of scores for the discriminant function from the analysis AN80 vs. AN84. The arrows indicate group centroids. While the discriminant function was not significant, the axis can be interpreted as a stems-cover axis. Actual nests in 1984 tended to have fewer stems within the nest space and more cover on the periphery of the shrub.

FIGURE 3. Frequency distribution of scores for the discriminant function from the analysis RP80 vs. RP84. The arrows indicate group centroids. The discriminant axis can be interpreted as a stems-height axis. After the ENSO, shrubs tended to be taller with less branching beneath the canopy.

thick canopies. Beginning in late 1983, a drought greatly reduced vegetative growth.

DENSITY OF BREEDING POPULATION

During the 1980 breeding season there were only 40 active nests at Y-site. Two years after the ENSO, in the 1984 breeding season, there were 77, a 92.5% increase. The shift in habitat struc-

ture, the demonstration of nest-site preference and stability of preferences over time, combined with the observed increase in number of active nests at Y-site suggest the possibility that breeding opportunities are limited by the availability of suitable nest sites.

BAND RETURNS

Figure 4 shows the probability of adult tropic-birds returning to Y-site as a function of years

TABLE 3. Summary of standardized canonical discriminant function coefficients (SCC)[a] and pooled within-group correlation matrix (PCM)[b] for the variables for each of the group comparisons.

| | AN84 vs. RP84 | | AN80 vs. AN84 | | RP80 vs. RP84 | |
	SCC	PCM	SCC	PCM	SCC	PCM
Stems	−0.064	−0.084	0.511	0.433	0.526	0.860
Height	0.089	0.412	0.120	−0.031	1.012	0.217
Nshrub	0.165	0.088	−0.025	0.026	0.109	0.088
Cover	0.685	0.749	−0.863	−0.861	−0.298	−0.020
Edge	0.370	0.561	0.261	0.155		
Neigh	−0.493	−0.460				
Center	−0.071	0.063				

[a] Standardized coefficients allow evaluation of the importance of variables while adjusting for differences in measurement scale. The magnitude of the score is a judgement of the importance of that variable to the discriminant function.
[b] PCM is the correlation of variables with the discriminant function which allows an evaluation of shared contribution of that variable in interpreting the standardized scores.
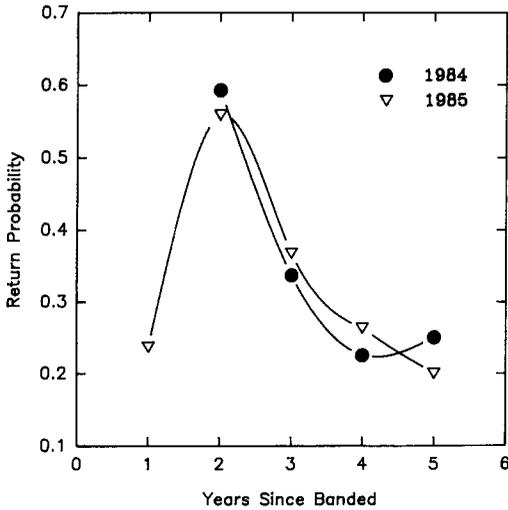
FIGURE 4. The probability of recovering banded tropicbirds as a function of the number of years since they were initially banded. Recoveries are reported for 1984 and 1985.

Time of Day

FIGURE 5. (A) The ambient (T_a) and black-body (T_B) temperature at a single nest site as a function of time of day. (B) The difference between the black-body temperatures of the nest site and locations underneath the shrub along the solar path as a function of time of day. Positive values indicate temperatures warmer than that recorded at the actual nest site. Points 1 ($\cdots$) and 2 (– – –) were 1.5 and 0.5 m east of the nest site, while points 3 (——) and 4 (–·–) were 0.9 and 1.8 m west of the nest site, respectively.

since banding for two post-ENSO years, 1984 and 1985. All the birds banded at Y-site and considered in Figure 4 were adults that established nest sites. The low probability of recapture for the first year after being banded is consistent with observations at other islands that the tropicbirds' breeding cycle is greater than 12 months (Stonehouse 1962). After 1 year, the probability of recapturing birds decreased exponentially over time. In 1984 and 1985 the return rate for birds banded during the ENSO was the same as for birds banded in pre- and post-ENSO years. This pattern suggests that the return rate was primarily a function of time, and that ENSO did not result in a pulse of breeding adults in post-ENSO years because some of these adults deferred breeding during the ENSO.

THERMAL ENVIRONMENT
AT NEST SITES

While vegetative characters, such as number of stems at ground level, may physically exclude birds from nesting, vegetative cover may be important in providing protection against wind and insolation. In 1980, we found that shade at the nest site at solar noon was not a good basis for discrimination between actual nest sites and randomly placed points (Clark et al. 1983). However, vegetation height was a good basis for discrimination, and height and shade covaried

significantly. We also found, in this and our previous study, that extensive peripheral vegetative cover was associated with actual nests, suggesting that midmorning and afternoon sun penetrating the leaf cover might limit insolation at the nest site. T_B at nest site A was relatively stable throughout the day, except for a brief period between 10:00–11:00 (Fig. 5A) when it exceeded T_a by 7°C. For the remainder of the day, T_B exceeded T_a by only 1–2°C. The T_B of four randomly placed points along the solar path are shown in Figure 5B. Prior to solar noon, points to the east of the nest site were warmer by as much as 12°C, and at no point were they cooler than the nest site. In all cases the integrated heat load (area under the curve) of random points was
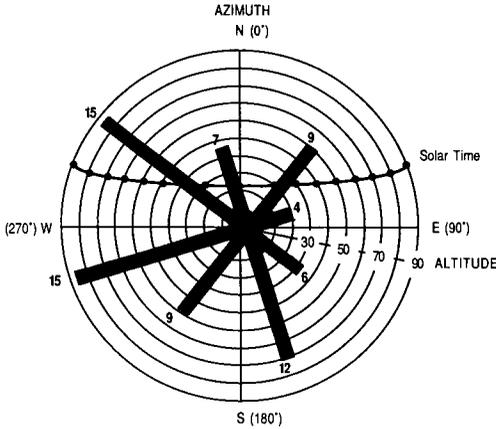
FIGURE 6.   The frequency distribution of actual nests in 1984 (solid bars) as a function of compass orientation (azimuth). Concentric circles depict the sun's altitudinal scale. The solid circles connected by the curved line represent the solar path at hourly intervals, as a function of the altitude and azimuth (Gates 1980). The frequency distribution of nests tends to be away from direct exposure to the sun.

greater than T_B recorded at the nest site. Points to the west of the nest site fared somewhat better prior to solar noon, and were 6°C cooler than the nest site T_B. However, after solar noon these westerly points were hotter than the nest site.

The polar distribution of nests supports the hypothesis that birds chose the coolest spot within a tree (Fig. 6). More nests were positioned on the west-southwestern side of trees, where integrated thermal load was least (based upon data derived from nest A), and which placed the maximum amount of foliage between the nest and the solar path.

Figure 7A depicts T_a and T_B at nest B. Heat loads for nest sites used in previous years were greater on average than for the active nest site (Fig. 7B). Taken together, the temperature data indicate that tropicbirds are sensitive to thermal load, and while tending to be site faithful (Schreiber and Schreiber 1987), will place nests to minimize insolation levels.

DISTRIBUTION OF NESTS

The essence of coloniality is the proximity of nesting birds. The question remains as to whether proximity results from aggregation around clumped resources, social attraction, or both. Within Y-site we found that the dispersion of actual nests was significantly clumped (Fig. 8,
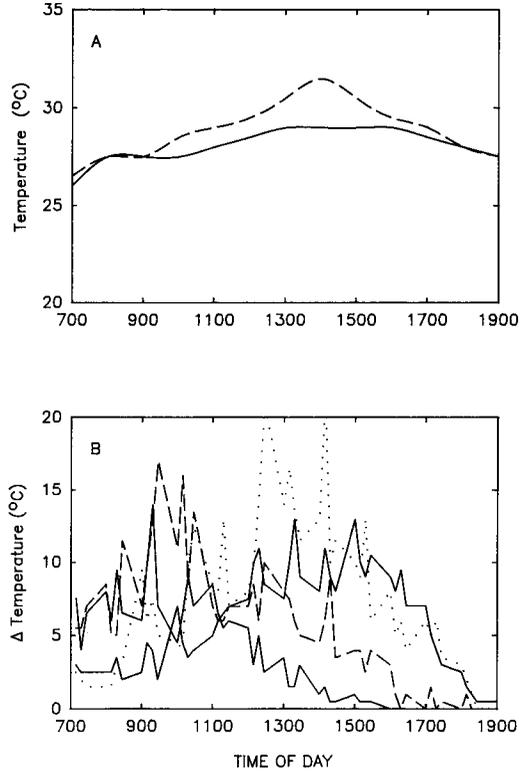
FIGURE 7.   (A) The ambient (——) and black-body temperature (– – –) at a single nest site as a function of time of day. (B) The difference between the black-body temperatures of the nest site and sites previously used by tropicbirds within the same shrub. Positive values indicate temperatures warmer than that recorded for the actual nest site.

Kolmogorov-Smirnov test, $P < 0.05$). This clumping pattern resulted from too few shrubs harboring one nest and too many harboring two or more nests (number of shrubs containing 0, 1, 2, 3, and 4 nests = 294, 44, 13, 1, 1, respectively, $\chi^2 = 61.29$, df $= 1$, $P < 0.001$ when tested against a Poisson distribution). As a control, we tested whether the placement of the RPs was indeed random. The dispersion of randomly placed points was in general accordance with an hypothetical random dispersion pattern. The minor deviation from linearity seen in Figure 8 represents constraints imposed upon nearest-point distances by the dispersion pattern of shrubs.

To what extent clumped resources are responsible for the tendency of tropicbirds to nest close to one another can be determined by comparing
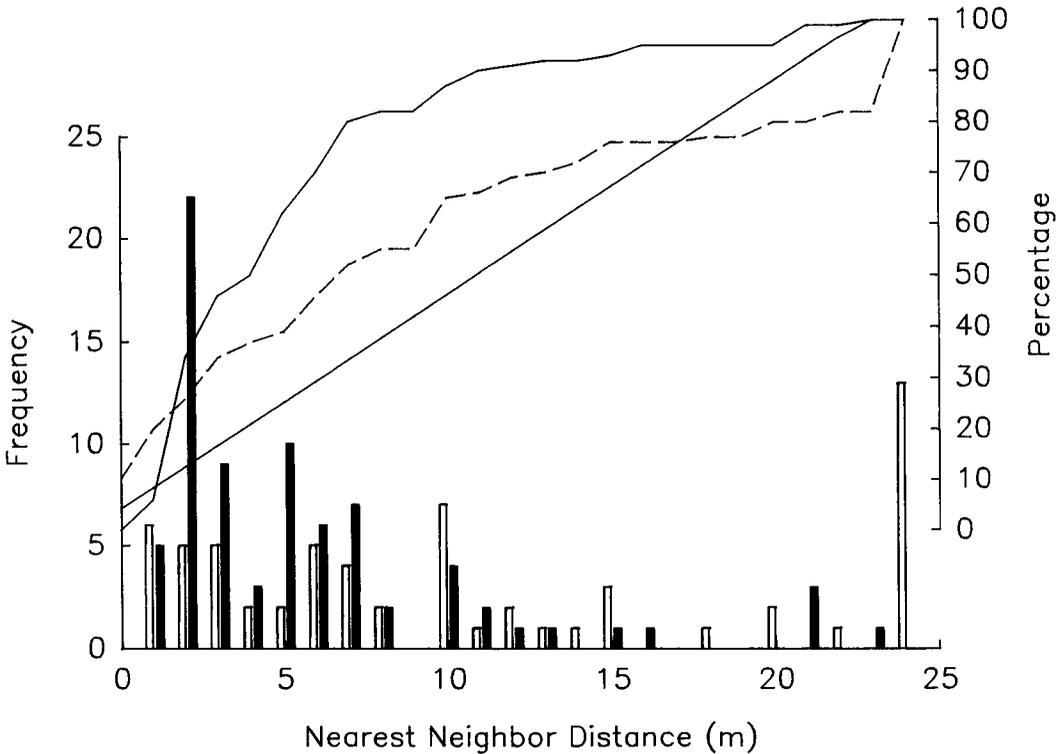
FIGURE 8. The cumulative frequency distribution of nearest-neighbor distances for actual nests (solid bars, solid line) and randomly placed points (open bars, dashed line). The solid diagonal line depicts a theoretical random dispersion pattern.

the dispersion pattern of vegetation structure for potential and actual nest sites. Vegetation associated with RPs with small nearest-point distances should be more similar than vegetation associated with RPs with large nearest-point distances, if only because close points are likely to be under shrubs experiencing similar microclimatic and soil conditions, or even within the same shrub. Figure 9A supports this hypothesis ($P < 0.05$, $r = 0.253$, df = 69).

Despite the vegetative similarity of near-point pairs, we found no relationship between nearest-nest distance and similarity of vegetation for actual nest sites (Fig. 9B, $r = 0.066$, $P < 0.1$). From the discriminant analysis we know that tropicbirds demonstrated specific, stable preferences for vegetation parameters associated with nest sites. Thus, the data indicate that the narrow spectrum of vegetative characters preferred by tropicbirds are exploited regardless of where they occur within the Y-site. The fact that some shrubs contain more than one nest reflects homogeneity

of vegetation resources that fall within the bounds of preferences expressed by tropicbirds, i.e., the occurrence of good nest shrubs. Therefore, the clumped dispersion of actual nests seen in Figure 8 is consistent with the utilization of clumped resources.

DISCUSSION

Our data do not exclude the possibility that social attraction is a factor in the formation and maintenance of tropicbird colonies. Birds may be attracted to specific habitat because of the presence of other birds. Such behavior would reduce the time and energy needed to locate suitable nesting habitat. However, if social attraction were the principal factor in the formation of colony structure then we might expect a tighter dispersion of nests coupled with a distribution of discriminant scores for actual nests that converged on the distribution seen for random points. Figure 9 does not support this expectation.

The strong site fidelity observed for tropicbirds
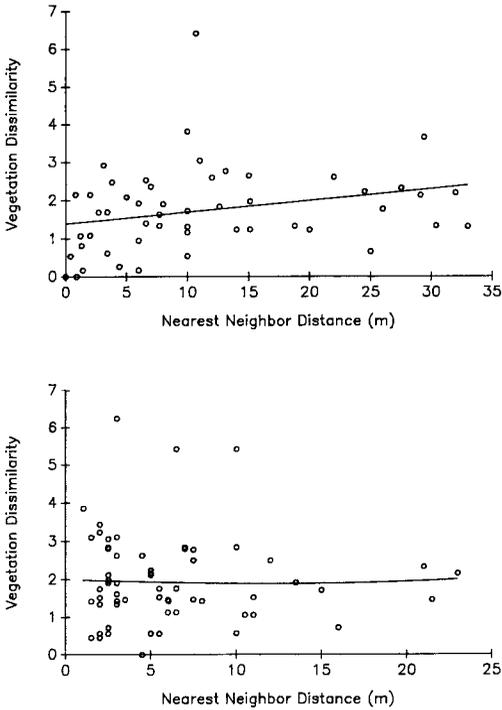
FIGURE 9.   The dissimilarity scores for the vegetation variables stems, cover, and height for pairs of random points (A, upper) or nests (B, lower) as a function of nearest-neighbor distances. A score of zero indicates identical vegetative structure.

may result from restricted availability of suitable sites, and the fact that good nest shrubs retain their features for long periods of time, even though the exact location of prime sites within the shrub may shift from year to year. Site fidelity and strong competition for limited nest sites may explain why a large percentage of tropicbirds nesting on Johnston Island (16°45'N, 169°31'W) did not nest in a year following the destruction of their nest shrub (Schreiber and Schreiber, unpubl. data).

After the 1982–1983 ENSO shrubs within the scaevola/turnefortia habitat had more extensive foliage cover and fewer stems at ground level. This difference in pre- vs. post-ENSO vegetation structure at the Y-site tropicbird colony was accompanied by an increase in the number of nests (AN80 = 40, AN84 = 77). Because nest-site preferences remained stable over time, our findings indicate that reproductive opportunities could be limited by availability of suitable nest sites. An alternative explanation is that the ENSO caused

adults to defer breeding, resulting in an increase in the number of active nests in post-ENSO years. Schreiber and Schreiber (1989) reported that tropicbirds initiated breeding during 1982 in a pattern similar to pre-ENSO years. They noted that the chicks were characterized by slower growth rates in July, and by fall many nests had failed. However, the ENSO did not appear to affect the probability of returning to Y-site for adult tropicbirds (Fig. 4). The low probability of being recaptured 1 year after banding is in agreement with an annual breeding cycle of more than 12 months as suggested by Stonehouse (1962). For periods greater than 1 year, the probability of recapturing previously banded birds decreased exponentially as a function of time. ENSO appears to have had little effect on the probability of recovering banded birds, implying that the ENSO did not cause birds to "pool-up" and defer breeding which would result in an increased number of active nests during post-ENSO years. If the ENSO caused birds to defer breeding, and these birds survived the ENSO, then the probability of returns should have deviated from the negative exponential pattern of return. This was not the case.

One underlying assumption of the interpretation that nest sites limit reproductive opportunities is that nonbreeding birds are always at hand ready to occupy optimal nest sites. While we had no way of quantifying the number of birds in the nonbreeding pool, visual inspection of birds displaying at colony sites suggested a number of nonbreeding birds were present. A second assumption of the hypothesis is that birds defer breeding because the cost (in terms of future fecundity and survivorship) is greater when suboptimal locations are used. Prys-Jones and Peet (1980) found that sheltered sites were used as nest sites first, then the more exposed sites were used. The latter were used only when vegetation grew to an extent to provide sufficient cover for shade (cf. Diamond 1975). Evaluation of the suitability of a nest site may occur by assessing the accessibility of the potential nest site. Fleet (1974) noted that 90% ($n = 2,000$) of tropicbird nests on Kure Atoll were within 3 m of the vegetation's edge, which could mean that the labored terrestrial locomotion of tropicbirds through the tangle of stems at ground level limits the distance they travel (Howell and Bartholomew 1969). Thermal load experienced by birds while sitting on the ground also is important. Young tropic-

birds, especially those in downy plumage, are highly sensitive to heat stress (Howell and Bartholomew 1962). Thus, direct exposure to insolation, even if only for a few minutes, can prove lethal to chicks. Choosing a nest site which minimizes direct exposure to the sun obviates the parent's need to brood the chick. Once released of the brooding obligation, parents can increase the time devoted to foraging activity (Clark and Ricklefs 1988). Many nonbreeding birds are observed to sit on the ground for long periods, presumably at potential nest sites. We suggest that once a bird selects a general area in which to breed, it then evaluates the quality of the site by experiencing the thermal load it would be likely to incur. Our data indicate that extant nest sites are at the coolest locations under shrubs. These observations are consistent with other descriptions of Red-tailed Tropicbird nest sites. Amerson and Shelton (1976) described shade to be a primary requirement for nest sites.

It is unlikely that tropicbird populations are regulated by any single factor. ENSO events may have unpredictable but devastating effects (Schreiber and Schreiber 1989). If the number of potential breeding pairs exceeds available sites, the rate of recovery from acute population crashes will be constrained. Alternatively, as was the case on Christmas Island, meteorological events actually increased the availability of potential nest sites, the population recovery may be facilitated. Thus potential energy and terrestrial habitat constraints on reproductive opportunities may shift in importance spatially and temporally ultimately influencing the structure and dynamics of tropicbird populations.

The importance of habitat constraints to reproduction is unresolved at present. Future studies should focus on a long-term correlational study of number of nests, availability of preferred sites, and habitat structure during non-ENSO years. More definitive studies might include logistically difficult habitat manipulation experiments guided by information about tropicbird nest-site preferences.

ACKNOWLEDGMENTS

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