NEST-SITE SELECTION BY THE
RED-TAILED TROPICBIRD

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Abstract.—Red-tailed Tropicbirds (*Phaethon rubricauda*) nest under shrubs in loosely associated groups on Christmas Island, Central Pacific Ocean. Aggressive interactions among adults at nest sites are high; yet, large areas of superficially similar habitat contain no tropicbird nests at all. We compared physiognomic features of nest sites with those of two sets of randomly generated "nest sites" by discriminant function analysis. Of those variables measured, the number of stems within a nest space and the amount of peripheral cover influenced the tropicbirds' choice of nest sites. Differences among localities existed. Areas where tropicbirds nested had shrubs with few stems and more peripheral cover. Preferred nest sites were rare in areas other than those in which tropicbirds were nesting already. This study demonstrates the utility of the discriminant function technique in quantifying nest-site selection and nest-site availability when the appropriate null data sets are used. *Received 22 November 1982, accepted 21 March 1983.*

Nest sites have been described in terms of general habitat and vegetation (e.g. Fleet 1974), multivariate assessment of nest placement (e.g. Gabaldon 1978), and environmental factors governing nest-site selection (e.g. Walsberg and King 1978). Among species that feed within nesting territories, suitable nest sites may not be used because nests are too widely spaced. In colonial and semicolonial seabirds, territory size is much reduced, and breeding populations may be restricted by the availability of suitable nest locations (Trivelpiece and Volkman 1979). Few researchers have addressed the problem of nest-site selection in seabirds (Lack 1934, Croxall and Prince 1980), and even fewer have attempted to test the hypothesis that nest sites may be limiting.

In this paper, we approach the problem of nest-site selection in the Red-tailed Tropicbird (*Phaethon rubricauda*) by comparing the characteristics of actual nest sites with those of randomly chosen sites both within active colonies and in areas of superficially similar habitat not used for breeding. Samples are compared by discriminant function analysis.

METHODS

Our fieldwork was conducted during July 1980 on Christmas Island (5°N, 153′W), where tropicbirds nest in small, discrete colonies (Schreiber and Ashmole 1970). Nests are typically located under small, scat-tered shrubs, most frequently tournefortia (*Messerschmidia argentea*) and scaevola (*Scaevola taccada*).

Our major study area was located on a peninsula near the center of the island (Y-site of Schreiber and Ashmole 1970), which has supported a colony of tropicbirds since at least 1967 (R. W. Schreiber unpubl.). At least 50 pairs of tropicbirds were nesting in the area during July 1980. Within this larger area we delimited three study areas of 60 × 60 m. Area I contained 19 active nests, Area II 12, and Area III 5 nests. These areas contained eggs or nestlings during our study and, together, were labeled AAAN (Actual Area, Actual Nest sites).

We established two sets of random nest sites (1) ARN (Actual Area, Random Nest sites). For Areas I, II, and III above, we located 19, 12, and 5 random "nest sites" by using a table of random numbers to select for each "nest site" a shrub along a transect across the length of the area. We oriented the site relative to a 45° octant, (with the center of the shrub as the origin) and to the distance from the nearest edge of the shrub. Random numbers designated intervals of distances, e. g. 1 = 0–0.5 m, 2 = 0.51–1.0 m, etc. The range of radii for shrubs was 1–4 m. (2) NULL (Null Area, Random Nest sites). We chose three 60- × 60-m areas in which there were no tropicbird nests but that had general physiographic features similar to areas where tropicbirds did nest. Random "nest sites" were located by the same methods as for ARN.

For each nest site, actual or random, we measured the following variables: (1) SPECIES, the species of shrub or bush under which the nest was placed; (2) HEIGHT, the maximum height (m) of the shrub un-
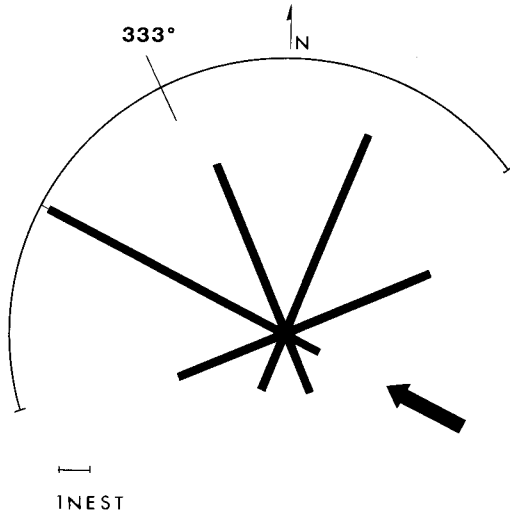
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Fig. 1. Nest dispersion patterns of Red-tailed Tropicbirds at shrubs used for nesting cover. The mean angle of orientation was 333° ± 80.83 SD. The arrow indicates the direction of the prevailing wind.

der which a nest was placed; (3) PERIMETER, the distance (m) around the edge of a shrub containing a nest; (4) EDGE, the shortest straight-line distance (m) between the nest and the outside edge of a shrub; (5) NEAREST, the shortest distance (m) between the edge of the shrub containing a nest and the edge of the nearest other shrub of any species; (6) STEMS, the number of stems intersecting a 0.5-m² area centered on the nest; (7) SHADE, the amount of shade covering an 0.5-m² area centered on the nest, estimated to the nearest 20% (shade was recorded between 1100–1300, PST); (8) ORIENTATION, the compass orientation of the nest. With the trunk of the shrub as a center of origin each nest was located in an octant of 45° (0–45°, 45–90°, etc) with respect to magnetic north. Trade winds consistently blow from the east (90°) to east southeast (145°) on Christmas Island; (9) COVER, the extent of vegetative cover on the outer surface of a shrub 0.6 m in height along the arc described by the octant containing the nest, estimated to the nearest 20%; and (10) SUBSTRATE, the predominant substrate around the nest scrape or random site. Five substrates were recognized: leaf, sand, shell, hardpan, and coral rubble.

We subjected each paired comparison of groups to a stepwise discriminant function analysis (SPSS, Nie et al. 1975). Using the Box's M criterion, we found that covariance matrices were not homogeneous between groups. Using the Malhalonobis distance between group centroids as the criterion for maximizing the separation of groups, we based the comparison between groups upon the pooled within-group covariance matrix. This method is most suitable when

covariance matrices do not meet the multinormal assumption for discrimination (Hand 1981). Discriminant function analysis provides a linear combination of a subset of the variables that optimally discriminates between two groups. Continuous variables (HEIGHT, PERIMETER, NEAREST, STEMS, SHADE, COVER) were entered into the stepwise procedure untransformed. The variable SUBSTRATE was entered as a dichotomous dummy variable: soft (leaf, sand) = 0 and hard (hardpan, coral rubble, shell) = 1. As each of the three groups of nest sites (AAAN, ARN, NULL) comprised pooled data with identical sample sizes ($n = 36, 36, 36$), the criterion for establishing prior probabilities for group membership was equal.

The comparison of ARN with NULL tested the null hypothesis that areas chosen for nesting did not differ from areas not used, and hence it tested whether or not tropicbirds may have chosen nesting areas according to habitat structure. The comparison of AAAN with ARN allowed us to determine whether or not nest sites differed subtly from physiognomically similar, randomly located "nest sites" and hence whether or not there was nest-site selection. By examining overlap of the two samples along the discriminant function in the comparison of AAAN with NULL, we determined whether or not areas not used for nesting contained suitable nest sites.

A separate analysis was performed for compass orientation of nest sites in the AAAN group. Because ARN and NULL were randomly positioned, no analyses of those data were necessary. The statistic for circularly distributed data, Raleigh's R, was used to test the null hypothesis of random orientation of nest sites (Zar 1974).

RESULTS

Characterization of actual nests.—Nests within the AAAN group were not randomly oriented with respect to the center of shrubs ($R = 13.32$, $P < 0.01$, $n = 36$). The dispersion pattern of nest sites, (Fig. 1) indicates that nests were positioned on the lee side of shrubs. This is consistent with two observations of tropicbird behavior. Tropicbirds stall into the wind when approaching the nest and then fall to the ground (often through the branches of the shrubs). Because their legs are positioned posteriorly, tropicbirds walk with great difficulty. Landing close to the nest site reduces the distance they have to walk. Of the 36 nests, 23 were within 1 m of the edge of the shrub. While the data indicate that tropicbirds favor nest sites that are easily accessible, given their constraints on landing and locomotion, they do not indicate that tropicbirds avoid exposure to
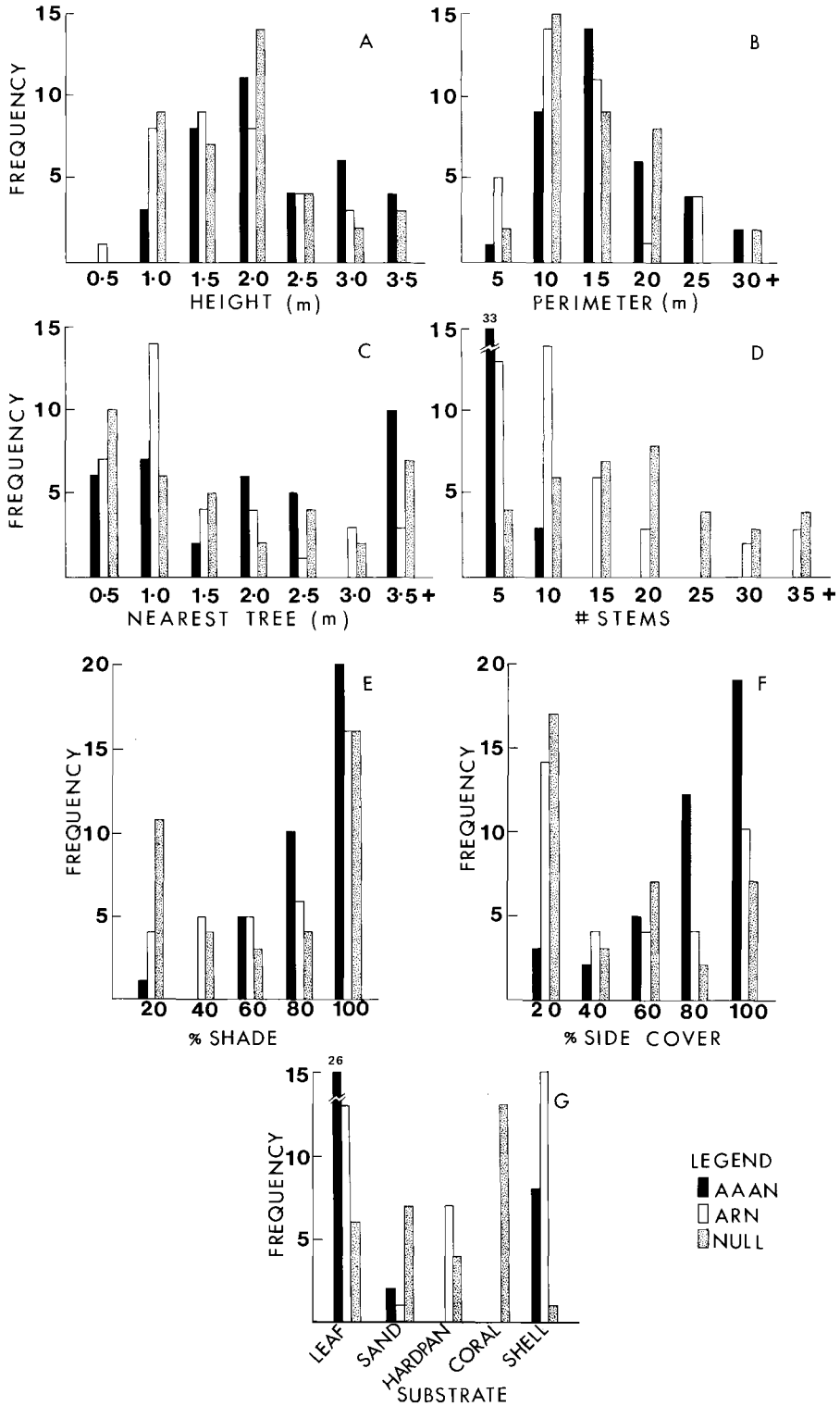
Fig. 2. Frequency distributions of seven variables measured for AAAN (solid bar), ARN (open bar), and NULL (stippled bar). See methods for a detailed description of the variables.

TABLE 1. Summary statistics of nest-site characteristics.

	AAAN	ARN	NULL
	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$
HT	2.11 ± 0.82	1.92 ± 0.91	1.81 ± 0.62
PERM	14.53 ± 6.29	11.17 ± 5.73	12.22 ± 7.28
NEGH	2.33 ± 2.37	1.94 ± 2.78	1.97 ± 1.63
STEM	3.22 ± 2.32	11.50 ± 11.39	17.39 ± 10.03
SHADE	82.92 ± 21.07	67.64 ± 31.04	62.22 ± 37.86
COVER	73.75 ± 27.01	47.64 ± 40.56	40.55 ± 34.86
SUBST	0.22 ± 0.42	0.61 ± 0.49	0.50 ± 0.51

the wind. For nest-site placement, distance from the edge of a shrub was not related to the deviation from the prevailing wind direction ($r = -0.089$), as would be expected if tropicbirds were avoiding exposure to wind at the nest site. Similarly, the percentage of cover on the side of a shrub was not related to distance from the edge ($r = -0.061$), nor was the percentage of cover related to deviation from the prevailing wind direction ($r = 0.005$).

The data presented in Fig. 2 and Table 1 indicate that the distribution of nest-site characteristics for the AAAN group is different from the distribution of characteristics for randomly selected potential "nest sites" (ARN, NULL), primarily by having fewer stems within the nest space (Fig. 2d) and a greater amount of cover of vegetation on the side of the shrub where the nest is located (Fig. 2f). These apparent differences are tested statistically using the discriminant procedure.

Comparison between areas.—A stepwise discriminant procedure was used to identify the subset of the variables that optimally distinguished the two groups of potential "nest sites" (ARN and NULL) in order to test for similarity between areas. EDGE was not included in this analysis, because, by definition, placement of the nest site was random in both groups. Thus, no differences for this variable would be expected. Three variables contributed significantly: STEMS, COVER, and PERIMETER (Table 2). The random potential "nest-sites" within the ARN group tend to have fewer stems and more cover on the side of the shrub adjacent to the "nest site" than do their NULL counterparts (Figs. 2b, 2f, 3). The group centroids differ significantly ($F = 2.841$, $P < 0.0442$, df = 3,68), indicating that tropicbirds possibly base their selection of locality on the number of stems within a potential "nest site" and the percent-

age of cover of vegetation on the side of a shrub adjacent to the "nest site" (Fig. 3, Table 2). Shrubs tended to be larger, and vegetation was qualitatively denser within the NULL area (Table 1, Fig. 2b). The discriminant function classified 64% of the nests correctly, indicating that random sites in the NULL area were not similar to the random nests of the "colony" area.

Comparison within areas.—We used a stepwise discriminant procedure to compare actual nest sites and randomly generated potential "nest sites" (AAAN and ARN) in order to test for nest-site preference. Compared to the ARN-NULL comparison, more variables entered the model at a significant level, and the discriminant function was more powerful in its ability to distinguish the two groups. Actual nest sites had many fewer stems within the nest space and more cover on the outer portion of the shrub than did the sample of randomly chosen potential "nest sites" (Fig. 2d, 2f). The group centroids were significantly separated along the stem-cover axis ($F = 10.534$, $P < 0.0001$, df = 4, 67; Fig. 4). Of random "nest sites" in nesting localities (ARN), 9 of 36 had features overlapping those of active nests (Table 3). The discriminant function classified 79% of the nests

TABLE 2. Summary of stepwise discriminant analysis for a comparison of random nest sites between areas (ARN vs. NULL).

Step	Entered[a]	Wilk's lambda	Minimum D^2	P	COEFF[b]
1	STEM	0.928	0.301	0.023	0.892
2	COVER	0.907	0.399	0.034	-0.697
3	PERM	0.889	0.487	0.044	0.484

[a] No variables were removed from the model.
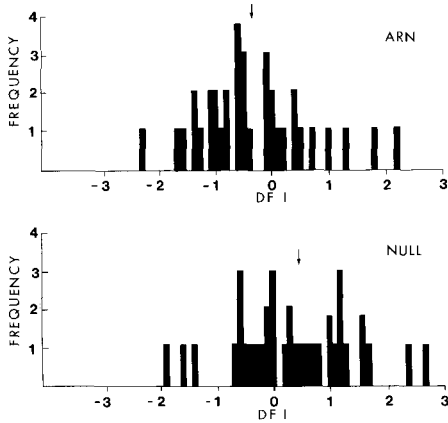[b] Standardized canonical discriminant function coefficient.

Fig. 3. Frequency distribution of scores for the first disciminant function from the analysis ARN vs. NULL. The arrows indicate group centroids. The first discriminant function is primarily a stem-cover axis. Randomly generated potential "nest sites" from "colony" areas (ARN) have fewer stems within the "nest space" and more cover along the side of the shrub.
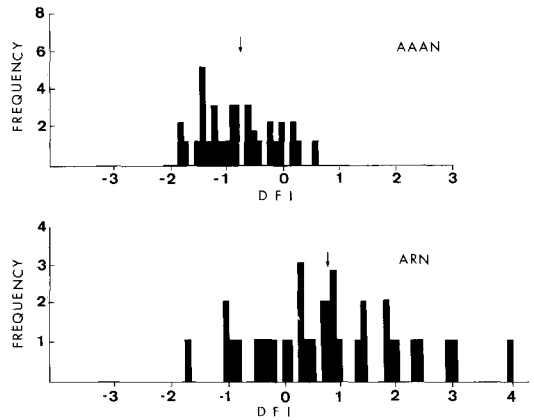

Fig. 4. Frequency distribution of scores for the first discriminant function from the analysis AAAN vs. ARN. Arrows indicate group centroids. The first discriminant function is primarily a stem-cover axis. Actual nests (AAAN) have fewer stems within the nest space and more cover along the side of the shrub.

correctly, indicating strong nesting-site preference (Table 3).

Comparison of actual nests and random "nest sites" in the null locality.—We used a stepwise discriminant analysis to distinguish actual nest sites from a random sample of potential "nest sites" at a different locality (AAAN and NULL). The discriminant function had three variables: STEMS, COVER, and SUBSTRATE, as in the AAAN-ARN comparison (Table 4). The group centroids were separated significantly ($F = 56.576$, $P < 0.0001$, df = 2, 69; Fig. 5). No nests were misclassified as belonging to the random "nest sites" in the null area, and only 5 of 36 randomly selected "nest sites" fell within the range of characteristics of actual nest sites. There were few randomly selected "nest sites" that could have served as adequate tropicbird nests within the null area. The total number of correct classifications was 93%.

Discussion

Tropicbirds showed subtle preferences for particular nest sites. Of the seven variables for shrubs that we measured, two were important to tropicbirds: in general, nest sites were best characterized as being under shrubs with few stems within a 0.5-m² nest space and with a high amount of peripheral cover on the sides

of the shrubs. Tropicbirds apparently were able to distinguish among areas of similar appearance primarily by means of these factors.

The range of discriminant function scores for AAAN had little overlap with a set of scores derived from NULL. Seven "nest sites" of the NULL area overlapped the scores of actual nest sites; 29 did not (Fig. 5). A similar comparison of overlap of discriminant scores between actual nest sites and those from the ARN group show that 15 "nest sites" of the ARN group overlap and 21 do not (Fig. 4). The amount of overlap of scores with actual nest sites is not independent of area ($\chi^2 = 4.19$, d. f. 1, $P < 0.05$). This is consistent with the notion that areas where tropicbirds choose to nest are different from other superficially similar areas. Tropic-

TABLE 3. Summary of stepwise discriminant analysis for a comparison of actual and random nest sites within areas (AAAN vs. ARN).

Step	Entered[a]	Wilk's lambda	Minimum D^2	P	COEFF[b]
1	STEM	0.793	1.015	0.001	0.778
2	COVER	0.676	1.863	0.001	−0.585
3	SUBST	0.635	2.231	0.001	0.486
4	HT	0.614	2.446	0.001	0.330

[a] No variables were removed from the model.
[b] Standardized canonical discriminant function coefficient.

TABLE 4. Summary of stepwise discriminant analysis for a comparison of actual and random nest sites between areas (AAAN vs. NULL).

Step	Entered[a]	Wilk's lambda	Minimum D^2	P	COEFF[b]
1	STEM	0.506	3.790	0.001	0.934
2	COVER	0.379	6.377	0.001	−0.634
3	SUBST	0.346	7.356	0.001	0.369

[a] No variables were removed from the model.
[b] Standardized canonical discriminant function coefficient.

birds nesting on Kure Atoll and Midway Island used very little of the apparently suitable habitat for nesting (Howell and Bartholomew 1962, Fleet 1974). This result and those of the discriminant analysis lead us to conclude that shrubs with the qualities necessary for nest sites did not commonly occur within areas that tropicbirds chose as "nesting colonies" and were even rarer on other wooded areas of Christmas Island.

The importance of stems to nesting tropicbirds is apparent. Tropicbirds move poorly on the ground and rarely move more than 2 m. Locomotion is achieved by pushing up with their wings and shoving forward onto their breasts (Howell and Bartholomew 1962). Most birds land directly beside the bush and move quickly underneath. A large number of stems under a tree would severely impede movement. Additionally, large numbers of stems within a nest space would probably make it physically impossible for a tropicbird actually to make a scrape for a nest.

Tropicbirds are not discriminating among potential sites on the basis of shade when the sun is at its zenith. All sites measured have approximately the same levels of protection at the times measured (Table 1). Peripheral vegetation cover, however, may reduce insolation levels when the sun is not at its zenith (morning and afternoon hours). That shade is important to tropicbirds has been shown by Howell and Bartholomew (1962). While in the shade, adults and chicks can effectively regulate their temperature when the air temperature is high. High-temperature thermal stress occurs within seconds for chicks and within minutes for adults, however, once tropicbirds are exposed to solar radiation. Adults nesting in sunny areas moved out of the sun when temperatures became too high. These adults experienced a high
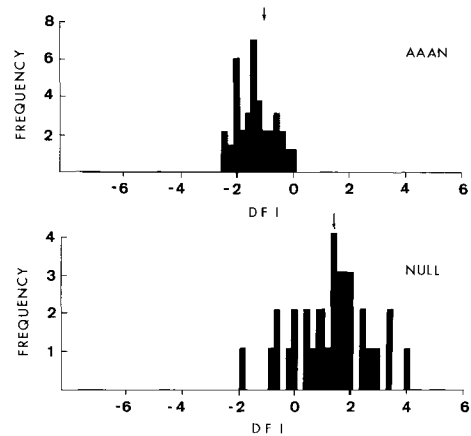

Fig. 5. Frequency distribution of scores for the first discriminant function from the analysis AAAN vs. NULL. Arrows indicate group centroids. Actual nests (AAAN) have fewer stems within the nest space and more cover along the side of the shrub.

degree of nest failure due to addling of the eggs. Surface temperatures can be substantially higher than temperatures only a few centimeters above the surface (Porter et al. 1973). If they are unshaded when the sun is low to midway on the horizon, the tropicbirds could face potentially large thermal loads due to solar insolation and re-radiation from the substrate.

Cover also may be important in obscuring nest locations from visually orienting predators, but, although Polynesian rats, feral cats, and feral pigs occur on the main island, we do not believe that predation is a factor influencing nest dispersion in tropicbirds. During the course of our study, no young were lost through predation. The majority of mortality for P. aethereus and P. lepturus on Ascension Island was due to antagonistic interaction among adults fighting for nesting space (Stonehouse 1962). Of the total mortality, 30% and 50% occurred at the egg stage for P. aethereus and P. lepturus, respectively. Of the mortality due to aggression, 17% and 18% occurred in neonates of P. aethereus and P. lepturus, respectively. Overall, most of the mortality occurred within the first 2 weeks after hatching. Predation is infrequently a cause of death among all species of tropicbirds (Howell and Bartholomew 1962, Stonehouse 1962, R. Shea per. comm., this study, although see Fleet 1974). We feel confident that,

during our 30 days of observation of tropicbird nesting, we were observing characteristic mortality patterns.

We realize that this study represents an analysis of nest-site distributions during a particular limited period of time. The period under consideration, however, is the time of peak breeding activity of tropicbirds on Christmas Island (Schreiber and Ashmole 1970). If nest sites are limiting, that limitation would occur during this time. We also suspect that the observed "colonies" of tropicbirds are not the result of social interactions designed to enable the birds to nest in close proximity to one another, especially in light of the causes of mortality (Stonehouse 1962). Rather, they represent an aggregation of animals in space and time about a clumped resource.

LITERATURE CITED

CROXALL, J. P., & P. A. PRINCE. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biol. J. Linnean Soc. 14: 103–131.

FLEET, R. R. 1974. The Red-tailed Tropicbird on Kure Atoll. Ornithol. Monogr. 16: 1–64.

GABALDON, D. J. 1978. Factors involved in nest-site selection in Pinyon Jays. Unpublished Ph.D. dissertation. Flagstaff, Arizona, Northern Arizona Univ.

HAND, D. J. 1981. Discrimination and classification. New York, John Wiley and Sons.

HOWELL, T. R., & G. A. BARTHOLOMEW. 1962. Temperature regulation in the Red-tailed Tropicbird and Red-footed Booby. Condor 64: 6–12.

LACK, D. L. 1934. Habitat distribution in certain Icelandic birds. J. Anim. Ecol. 3: 81–90.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, & D. H. BENT. 1975. Statistical package for the social sciences (SPSS), 2nd ed. New York, McGraw-Hill.

PORTER, W. P., J. W. MITCHELL, W. A. BECKMAN, & C. B. DeWITT. 1973. Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their microenvironment. Oecologia (Berlin) 13: 1–54.

SCHREIBER, R. W., & N. P. ASHMOLE. 1970. Sea-bird breeding seasons on Christmas Island, Pacific Ocean. Ibis 112: 363–394.

STONEHOUSE, B. 1962. Tropicbirds (genus *Phaethon*) of Ascension Island. Ibis 103b: 124–259.

TRIVELPIECE, W., & N. J. VOLKMAN. 1979. Nest-site competition between Adelic and Chinstrap penguins: an ecological interpretation. Auk 96: 675–681.

WALSBERG, G. E., & J. R. KING. 1978. The energetic consequences of incubation for two passerine species. Auk 95: 644–655.

ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice-Hall, Inc.