

NEST-SITE SELECTION AND NESTING SUCCESS OF WHITE-TAILED TROPICBIRDS (*PHAETHON LEPTURUS*) AT CAYO LUÍS PEÑA, PUERTO RICO

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ABSTRACT.—I studied nest-site selection and nesting success of White-tailed Tropicbirds (*Phaethon lepturus*) at nesting colonies located in coastal boulder talus on Cayo Luís Peña, in the Culebra National Wildlife Refuge, Puerto Rico, during 1983–1988. Twenty-nine to 38 pairs attempted to nest at each of two colonies, Punta Cruz and South Peninsula, in each season. Nests were distributed along different coastline distances: 170 m at Punta Cruz and up to 420 m at South Peninsula. Nearest-neighbor distances of nest sites were 2–4 m at Punta Cruz and 6–10 m at South Peninsula. Nests averaged 2 m from the forest edge, within 6 m of the waterline and 2 m above mean high tide. Temperatures in nest crevices fluctuated between 20°C and 35°C. Incubation times averaged 41 days (range: 40–43). Mean fledging times (\pm SD) were 73 ± 5.25 days in 1984, 71 ± 2.65 days in 1985, and 71 ± 1.57 days in 1986. Overall nesting success (laying through fledging), estimated by the Mayfield method, for the two colonies combined was low (0.15 in 1984 to 0.26 in 1986), although it was similar to that reported for White-tailed Tropicbirds at other colonies worldwide if estimated by the traditional method. Most nesting failures occurred early in the egg stage. The most important causes of nest failure at Punta Cruz were abandonment and agonistic encounters between conspecifics during the egg stage, including overt and severe fighting. In contrast, the most common cause of nesting failure at South Peninsula was predation. At South Peninsula, reduced predation by black rats (*Rattus rattus*) and increased hatching success were concurrent with intensive predator control efforts, especially the use of poisoned rat bait. Received 11 December 1989, accepted 13 May 1991.

CURRENT knowledge of the status, nesting success, and distribution of seabirds in the Caribbean Sea and adjacent tropical western Atlantic Ocean is at present incomplete. Available information suggests that Caribbean seabird populations have suffered significant declines due to human activity and introduced animals (Westerman 1953, Dewey and Nellis 1980, van Halewyn and Norton 1984). I examined the breeding biology of the Caribbean White-tailed Tropicbird (*Phaethon lepturus*), at Cayo Luís Peña, Culebra, Puerto Rico. My objectives were to determine the size and nesting success of the nesting colonies at Cayo Luís Peña, to describe the characteristics and distribution of nest sites, and to identify causes of nesting failure.

STUDY AREA AND METHODS

I studied nesting colonies on Cayo Luís Peña, an uninhabited islet in the Culebra National Wildlife

Refuge, at Isla de Culebra, Puerto Rico (18°20'N, 65°18'W). Cayo Luís Peña is located about midway between the main island of Puerto Rico and St. Thomas, U.S. Virgin Islands. White-tailed Tropicbirds were first reported in the vicinity of Culebra by Wetmore (1917). The nesting colonies were first identified and described by Kepler and Kepler (1978), and first censused by Furniss (1983). About a half-dozen pairs of Red-billed Tropicbirds (*P. aethereus*) also nested at Cayo Luís Peña during 1983–1988.

Two nesting colonies were at Punta Cruz and South Peninsula on Cayo Luís Peña (Fig. 1). Punta Cruz consists of a low-lying volcanic boulder talus along the entire shoreline. The adjacent subtropical dry forest (Ewel and Whitmore 1973) occupies a narrow peninsula extending to <15 m above the waterline. This colony had a distinctly windward side, with no shelter from the wind, and a sheltered leeward side. South Peninsula consists of a low-lying talus of large boulders sparsely strewn along the northern extent of the shoreline, changing to smaller more densely strewn boulders at the southern extent. The arrangement of these boulders suggests an origin as products of the erosion of the cliffs and steep slopes of the adjacent forested hillside, which extended to >30 m and provided the colony with moderate shelter from the wind. Midafternoon air temperatures at Punta Cruz varied from 26°C to 44°C, whereas those at South Peninsula

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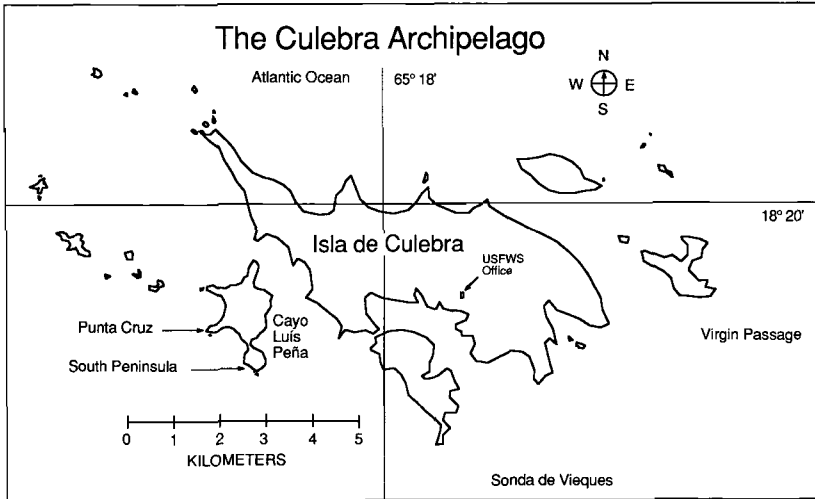


Fig. 1. Map of the Culebra archipelago, showing location of study areas (Punta Cruz and South Peninsula) on Cayo Luis Peña.

were typically 29°C to 37°C. Lowest midafternoon temperatures occurred on the windward side of Punta Cruz, while the highest temperatures were on its leeward side. Surface temperatures on the rocks ranged up to 66°C. Nighttime ambient temperatures could fall to 18°C at all locations. The colonies experienced strong trade winds (6.8 m/s, gusting to 9.2 m/s), which were easterly to northeasterly early in the nesting season (February to March), and shifted to south-easterly from April to May onwards, with the progression of the Intertropical Convergence (see Fuller et al. 1989, Pennycuick et al. 1990, Schaffner 1990a).

Nest sites.—Data for 1983 were collected by U.S. Fish and Wildlife Service personnel (Furniss, Taylor, and Griffen-Taylor MS). During February to June (1984) and February to August (1985 and 1986), I visited each colony two or three times per week. On each visit all likely looking crevices were searched for evidence of nesting activity. From a blind located in the adjacent forest, or from a boat, I also found likely nesting sites by observing adults entering and leaving the colony. All known visitation sites (where an adult was captured or observed, but no egg was laid—most became nest sites in subsequent seasons) and nest sites were uniquely marked, and I captured and banded adults in all accessible locations. Periodic visits allowed me to determine the nesting success of the breeding birds, observe evidence of predators, and document other phenomena at the colonies. Although Caribbean White-tailed Tropicbirds do not exhibit the obvious sexual dimorphism reported by Stonehouse (1962) for South Atlantic (Ascension Island) individuals, I usually was able to infer the sex of nesting individuals by incubation order (males take the first full [>36 h] incubation shift after egg laying) and by observation of which pair member laid the

egg (Schaffner 1988, 1990a, b; Schaffner and Swart 1991). I made additional visits to the nesting colonies during late March of 1987 and 1988, 25 May to 1 August of 1987, and 14 May to 2 June of 1988. However, the number of visits made during the egg stages of 1987 and 1988 was inadequate for reliable estimation of nesting success, and during visits to Cayo Luis Peña during the chick stages of 1987 and 1988, I did not always examine all nests (see Fuller et al. 1989, Pennycuick et al. 1990).

I painted transect markers at 10-m intervals on boulders along the coastline of each colony by suspending a 10-m cord horizontally from marker to marker through the colony. The heights of the marker locations approximately bisected the vertical distribution of the nest sites in each 10-m interval. These lines provided measures of the linear extent of the nesting colonies, which could be directly compared because of the standardized 10-m step lengths (see Pennycuick and Kline 1986).

I measured nearest-neighbor distances of nest sites by means of a tape measure suspended between the site entrances. Sites sharing an entrance were recorded as having 0.0 m nearest-neighbor distances. Using a clinometer mounted on a tripod (Fig. 2), I measured the height above the approximate mean high-tide line (waterline) and the distance inland from the waterline for each site. I suspended a tape measure to determine the distance (d_1) from the site entrance to the clinometer, and I suspended a tape measure from the waterline to the clinometer to determine that distance (d_2) as well. I also recorded the respective angles (θ_1 , θ_2) between the horizontal plane of the clinometer and d_1 and d_2 . Thus, $H_1 = d_1 \sin \theta_1$; $H_2 = d_2 \sin \theta_2$; $L_1 = d_1 \cos \theta_1$, and $L_2 = d_2 \cos \theta_2$.

Nest temperatures and ambient temperatures were

recorded on many visits. Three nests in 1985 and four in 1986 were fitted with remote reading thermometers for at least half of the nesting period. Thermometers at six of these nests also provided readings of the highest (max.) and the lowest (min.) temperatures in these nest crevices between visits, as well as the temperature at the time of my visit (usually late afternoon). The thermometers were then reset.

Nesting success.—I calculated nesting success by the traditional estimation method and by Hensler's (1985) modification of the Mayfield method. The traditional method considered all known eggs and chicks, regardless of age at discovery, and assumed survival for all offspring remaining in the colony at time of observer departure. Hatching and fledging (normal departure of the chick from the nest) success of the nests at each colony were calculated as number of eggs laid or chicks hatched minus the number known failed, divided by the number of eggs laid or chicks hatched. Hatching and fledging success were multiplied together for an estimate of overall success.

For events (such as hatching, fledging, or predation) that occurred between consecutive visits, I occasionally used circumstantial information (such as degree of decomposition of the remains of failed eggs or dead chicks, or very high or very low body masses of incubating adults) to judge when the event occurred. Most often, however, I assumed that an event occurred on the exact middle day for intervals of odd numbers of days or on the earlier of the middle two days for intervals of even numbers of days, because failures may be more likely to occur early in the cycle (Miller and Johnson 1978). For long intervals, as in 1983, I assumed that an event occurred on the day closest to the 40% point of the interval (Johnson 1979). Nest exposure (number of days of observation) was taken to be the period from discovery to fate or my last visit of the season. For chicks that were also known from eggs shortly before hatching, exposure began on the estimated day of hatching. Because nests often were inspected twice in a single day (early morning and late afternoon), nests known from a single day were allotted an exposure of 1 day.

I assumed a typical incubation time to be 41 days for all years, and I assumed the typical chick fledging time to be 72 days for 1983, 73 days for 1984, and 71 days for 1985 and 1986. A successful nest for a period (e.g. egg stage or chick stage) is one in which at least one young survives through the specified period. Thus, nest survival is the same as the survival of individual young because White-tailed Tropicbirds always lay only one egg per nest.

Predator control.—During 1984 I controlled predators with snap traps set at the colony-forest edges. In 1985–1987, in response to management concerns regarding predation on eggs and chicks, I continued predator control, aimed primarily at black rats (*Rattus rattus*), and to a lesser extent land crabs (*Gecarcinus* spp.) and large land hermit crabs (Coenobitidae: *Co-*

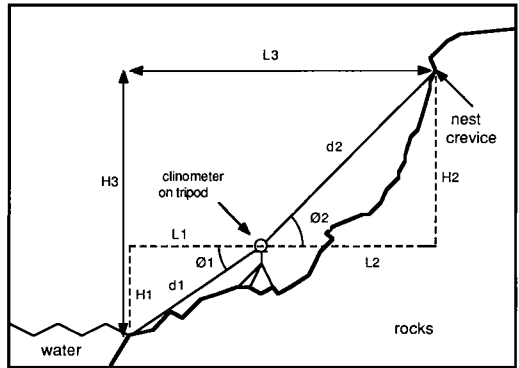


Fig. 2. Method of determining height above the waterline (H_3) and distance inland from waterline (L_3) of nest sites and visitation sites. Distances d_1 and d_2 were measured directly with a tape measure.

nobita clypeatus). I used snap traps and poisoned bait (diphacinone-impregnated baited paraffin blocks, i.e. "Eaton's All-Weather Bait Blocks") to control rats, and I removed large land crabs and hermit crabs physically from the colony areas. I made the first bait block application in April of 1985, after some egg losses had already occurred. I placed bait blocks near entrances of previously destroyed nests, and at regular intervals along the forest edges at both colonies. In June and August of 1985, I also placed bait blocks inside empty nest crevices, and I applied poisoned bait upon my arrival at Culebra in February, March, April, and August of 1986, and March and July of 1987.

RESULTS

Colony and nest-site characteristics.—White-tailed Tropicbirds nested along 170 m of contiguous coastline at the Punta Cruz colony during 1984–1988. At the South Peninsula colony nests occurred along 220 m of coastline in 1984, 330 m in 1985, and 420 m in 1986–1988.

Nests were situated in crevices that provided shelter from wind and direct sunlight. Nest scrapes were placed from immediately adjacent to the crevice opening to a few meters within the crevice. Some nest sites shared entrances. The birds brought no nest material to the crevices. They placed their single egg on bare rock or soil, or on whatever litter may have fallen into the crevice. Daily variation in ambient temperatures within the crevices ranged from 20° to 35°C (Fig. 3).

Nearest-neighbor distances (NNDs) for nest sites at Punta Cruz were one-half to one-third those at South Peninsula (Table 1). The number of nest sites per unit coastline distance at Punta

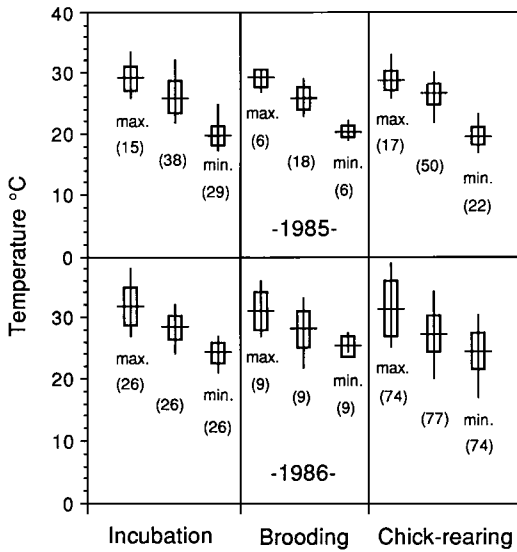


Fig. 3. Temperature regimes of 3 White-tailed Tropicbird nest sites at Punta Cruz in 1985 and 4 in 1986, during the incubation, brooding, and the post-brooding chick-rearing phases of the nesting cycle. Measurements were obtained using maximum-minimum thermometers with thermistors installed in the nest crevices. For each stage (incubation, brooding, or chick-rearing), the middle reading is the midday temperature at the time I visited the nest. Designations "min." and "max." indicate lowest and highest temperature which occurred between my visits. Horizontal lines represent the mean temperatures, vertical lines represent the ranges, and boxes represent standard deviations. Total number of measurements within each category is indicated below the points.

Cruz (28–30 nests/170 m) was greater than at South Peninsula, where similar numbers of nest sites were dispersed over increasing coastline distances from 1984 to 1986 (33 nest sites/220

m in 1984, 32 nest sites/330 m in 1985, and 33 nest sites/420 m in 1986).

Despite the differences in topography and nesting density of the two colonies, nest placements were strikingly similar. Distance from the forest edge was approximately 2 m for nests at both colonies in 1984–1986, and horizontal distances from the waterline ranged from 4.09 to 6.49 m (Table 1). All nest sites were less than 10 m above the water, and heights above the waterline were between 1.73 m and 2.83 m for the 3 yr data were collected (Table 1).

Population size.—The total number of nest sites at Cayo Luís Peña was similar in 1984–1986 (63, 61, 62) as was the total number of clutches initiated (69, 69, 68) (Table 2). The smaller number of nest sites and clutches in 1983 (Table 2) reflect fewer surveys of the colonies that year; clutches that started and failed between observer visits were overlooked (Table 3).

The number of nest sites known to be active midway through the nesting seasons (mid-May) was similar at Punta Cruz for the years 1971 and 1983–1988 (Table 3), whereas the number of known active sites mid-season at South Peninsula was lower for 1983–1984 vs. 1985–1988 (Table 3).

More frequent visits in 1984–1986 revealed nests that started and failed in periods of 2 days to 4 weeks. The between-year difference in the number of known nesting attempts (including failures) at mid-season was greater than the difference in the number of remaining active nests (Table 3). The difference varied with the number of observer visits to each colony at mid-season (Spearman rank correlation [Siegel 1956]; Punta Cruz $r_s = 0.995, P = 0.0193, n = 7$; South Peninsula $r_s = 0.902, P = 0.0273, n = 7$). Simi-

TABLE 1. Placement (m) of nest sites at Cayo Luís Peña, 1984–1986. Abbreviations: NND = nearest-neighbor distances, DNV = distance from nearest vegetation, DWL = horizontal distance from waterline, and HTL = height above mean high tide line. Data are $\bar{x} \pm SD$; sample sizes are in parentheses.

	NND	DNV	DWL	HTL
1984				
Punta Cruz	3.96 ± 7.03 (31)	2.09 ± 1.41 (30)	5.34 ± 2.75 (30)	2.44 ± 1.28 (30)
South Peninsula	6.32 ± 14.00 (33)	2.37 ± 1.31 (32)	4.09 ± 2.59 (32)	1.73 ± 1.24 (32)
1985				
Punta Cruz	3.24 ± 2.28 (31)	2.18 ± 1.50 (28)	6.46 ± 2.62 (28)	2.83 ± 1.60 (29)
South Peninsula	9.84 ± 14.19 (32)	2.25 ± 1.60 (31)	5.27 ± 3.13 (31)	2.11 ± 1.26 (31)
1986				
Punta Cruz	2.24 ± 1.65 (30)	2.11 ± 1.48 (28)	5.92 ± 1.96 (27)	2.37 ± 1.26 (28)
South Peninsula	7.80 ± 9.28 (35)	1.94 ± 1.68 (33)	5.46 ± 3.16 (33)	2.16 ± 1.19 (33)

TABLE 2. Nest sites and clutches at Cayo Luis Peña. Designations "1 clutch," "2 clutches," and "3 clutches" indicate the number of clutches laid (i.e. the number of nesting attempts) at a particular site.

	1983	1984	1985	1986
Punta Cruz				
Clutches				
Discovered as chicks	2	7	1	2
Discovered as eggs	19	24	33 ^a	32 ^b
Total known	21	31	34	34
With egg and chick data	7	8	12	14
Sites				
1 clutch	21	29	26	25
2 clutches	0	1	3	3
3 clutches	0	0	0	1
Total	21	30	29	29
South Peninsula				
Clutches				
Discovered as chicks	1	9	5	7
Discovered as eggs	12	28 ^a	30	27
Total known	13	38	35	34
With egg and chick data	7	8	11	13
Sites				
1 clutch	13	29	29	32
2 clutches	0	3	2	1
3 clutches	0	1	1	0
Total	13	33	32	33
Total Luis Peña				
Clutches				
Discovered as chicks	3	16	6	9
Discovered as eggs	31	53 ^a	63 ^a	59
Total known	34	69	69	68
With egg and chick data	14	17	23	28
Sites				
1 clutch	34	57	56	57
2 clutches	0	4	5	4
3 clutches	0	1	1	1
Total	34	63	61	62

^a 1 no data.

^b 2 no data.

larly, at both colonies the number of nesting attempts known for the entire season varied with the number of observer visits for the entire season (Spearman rank correlation; Punta Cruz $r_s = 0.991$, $P = 0.0152$, $n = 7$; South Peninsula $r_s = 0.821$, $P = 0.0442$, $n = 7$).

Nesting phenology.—Nesting activity was unsynchronized, continued over 6 months, and peaked in mid-May (Fig. 4). Incubation times (laying to hatching) ranged from 40 to 43 days (means [\pm SD] = 40.7 ± 1.21 , $n = 6$ [1984]; 41.2 ± 0.86 , $n = 15$ [1985]; and 41.2 ± 0.86 , $n = 18$ [1986]. Fledging times (hatching to normal departure from the nest) of chicks ranged from 66

to 81 days ($\bar{x} = 73.3 \pm 5.25$, $n = 4$ [1984]; 71.2 ± 2.65 , $n = 17$ [1985]; 71.1 ± 1.57 , $n = 18$ [1986]).

Nesting success and predator control.—By the traditional method, I estimated nesting success during the egg stages at Cayo Luis Peña: 55.9%, $n = 34$ (1983); 50.7%, $n = 69$ (1984); 42.0%, $n = 69$ (1985); and 53.7%, $n = 67$ (1986). I estimated nesting success during the chick stage (79.0%, $n = 19$ [1983]; 81.8%, $n = 33$ [1984]; 93.3%, $n = 30$ [1985], and 80.6%, $n = 36$ [1986]), with overall nesting successes (hatching \times fledging) of 44.1% (1983), 41.5% (1984), 39.1% (1985), and 43.3% (1986).

Nesting success (probability of survival) estimates for the egg stages at both colonies, estimated by the Mayfield method, were (\pm SD) 0.3609 ± 0.09497 for 1983, 0.2168 ± 0.05685 for 1984, 0.2724 ± 0.05601 for 1985, and 0.3883 ± 0.06598 for 1986, based on 31, 52, 63, and 58 nests for which sufficient egg data were recorded. Nesting success during the chick stage was 0.6298 ± 0.1456 , 0.7075 ± 0.09993 , 0.9190 ± 0.07763 , and 0.6742 ± 0.08405 , based on 19, 33, 29, and 33 nests with chicks, for 1983–1986. Overall nesting success was estimated to be 0.2273 ± 0.08081 (1983), 0.1534 ± 0.04604 (1984), 0.2497 ± 0.05369 (1985), and 0.2648 ± 0.05515 (1986). There was a trend towards increased overall nesting success, primarily due to increased egg survival, at South Peninsula from 1984 to 1986, while nesting success at Punta Cruz remained relatively constant (Fig. 5).

Ages of eggs and chicks at time of discovery indicate increased proficiency in locating nest sites early after both egg laying and hatching in successive seasons (Table 4). The exception, egg age at time of discovery at South Peninsula in 1986, is consistent with my later arrival that season and the greater nesting activity at South Peninsula than at Punta Cruz in mid-February of all seasons (Fig. 4).

Most egg loss occurred early in the cycle (Table 4), usually at the end of the first full incubation shift (of the male) and before the return of his mate (see also Schaffner 1988). Predation on chicks by land crabs or hermit crabs (see below) always occurred <10 days after hatching. Important causes of nesting failures during the egg stage were nest abandonment, agonistic encounters at the nest site between parents and conspecific intruders, and predation by rats, land crabs, or hermit crabs (Table 5).

Two egg losses due to agonistic encounters between adults occurred at Punta Cruz in 1984,

TABLE 3. White-tailed Tropicbird nesting attempts (including failures), observer visits, and active nest sites at Cayo Luís Peña in mid-May of 1971,^a and 1983–1988.^a Note the relationship between number of observer visits and number of known nesting attempts.

	1971 (14 May)	1983 (mid- May)	1984 (15 May)	1985 (15 May)	1986 (15 May)	1987 (25 May)	1988 (14 & 15 May)
Punta Cruz							
Active nests on above date	11	14	13	11	14	14	14
Known attempts to above date	11	19	25	24	28	23	20
Known attempts for season	11	21	31	34	34	25	22
No. observer visits ^b to above date	1	4	38	28	31	8	4
Season total observer visits ^b	1	6	51	65	80	22	9
South Peninsula							
Active nests on above date	6	9	10	15	15	15	16
Known attempts to above date	6	13	35	32	28	28	22
Known attempts for season	6	13	38	35	34	30	23
No. observer visits ^b to above date	1	6	34	23	25	7	3
Season total observer visits ^b	1	7	45	46	62	15	5
Total Luís Peña							
Active nests on above date	17	23	23	26	29	29	30
Known attempts to above date	17	32	60	56	56	51	42
Known attempts for season	17	34	69	69	68	55	45
No. observer visits ^b to above date	2	10	72	51	56	15	7
Season total observer visits ^b	2	13	96	111	142	37	14

^a Sources: for 1971, Kepler and Kepler 1978; for 1983, Furniss, Taylor and Griffen-Taylor MS; for 1984–88, this study, Schaffner 1988, unpubl. data.

^b Observer visit defined as any visit during which any census data were recorded, regardless of number of observers.

four in 1985, and six in 1986. There were only three such losses at South Peninsula for 1984–1986 (Table 5). I witnessed overt and severe fighting, resulting in injuries and loss of blood, at nest and visitation sites in 1984 and 1986. The first such encounter in 1984 occurred at a nest site shortly after egg laying and resulted in the abandonment of the intact egg and nest site. I found two bloodied birds (later identified as males) exhausted and immobile in a nest crevice, their bills locked together. This site remained unused until one of the combatants and his mate from 1984 nested there successfully in 1986.

A second event at Punta Cruz in 1984 involved three birds at a visitation site. I discovered two of the birds struggling with their bills interlocked. All three birds exhibited minor lacerations and blood stains. One of the interlocked birds (a male) and the third bird nested together at that site one month later.

In a third incident at Punta Cruz in 1984, one pair of nesting White-tailed Tropicbirds was displaced by conspecifics. The original inhabitants abandoned the site and the intact egg, but the site remained unused, until it was occupied by Red-billed Tropicbirds in 1987 and 1988.

At a nest site at Punta Cruz in 1986, a fight between the resident female and a female intruder resulted in the destruction of the egg. The intruder displaced the resident female and nested with the original male later that season. I observed wounds on another incubating female at Punta Cruz in 1986. This female and her egg disappeared 4 days later and a second female nested at that site with the original male a few weeks later. Other losses believed to have resulted from agonistic encounters were followed by nesting at the same site by one or two new individuals within 30 days.

During 1984 I observed black rats (*Rattus rattus*) in the tropicbird colonies and adjacent forest, as well as rat fecal material in nest crevices. With snap traps (1984) I collected 12 rats at Punta Cruz and 15 at South Peninsula. I trapped 7 rats in 1985 and 4 in 1986 in the two colonies. In April and May of 1985, ca. 2 weeks after the first application of poisoned bait, I found dead rats in the colonies and adjacent forest edges. Dead rats were found in both colonies 5–15 days after the first application of rat bait in 1986, and by the end of that season I had discovered 4 dead at Punta Cruz and 6 at South Peninsula. In both 1985 and 1986, the presence of other

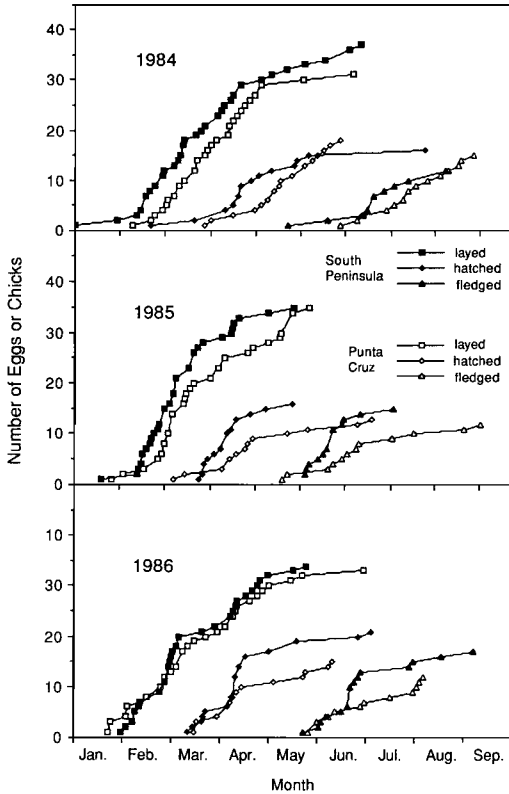


Fig. 4. Sequence of laying, hatching, and fledging at Cayo Luis Peña in 1984–1986. Number of eggs and chicks are cumulative for each season.

dead rats deep in the rock crevices and adjacent brush was revealed by the odors emanating from those areas.

I also observed large land crabs (*Gecarcinus* spp.: 8–12 cm carapace diameter), and large land hermit crabs (Coenobitidae: *Coenobita clypeatus*; >7 cm shell length) in the colonies and in the vicinity of recently damaged eggs and dead or moribund chicks (for crab identifications, see Voss 1976). More than half of the damaged eggs had large oval holes, which implicated rats. Approximately one third of the apparently predator-destroyed eggs had paired large and small holes, corresponding to the large and small claw tips of large *Gecarcinus* land crabs. In most cases the eggs were pushed against a rock and punctured with the claw tips. One adult male tropicbird with a severe neck wound was killed by rats at Punta Cruz in 1985. Rat feces were found in this nest, and the egg disappeared. The proportion of eggs lost to predators and unknown causes did not change greatly in 1984–1986 at

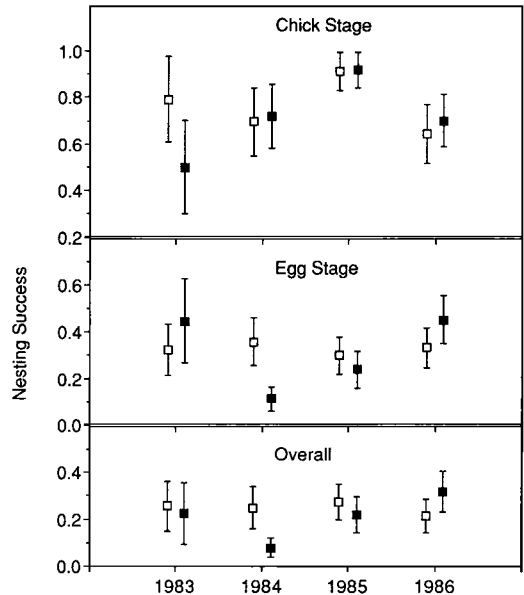


Fig. 5. Nesting success estimated by the Mayfield method (Hensler 1985). Open symbols represent data for the Punta Cruz colony and closed symbols represent data for the South Peninsula colony. Vertical lines represent the estimated standard deviation of the Mayfield estimate of nesting success.

Punta Cruz. At South Peninsula 12 eggs in 1984 and 16 in 1985 were lost to predators and unknown causes combined, but just 5 in 1986 (Table 5).

Total counts of chicks lost at both colonies in 1986 were higher than in previous years (Table 5). Predation on chicks always occurred when chicks were less than 2 weeks of age. The Punta Cruz chicks lost to predation in 1985 and 1986 were killed at <5 days of age by large (>7 cm shell diameter) hermit crabs, which fed on the freshly killed chicks. In one case (Punta Cruz in 1985), I found a large hermit crab feeding on a freshly killed, newly hatched chick. The parent was still sitting in the nest on both the chick and the hermit crab. I also found hermit crabs in nests with newly hatched chicks and brooding adults in 1984 and 1986 at Punta Cruz, and twice in 1984 at South Peninsula. I observed Sally Lightfoot crabs (Grapsidae: *Grapsus grapsus*) feed on a chick carcass at Punta Cruz in 1984 and 1986, and on fish or rat carcasses at both colonies in all years. I also observed *Grapsus* and *Coenobita* scavenge previously damaged eggs and dead chicks.

Two chicks at Punta Cruz and three chicks at

TABLE 4. Estimated age (days) of all eggs and chicks at the time of discovery and failure (destruction, death, or disappearance), at Cayo Luís Peña during 1983–1986. Data are $\bar{x} \pm \text{SD}$; sample sizes are in parentheses. Times of occurrence of laying and hatching events were estimated in the same fashion as events in Mayfield analyses.

	1983	1984	1985	1986
Egg age at discovery				
Punta Cruz	14.0 \pm 9.62 (14)	5.4 \pm 9.86 (24)	3.6 \pm 5.59 (32)	3.4 \pm 6.25 (29)
South Peninsula	24.6 \pm 6.20 (8)	6.2 \pm 10.16 (29)	6.1 \pm 9.31 (30)	8.7 \pm 6.25 (27)
Total Luís Peña	17.9 \pm 9.88 (22)	5.8 \pm 9.94 (53)	4.8 \pm 7.65 (62)	5.9 \pm 8.41 (56)
Egg age at failure				
Punta Cruz	27.4 \pm 9.13 (5)	15.8 \pm 16.17 (13)	17.6 \pm 14.07 (20)	12.6 \pm 15.03 (16)
South Peninsula	—	14.0 \pm 11.30 (21)	13.7 \pm 11.26 (17)	23.5 \pm 13.04 (13)
Total Luís Peña	27.4 \pm 9.13 (5)	14.7 \pm 13.17 (34)	15.8 \pm 11.80 (37)	17.5 \pm 14.98 (29)
Chick age at discovery				
Punta Cruz	35.5 \pm 14.19 (8)	13.6 \pm 20.51 (18)	2.0 \pm 1.29 (13)	2.2 \pm 2.15 (15)
South Peninsula	20.6 \pm 7.13 (9)	18.6 \pm 21.96 (15)	15.8 \pm 22.3 (16)	8.7 \pm 17.03 (18)
Total Luís Peña	27.6 \pm 13.28 (17)	15.9 \pm 20.99 (33)	9.7 \pm 17.18 (29)	5.7 \pm 12.92 (33)
Chick age at failure				
Punta Cruz	25.0 \pm 0.0 (1)	18.7 \pm 20.13 (3)	31.0 \pm 0.0 (1)	21.8 \pm 25.24 (5)
South Peninsula	35.7 \pm 40.04 (3)	38.0 \pm 10.0 (3)	9.0 \pm 0.0 (1)	42.2 \pm 20.36 (5)
Total Luís Peña	33.0 \pm 6.27 (4)	28.3 \pm 17.73 (6)	20.0 \pm 15.56 (2)	32.0 \pm 24.15 (10)

South Peninsula were abandoned in 1986. These chicks were the first hatched at these nest sites, although the nesting attempts of these parents failed during the egg stage in previous years. Abandonments occurred when chicks were between 40 and 60 days of age. In nearly all cases, 10–18 days passed between the last feeding of the chick by one parent (female or unidentified) and the last feeding by the second parent (male or unidentified).

One Red-billed Tropicbird egg at South Peninsula (of the two nests there that season) was destroyed by White-tailed Tropicbirds in 1984. A pair of White-tailed Tropicbirds was found just inside the entrance of a crevice where a Red-billed Tropicbird was incubating its egg. All three birds called loudly. I subsequently found the Red-billed Tropicbird egg broken and rolled out of the nest crevice, and the same pair of White-tailed Tropicbirds occupying the nest depression. Within a month these White-tailed Tropicbirds produced an egg, and the site was used by White-tailed Tropicbirds in subsequent years.

During 1984 one Red-billed Tropicbird chick at Punta Cruz (of the only nest there that season) was killed by White-tailed Tropicbirds. The 3-week-old chick was found with a severe open wound on its back, displaced from the nest depression; and a White-tailed Tropicbird adult, with a blood-stained bill and breast, occupied

the depression. On my next visit to this site, the same White-tailed Tropicbird adult was present, and the Red-billed Tropicbird chick was missing. Three weeks later this White-tailed Tropicbird adult (a male) was incubating an egg at this site. White-tailed Tropicbirds used this site in 1985 and 1986, but the site was reclaimed by Red-billed Tropicbirds in 1987 and 1988.

DISCUSSION

Wetmore (1917) observed "six or eight tropicbirds circling about a rocky point on Cayo Luís Peña," on 11 April 1912. A similar observation could have been made at Punta Cruz midmorning on 11 April, 1984–1988. Kepler and Kepler (1978) censused both colonies in May 1971 and located 17 nesting pairs on their single visit to each colony. My more frequent visits in subsequent seasons revealed nests that started and failed in periods of 2 days to 4 weeks, which resulted in larger numbers of known nesting attempts. Thus, different estimates of nesting population size are, at least in part, artifacts of the frequency and number of observer visits. The results of my study do not suggest dramatic changes in nesting population size, and the Cayo Luís Peña nesting population appears to have been fairly stable since 1971 (and perhaps since 1912) through 1988. However, there was a substantial turnover among individuals that at-

TABLE 5. Causes of nesting failures during the egg stage and chick stage. Abbreviations: Abd = egg/chick abandoned; Agn = loss as a result of agonistic interactions between adults; Prd = destroyed by a predator; Ukn = disappearance due to an unknown cause; Ald = egg found rotten while still being incubated; DH = died while hatching; Fld = nest flooded; Bkn = egg broken.

	Egg stage							Chick stage					
	Abd	Agn	Prd	Ukn	Ald	DH	Fld	Bkn	Abd	Agn	Prd	Ukn	Fld
Punta Cruz													
1984	3	2 ^a	3	3	0	1	0	1	1	0	1 ^b	0	1
1985	9	4	2	3	3	0	0	0	0	0	1 ^c	0	0
1986	9	6 ^a	0	2	1	0	0	0	2 ^d	0	2 ^c	0	1
South Peninsula													
1984	8	0	7	5	1	0	0	0	0	1 ^e	0	1	0
1985	1	1	10	6	1	0	0	0	1	0	0	0	1
1986	1	2	2	3	2	1	2	0	3 ^d	0	0	1 ^f	1

^a Includes one failure each in 1984 and 1986 due to Red-billed Tropicbirds, as inferred by the change in site ownership.

^b Due to rats.

^c Due to hermit crabs.

^d Punta Cruz—one chick fed in the field, one hand-reared, both of these fledged. South Peninsula—one chick hand-reared and fledged.

^e Due to Red-billed Tropicbirds.

^f Emaciated, apparently starved but not abandoned.

tempted to nest in a given year. Approximately 10 nest sites discovered in 1983 were not reused in 1984–1988. During 1984–1988 I discovered a total 104 active nest sites and identified 110 nesting pairs, but only about two thirds of this number actually nested at Cayo Luís Peña in any single year (see Tables 2 and 3).

Estimates of nesting success can be affected profoundly by sample size, frequency of sampling, and method of calculation. Diamond (1975) calculated overall nesting success for White-tailed Tropicbirds at Aldabra Atoll as the number of successful nests per number of nests of known fate. This resulted in 50.0% (7/14) for 1967–1968, and 42.9% (12/26) for 1969. On Ascension Island, Stonehouse (1962) calculated overall nesting success of White-tailed Tropicbirds similarly for 1957–1959 as 30.3% (249/821). Prys-Jones and Peet (1980) reported an overall nesting success of 46% for White-tailed Tropicbirds at Aldabra Atoll for 1976–1977. They used the number of chicks survived per number of eggs laid, which is the same as (number laid – number failed)/number laid, assuming that all large chicks present at the end of the study period survived to fledging. By this method, overall nesting success at Cayo Luís Peña would be 44.1% (15/34) for 1983, 39.7% (27/69) for 1984, 39.1% (27/69) for 1985 and 38.2% (26/68). Kepler and Kepler's (1978) data for 1971 would estimate 100% (17/17) overall nesting success, for their single visit.

The estimates of nesting success from Aldabra Atoll (see also Phillips 1987), Ascension Island, and Cayo Luís Peña in 1983 must be considered maxima because they unavoidably excluded any nests that started and failed between the monthly observer visits, whereas estimates at Cayo Luís Peña in 1984–1986 are derived from data collected at more frequent intervals. The majority of White-tailed Tropicbird nesting failures at Cayo Luís Peña occurred from 6 to 21 days after laying, and it seems reasonable to suppose that nesting failures at other locations would also tend to occur early in the cycle. Therefore many nesting attempts would be missed by monthly sampling only.

Monthly sampling for 1984–1986 cannot be reliably simulated by simply considering only records at intervals of 30 or 31 days. Although some nests would be excluded correctly because they started after one visit and failed before the next visit, I discovered nests by many different means. Often nest discovery was the result of several days of prior observation of displaying birds, or due to observing birds entering or leaving a crevice. This was especially true in 1984, when I also discovered nests that had previously escaped my attention until the incubating or brooding adult inside the crevice called loudly as I passed.

The Mayfield method yields realistic estimates of nesting success. It involves few assumptions, yet accommodates incomplete data

series and allows use of nearly the entire data set. This avoids reduction of sample sizes to unreliably low levels. However, Mayfield estimates are time sensitive, assuming equal probability of success on all days of a given period (Johnson 1979, Hensler 1985). Losses in my study tended to occur early in a period (egg stage or chick stage), and therefore the Mayfield estimates reported here are probably slightly lower than actual reproductive success.

Although a strictly controlled experimental examination of the effectiveness of predator-control efforts was impossible, the decreases in egg predation (Table 5) and trend towards increasing nesting success at South Peninsula (Fig. 5), coincident with rat-control efforts in 1985–1986, are encouraging. Moreover, at South Peninsula, the number of surviving nests midseason in 1985–1988 was 50% greater than in pretreatment years (1983 and 1984) (Table 3).

Black rats and land crabs can influence tropical island avifaunas (Atkinson 1985), and predation by land crabs on birds and their eggs has been reported (Sprunt 1948, Amerson 1969, and King 1973). Land hermit crabs destroyed eggs of White-cheeked Pintails (*Anas bahamensis*) at Green Cay, St. Croix, in a fashion similar to *Gecarcinus* predation on tropicbird eggs (Meier et al. 1989). At Cayo Luís Peña rats were the most important predators on eggs, with *Gecarcinus* of lesser importance. Many of the disappearances classified as “unknown” are presumably due to predators, particularly rats, dragging eggs away from nest sites. I observed adult White-tailed Tropicbirds vigorously attacking and killing intruding *Gecarcinus*. I presume they attack rats as well. Some of the rat damage, therefore, must occur when adult tropicbirds leave their egg unattended or after they abandon eggs. Thus there is some uncertainty as to the number of losses due to primary predation versus the number due to scavenging on abandoned eggs.

Gecarcinus are likely to destroy eggs only when they can push the egg beyond the adult's bill-jabbing range or push the egg against a rock to puncture it, and wait for the adult to abandon the nest. Both *Coenobita* and *Grapsus* are primarily scavengers, although *Coenobita* occasionally enter nest crevices to feed on newly hatched chicks, and parents seem unaware of them.

At South Peninsula, with low nesting density and large nearest-neighbor distances, predation and “unknown” causes (which could have been

predation) accounted for most nesting failures. At Punta Cruz, with a high nesting density and small nearest-neighbor distances, agonistic encounters and abandonment accounted for most nesting failures in 1985 and 1986. Tropicbirds are well-known for hostile interactions at their nesting colonies (Stonehouse 1962, Snow 1965, Harris 1966). The relatively constant nesting success during the egg stage at Punta Cruz (Fig. 5), despite predator control efforts, highlights causes other than predation for nesting failures at that colony. Agonistic encounters between adults were especially important causes of nesting failures at Punta Cruz during the egg stage in 1986, and they might also have led to abandonments. Punta Cruz and South Peninsula had similar numbers of nests, but the nests were more crowded at Punta Cruz (170 m of coastline versus up to 420 m at South Peninsula). The nearest-neighbor distances at Punta Cruz during 1984–1986 were only 28–63% of those at South Peninsula (Table 1), which provided more opportunities for nesters and would-be nesters to interact and compete directly for sites. Furthermore, although abandonment was an important cause of failure during the egg stage at Punta Cruz in all years, it was important at South Peninsula only in 1984 (Table 5), the year in which nest sites were most concentrated (along only 220 m of coastline), and nearest-neighbor distances smallest (Table 1). Chick abandonment in 1986 also may have been related to changes in the food resource that year, as these abandonments were coincident with the almost complete absence of an entire family of important food fishes, the Belonidae (needlefishes), in the regurgitations collected that year (Schaffner 1988: appendix 1).

During May to July, 1984–1988, nonnesting adults often followed provisioning parents back to the nesting colony and visited sites containing chicks, as well as empty sites in other crevices. On eight occasions at three sites at Punta Cruz during 1985–1987, as many as six birds at one time entered a single crevice (Schaffner unpubl. data). Such piling-in visits always led to hostile interactions. The first of these popular sites changed ownership and the second did not; but the third site was never used. Most empty sites visited by nonnesting adults in 1984–1987 were eventually nested in by *other* individuals one to four seasons later. Thus, a method of nest-site acquisition for White-tailed Tropicbirds at Cayo Luís Peña, and particularly

at Punta Cruz, may have been to usurp a site already visited or in use by other individuals rather than to locate a completely new site. Ironically, this occurred despite an apparent abundance of suitable crevices (Stonehouse 1962, Snow 1965, Harris 1966, this study).

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