

THE RED-TAILED TROPICBIRD  
ON KURE ATOLL

BY  
ROBERT R. FLEET

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## INTRODUCTION

The family Phaethontidae (Order Pelecaniformes) contains three species: the Yellow-billed Tropicbird (*Phaethon lepturus*), the Red-billed Tropicbird (*Phaethon aethereus*), and the Red-tailed Tropicbird (*Phaethon rubricauda*) (Peters, 1931). There are five recognized subspecies of *Phaethon rubricauda* (*rubricauda*, *westralis*, *roseotincta*, *melanorhynchos*, and *rothschildi*). The subspecies *rothschildi* from the Hawaiian Island chain was described by Mathews (1915) from 13 specimens from Laysan and Niihau in the Leeward Hawaiian Islands.

The Red-tailed Tropicbird (*Phaethon rubricauda*) an oceanic, colony-breeding bird, is the least studied of the three species of the genus. Although it occurs throughout much of the Pacific and Indian Oceans, most of the literature represents work in the southern hemisphere, whereas island populations of the north-central Pacific are virtually unstudied. Most literature on *Phaethon rubricauda* deals with description, taxonomy, and notations of unusual occurrence.

The range of the species includes tropical and subtropical portions of Indian and Pacific Oceans, from Madagascar and Mauritius eastward to the Galapagos Islands, northward to the Bonin and Hawaiian Islands and southward to Australia and to Lord Howe, Norfolk and the Kermadec Islands (Bent, 1922; Mayr, 1945; Oliver, 1955; Thomson, 1964). Numerous short papers have dealt with the accidental occurrence of this species (Oberholser, 1919; Sclater, 1927; Whittell and White, 1940; Courtney-Latimer, 1955; Clancey, 1955; Hindwood, 1947, 1955, and Gibson and Sefton, 1956).

Other studies concentrated on description of the bird. The following was abstracted from Munro (1944), Mayr (1945), Oliver (1955), and Thomson (1964). The adult Red-tailed Tropicbird measures 45 centimeters in body length and weighs 600 to 800 g. Its plumage is white except for the following black areas: a spot anterior to eye, shafts of wing feathers, a small patch in the axillary region that continues posteriorly on flanks. The fully grown central rectrices are narrow-vaned, red, and longer than the body. The bill is serrated, stout, slightly decurved, and coral red, tending toward orange ventrally with black around the external nares. New white plumage is flushed with pale roseate pink. The tarsi and proximal one-third of the totipalmate feet are blue-gray; the distal two-thirds of the feet are black. Immature plumage lacks the pink flush and the elongated central rectrices. The bill of immature (juvenal) birds is gray-black and feathers of head, back, wings and tail are barred and speckled with black (Figures 1, 2). Hatchlings are covered with white down which is usually gray-tipped on head, back and in a ring around the neck. The tarsi and feet are pale pink.





FIGURE. 1. White adult plumage of the Red-tailed Tropicbird. Note black feathers in front of eye and on flanks. Bill and central rectrices are bright red.

Red-tailed Tropicbirds are sexually monomorphic. I was positively able to determine sex of nesting tropicbirds only in females that had a shelled egg in their oviduct or females whose cloacas temporarily were enlarged from egg laying. The mates of the birds positively identified as females were assumed to be males.

#### LOCATION AND PHYSIOGRAPHY OF KURE

Kure is a low volcanic-coral atoll lying at the northwestern end of the Hawaiian Island chain. It is approximately 1,890 kilometers northwest of Honolulu, Hawaii at coordinates  $28^{\circ} 25' N$  latitude and  $178^{\circ} 10' W$  longitude (Figure 3).

Kure Atoll has a nearly circular coral reef, approximately 24 km in circumference and 8 km at its greatest diameter. The reef is highest along its eastern and northern sides where it is marked by emergent coral boulders. The remainder of the reef is solid, several meters wide and awash at high tide, except for an opening of about 274 meters on the south side (near the southeastern tip of Green Island) and a break of about three km on the southwestern curvature. The enclosed lagoon is dotted with submerged coral growths and reaches a depth of 15 m in the center and in the southwest quarter.

Green Island, the largest and only stable land mass within the atoll,



**FIGURE 2.** Completed immature plumage of Red-tailed Tropicbird. White feathers of dorsum are checkered with black. Elongated central rectrices are absent and bill is gray-black.

lies in the southeast section of the lagoon about 400 m inside the reef (Figure 4). Several (usually two) fluctuating and occasionally disappearing sand spits are located west of Green Island and known collectively as Sand Island. These spits make up the only other land mass of the atoll.

Green Island is crescent-shaped, with the axis of the crescent curving from north to southwest. The island is approximately 2.30 km in greatest length along this axis and 0.60 km wide in the northern half. The island is bordered by a nearly continuous series of sand dunes that reach their maximum height (and that of the island) of about 7.5 m along the western (lagoon) beach. A similar line of dunes along the northeastern and southern beaches ranges from 2.4 to 4.6 m above sea level; however, the dune structure is less discernible because the island itself rises to a greater height on this side. Dunes in the southwestern interior are from 1.8 to 4.9 m in elevation, while the north central plain is only 1.8 to 2.4 m above sea level.

The beaches along the eastern and southern sides of the island are moderately sloping, up to 30 m wide, and strewn with small stones. Fluctuating sand points at the northern and western ends of the island may

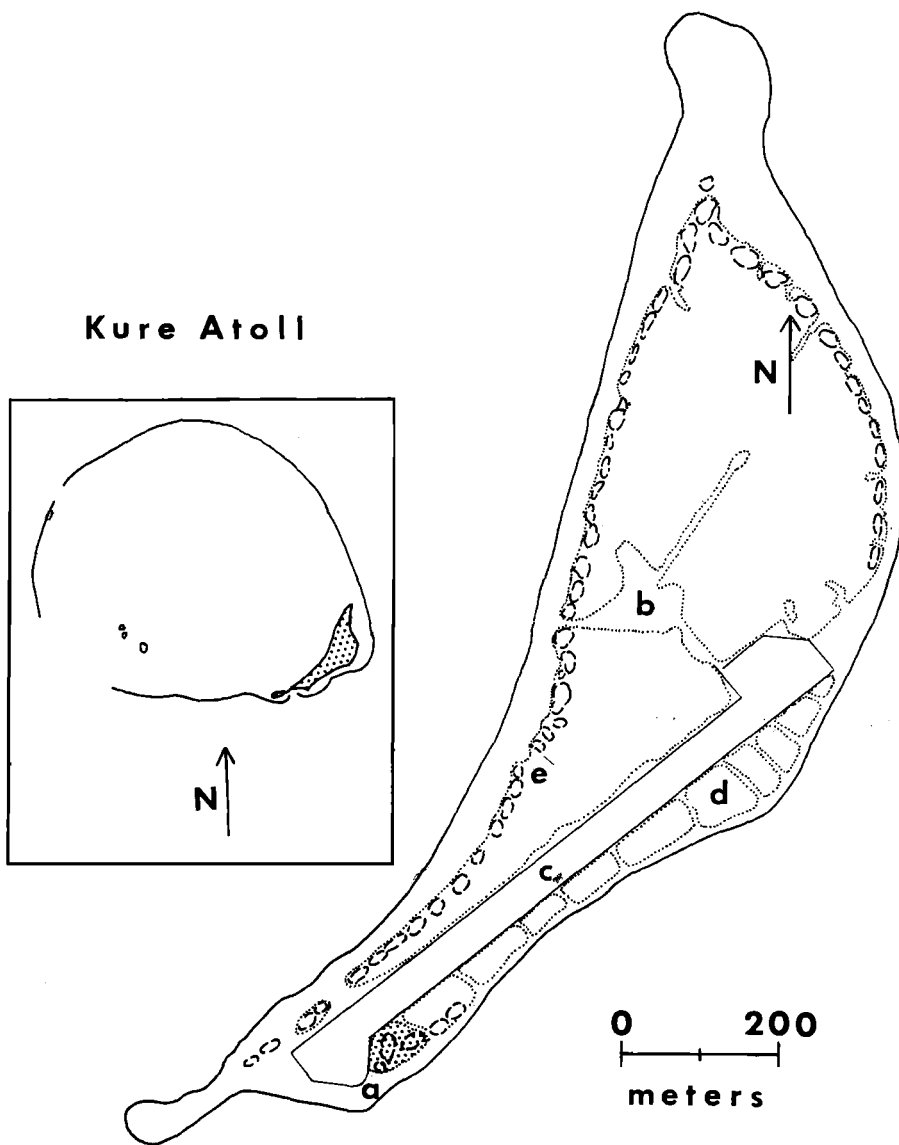


FIGURE 3. Map of Green Island, Kure Atoll. (a) Red-tailed Tropicbird study area. (b) U. S. Coast Guard Station buildings. (c) Runway. (d) Dotted lines enclose vegetated areas. (e) Dash lines indicate sand dunes. Inset shows entire atoll.



FIGURE 4. Aerial photograph of Green Island, Kure Atoll. Coast Guard station and runway are visible. Red-tailed Tropicbird study area was southeasternmost vegetated area. Photograph was taken from the southwest.

extend more than 450 m or, after storms, be completely obliterated by wind and wave action. The beaches along the lagoon side of the island are wider (up to 60 m), gently sloping, and composed of fine sand.

Total land area of the island is 86.6 hectares. However, modification from construction has reduced the vegetated area to approximately 58.2 ha.

Jurisdiction over the island was transferred to the U. S. Navy during World War II. After the war Kure was turned over to the State of Hawaii, which in turn, granted license to the U. S. Coast Guard to occupy the island for an indeterminate period. Under the licensing agreement the Coast Guard was charged with the protection of all plant and animal life, except rodents, so far as was practical and compatible with Coast Guard operational requirements.

#### CLIMATE

Extensive climatic data for this area of the Pacific are available only from Midway Naval Station located 90 km east of Kure. The statistics

cited in this section are from a summary of the years 1953–63 in the NavSta Midway Forecast Handbook and Air Weather Service, MATS Climate Center USAF (Wirtz, 1965).

The climate of this area is influenced by marine tropical or marine Pacific air masses depending upon the season. During summer the Pacific High becomes dominant, extending across the Pacific north of Kure and Midway. This places the region under the influence of easterlies with marine Tropical winds and trade winds prevailing. During the winter the Aleutian Low moves southward over the North Pacific, displacing the Pacific High. The Kure-Midway region is then affected by either marine pacific or marine tropical air, depending upon the intensity of the Aleutian Low and/or the Pacific High.

Temperature variation is indicative of a marine environment. Mean annual range is 9°C. From December through April monthly means range between 18.9°C and 20.6°C, and during the remainder of the year between 21.1°C and 27.2°C. The warmest months are July, August and September, and the coolest are January, February and April.

Rain is most frequent from December through May and least frequent in June and July. The mean annual precipitation for the 10 year period is 108.13 cm.

During periods for which data are available, no tropical storm or typhoon passed through the area. However, storms of tropical character passed within 800 km and caused noticeable increases in precipitation and wind in September of 1957, 1958 and 1959, October and November 1962, and December 1964.

Prevailing wind direction 10 months of the year is easterly (from the east), but during December and January it is westerly. Annual mean wind speed is 10 knots. Peak wind gusts of 77 and 67 knots have been recorded in December and January respectively.

#### VEGETATION OF GREEN ISLAND

The vegetation of Green Island was altered in 1959 by habitat modification intended to improve its potential as an albatross nesting site. In 1961 further alteration resulted from construction of a U. S. Coast Guard LORAN (Long Range Navigation) Station. Prior to this time there was a flora of 13 species (reported by the Tanager Expedition in 1923) dominated by a dense, shrubby growth of *Scaevola taccada* (Goodeniaceae) except on a 6 ha open plain in the interior of the northern half of the island where herbs and grasses dominated (Clay, 1961; Lamoureux, 1961).

In October 1959 a team from the U. S. Bureau of Sport Fisheries and Wildlife, assisted by U. S. Navy personnel bulldozed trails from the beach to the interior in 18 places in an effort to make the island more suitable

as a breeding ground for albatrosses. Grasses and herbs have since overgrown these paths, but *Scaevola* replacement has been much slower.

Alterations on the island for the Coast Guard station included buildings, roads, water and fuel tanks, a 1,219 m coral runway, and a 190.5 m antenna with its extensive system of moorings, guy and ground wires. Most of the vegetation removed was *Scaevola*; regrowth, where it was possible, consisted of grasses and herbs.

During my study the beach crests, dunes, and much of the interior of the island are covered with dense stands of *Scaevola taccada* that sometimes reached 2.4 m in height. The 6 ha central plain in the northern half of the island as well as small scattered clearings elsewhere are dominated by bunch grass (*Eragrostis variabilis*) and several prostrate herbs (e.g., *Boerhavia diffusa*, *Tribulus cistoides*, *Ipomoea indica*, *Solanum nelsoni*, *Solanum nigrum*). The beach edges and exposed sides of dunes are occupied primarily by bunch grass (*Eragrostis whitneyi* variety *caumii*) and *Boerhavia diffusa*.

Several cultivated plant species are common on the Coast Guard station grounds, and additional introduced species are found primarily in other disturbed areas. Of these only *Verbesina encellicides*, a fast-growing composite, seems capable of replacing native species. Lamoureux's (1961) list of 41 species of vascular plants from Green Island included 22 introduced weeds and cultivated plants. A list of plants known from Kure Atoll via collections of Clay (1961), Lamoureux (1961) and POBSP personnel includes 16 species presumed to be native to Kure and 30 introduced or cultivated species.

#### VERTEBRATE FAUNA OF GREEN ISLAND

Two species of mammals are native. The Hawaiian monk seal (*Monachus schauinslandi*) is endemic to the Leeward Island chain, and in 1965 a herd of approximately 200 adults inhabited Kure Atoll. The Polynesian rat (*Rattus exulans*) is known in the Leeward chain only from Kure. The earliest record of *R. exulans* on Kure is in accounts by the crew of the U.S.S. *Saginaw* that wrecked there on 29 October 1870 (Read, 1912). Densities of the rat population were estimated by live-trapping a 2.8 ha study plot from 1963 through 1965. Estimates were based on calculated number per hectare within the study plot multiplied by the number of hectares of suitable habitat on the island. The Hayne equation, utilizing the changing ratio of new to previously handled animals in a given trapping period, was used to calculate the monthly population within the study plot (Hayne, 1949). Densities were lowest in April and May (2,880 individuals) and highest in September and October (10,800 individuals). Population size is dependent upon natality and mortality, both of which appear related to seasonal weather conditions and food abundance (Wirtz, 1972). Rats

prey on young and adults of the Laysan Albatross, on young of the Wedge-tailed Shearwater and Brown Booby, on eggs and young of the Sooty Tern, Noddy Tern and Red-tailed Tropicbird and on eggs of the Bonin Island Petrel (Kepler, 1967). Predation by rats is the major cause of egg and nestling mortality of the Red-tailed Tropicbird on Kure (Fleet, 1972).

There are two species of reptiles on Kure Atoll. The Green Sea Turtle (*Chelonia midas*) has been recorded historically (Bryan, 1942) and individuals were observed by Pacific Ocean Biological Survey Program (POBSP) personnel on several occasions. Turtles came out onto the beach and dug several presumed nests several nights during August 1964; however, no eggs were found. Green turtles are known to breed on other Leeward Islands. Geckos (species unknown) are found occasionally around the Coast Guard Station. They are probably recently introduced from Midway Atoll where they are common.

The recorded avifauna of Kure Atoll has increased considerably due to POBSP efforts. Prior to 1963, 15 species of resident seabirds and 9 species of migrants or accidentals were recorded for Kure. Now the known avifauna consists of 16 species of seabirds (14 of which are annual breeders on Kure) and 44 species of migrants or accidentals (Clapp and Woodward, 1968).

#### DESCRIPTION OF STUDY AREA

Originally I had hoped to use the entire island as a study area, but this was impractical due to the large number of nesting tropicbirds. In order to insure sufficient study pairs within a workable area, I chose an area over which many tropicbirds were displaying. This location, the southeasternmost sand dune on Green Island, turned out to be an area of high nesting density. The study site has the shape of a trapezoid and an area of 0.57 ha. The dune is capped with *Scaevola taccada* reaching 1.8 m in height and is isolated by an asphalt runway on the north and west sides, by a beach access road on the east side, and by a sand beach on the south side. In 1964 only part of the dune was used as the study area, but in July of that year study was expanded to include the entire area of the dune. Henceforth the entire area was used until the study ended on 15 August 1965. The original area and the area subsequently added appeared similar and seemed to be used with equal intensity by nesting tropicbirds.

A secondary study area was established in a scaevola thicket immediately south of the U. S. Coast Guard station quarters near the center of the island. Within this study area, 18 nests were marked and monitored during the first half of the 1964 breeding season. When these nests were abandoned by the adults or preyed upon by *Rattus exulans*, study in this area was discontinued.

An additional 200 nests were marked at locations scattered throughout the island to provide additional information about nest site preference, nest construction, egg size and pigment pattern, and nesting behavior.

#### METHODS OF STUDY

All Red-tailed Tropicbirds captured on Green Island were banded on the right leg with size five U. S. Fish and Wildlife Service aluminum leg bands. After each female laid her egg, the nest site was marked. Because of the dense vegetation it was necessary to double-mark each nest within the main and secondary study areas. Conspicuous nest markers made from one meter lengths of bamboo were placed in the open sand area nearest each nest. Poles were painted red and a cirlet of masking tape upon which the nest number was written was placed near the top. In addition, a 15 cm yellow marker was driven into the ground at the outer edge of the nest depression. The additional 200 nests marked throughout the island were marked only with yellow garden markers.

The birds of each pair were marked with different colors to facilitate recognition and to reduce the necessity for handling. A 5 cm diameter spot was spray-painted on the head of each bird; red and blue were used in 1964 and red and green in 1965. Since Red-tailed Tropicbirds are sexually monomorphic and sex could seldom be determined no attempt was made to mark sexes with a particular color. Care was taken, however, to insure that the members of pairs were marked with different colors.

The main study area was checked daily during the breeding seasons, from March 1964 to mid-August 1965. Following a fixed west-east route along a beach path and spreading apart the leafy canopy every few steps, I was able to see far into the tangle of scaevola stems. The white plumage of tropicbirds was conspicuous against the dark leaf litter. This beach path route was effective because adult birds must push themselves into an open area for takeoff, and consequently more than 90% of the nests were within 3 m of the edge of the scaevola.

Every third day all nestlings within the study area were measured and weighed. As a result of this technique, the data reflect three different age groups; i.e., some individuals were measured at ages 1, 4, 7 days etc., others at ages 2, 5, 8 etc., and still others at ages 3, 6, 9 etc. Measurements of culmen, tarsus, foot, wing, and tail length were taken. Culmen length was measured from the basal (proximal) bony end of the maxilla to the distal end of the maxilla. This measurement and those of tarsus and foot were taken with calipers or, in the field, with dividers. The tarsus measurement was taken with tibiotarsus, tarsus, and digits bent to form the shape of a Z. One end of the dividers was placed on the knob of the proximal end of the tarsus which projects beyond the tibiotarsus joint. The other end



was placed on the dorsal side in the notch of the joint between tarsus and phalanges. The foot was measured from dorsal notch of the joint between tarsus and phalanges to end of longest toe including claw. The wing measurement was taken by measuring the length of the manus, bent at a right angle to the wrist (carpus). The length was read directly from a mm rule. Down of young nestlings was not included in measurements but primary feathers were included. The tail was measured by placing one end of a mm rule between the central rectrices and solidly against the pygostyle. Small nestlings were weighed (in grams) with an Ohaus triple beam balance. Later, when larger and more active, nestlings were weighed (in ounces) by suspending them in a wire cage from a Chantillion spring balance. Weights in ounces were subsequently converted into gram equivalents.

The size of the population was determined by searching the entire island for nesting pairs and counting them. I discovered that nesting birds never made the aerial display characteristic of pre-nesting birds. The sum of nesting birds and birds in aerial display was then used as a population estimate.

Aerial activity of tropicbirds was monitored on an average of one full daylight period per week throughout the 1964 breeding season. Behavioral information, especially concerning prebreeding aerial display, was gathered by observation from a 18.3 m radar reflector tower in the southern half of the island and from a 6.1 m wooden platform built by POBSP personnel in the northern half of the island.

Other behavioral information was collected as opportunities arose and was recorded in field notes. All information about birds within the study area was recorded on daily work sheets and later transferred to mimeographed nest record sheets. Black and white and color photographs were obtained with a 35 mm camera. Statistical testing of the data was carried out according to methods of Simpson, Roe, and Lewontin (1960). Mean values within the text are accompanied by plus or minus one standard error.

#### REVIEW OF LITERATURE

Ecological and population oriented studies on *P. rubricauda* are few. Howell and Bartholomew (1962) studied temperature regulation, and in a later paper (1969) they investigated nesting behavior through experiments involving egg retrieval, egg and nestling substitution, and gaping response of chicks in relation to visual and tactile stimuli. Locke, Wirtz, and Brown (1965) studied pox infection in adults and young on Midway Atoll. Gibson-Hill (1947) reported on fishing habits of adults and examined stomach contents of 28 birds from Christmas and Cocos-Keeling Islands in the Indian Ocean. He concluded that the normal foods of *P.*

*lepturus* and *P. rubricauda* are cephalopods and flying fishes of the species *Cypsilurus bahiensis* and *Exocoetus volitans*. Adults took approximately 50–65% flying fish and 50–35% cephalopods; juveniles still on the nest showed a higher proportion of cephalopods, while young nestlings were fed cephalopods almost entirely.

Numerous authors summarized natural history information on *P. rubricauda* for various islands, island groups, or regions. Crowfoot (1885) noted breeding on Norfolk, Nepean, and Philip Islands (southwest Coral Sea) and included descriptions and measurements of eggs. Oliver (1955) reported eggs present in December and January on the Kermadec Islands. Hindwood, Keith and Serventy (1963) summarized information from the southwest Coral Sea and reported eggs present between September and November for several islands. McKean and Hindwood (1965) reported on an incubating tropicbird, banded three years previously on the same site, in November 1962 on Lord Howe Island.

Betts (1940) reported that the species breeds in the Seychelles group, but gave no dates. Storr (1964) found a nest and egg on Rottnest Island in the Indian Ocean off western Australia in October and included a description of the nest.

Murphy, Bailey, and Niedrach (1954) reported eggs in May and June on Canton Island. Williams (1960) reported a breeding peak in June for Oeno Island (near Pitcairn Island), which, like Canton Island, is situated at about 3° S latitude.

Breeding records and other natural history information from the Hawaiian Leeward Islands was summarized by Rothschild (1900), Bent (1922), Munro (1944) and Bailey (1956). Generally this information indicates a breeding peak between April and June for this island group.

Combined breeding records and egg dates show a trend in breeding peaks from April-June in the northern islands (Hawaiian Leewards) to slightly later (June) in the equatorial islands (Oeno, Canton) to October-December in the southern islands (Lord Howe, Philip, Norfolk, Nepean). Recent work on Christmas Island (Schreiber and Ashmole, 1970) in the central equatorial Pacific substantiates this trend. Egg dates for this population are June through November. Schreiber and Ashmole (1970) also discuss re-nesting capabilities and molt of the tropicbird population.

Three extensive studies on the breeding cycle of tropicbirds have been conducted; one by Gross (1912) on the Yellow-billed Tropicbird (*Phaethon lepturus*), one by Snow (1965) on the Red-billed Tropicbird (*Phaethon aethereus*), and one by Stonehouse (1962) on both *P. lepturus* and *P. aethereus*.

Gross' (1912) investigations were carried out in the Bermuda Islands and

emphasized food and feeding habits, nest site description, egg description and measurements, nestling growth and development and behavior.

Snow (1965) compared breeding season pattern and density of nests of *P. aethereus* in two colonies in the Galapagos Islands. Daphne Island has a high population density of *P. aethereus* that lacks any apparent breeding pattern in that birds nest in approximately equal numbers in all months. In comparison, South Plaza Island has a low population density of *P. aethereus* that shows a well defined breeding peak in October and November. Snow suggests that the most likely explanation of continuous breeding and lack of any obvious breeding pattern on Daphne Island is that competition for nest sites has spread breeding more or less evenly throughout the year. He concludes that this is possible only because the birds' responses to proximate factors regulating the annual cycle are weak and easily overridden by other pressures. Proximate factors are weak because the advantages of nesting at one season rather than another in the Galapagos Islands are slight.

Stonehouse (1962) investigated the breeding biology of *P. aethereus* and *P. lepturus* on Boatswain Bird Island near Ascension Island in the southern Atlantic Ocean. Both species initiate the breeding cycle and lay in every month of the year. Individual birds were found to breed at intervals of 5 to 10 months (*P. lepturus*) or 9 to 12 months (*P. aethereus*) depending on whether the previous cycle was successful. Unsuccessful breeders tended to re-lay sooner, usually following a postnuptial molt. The main cause of unsuccessful breeding cycles was competition for nest sites. Details of breeding behavior, food, egg measurements, growth rates of nestlings, causes of nestling mortality and fledging success were also studied.

#### ACKNOWLEDGMENTS

While in the field, I was employed by the Pacific Ocean Biological Survey Program (POBSP) of the Smithsonian Institution. The research upon which this paper is based was made possible through the cooperation of Charles A. Ely and Philip S. Humphrey, then of POBSP. I thank those members of POBSP who assisted me in the actual field work. Special thanks are due to William O. Wirtz whose guidance and encouragement in the field were instrumental in completion of this work. Living quarters, food, and other assistance in the field were provided by officials of the U. S. Coast Guard station on Kure Atoll. Photographs comprising figures 18, 19, and 32 are available through the courtesy of Thomas R. Howell.

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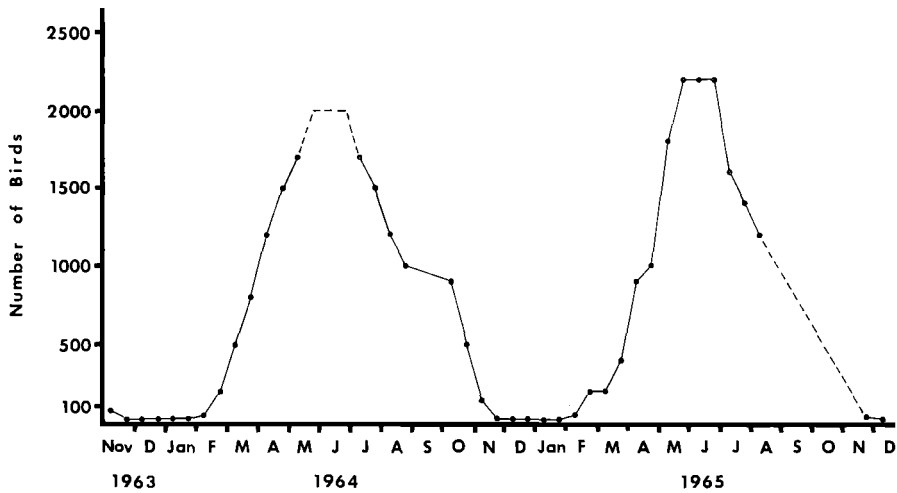


FIGURE 5. Population cycles of the Red-tailed Tropicbird on Kure Atoll from November 1963 through December 1965. Dots indicate population estimates. Dashed lines indicate assumed population levels during times for which estimates are unavailable.

preparation and review of this manuscript. Thanks are due Kathleen J. Oaks who cheerfully typed the several versions of the manuscript. For photographic assistance I thank Richard J. Baldauf. Finally, the inestimable patience of my chairman, Donald R. Clark, Jr., will always be appreciated.

This paper is contribution 91 of the POBSP.

## BREEDING CYCLE

### POPULATION DYNAMICS

In the Leeward Hawaiian Islands, Kure Atoll is second only to Midway Atoll in its number of Red-tailed Tropicbirds. Red-tailed Tropicbirds are present on Kure all year but are few in number between mid-November and mid-February. Population lows of five individuals were recorded in January 1964 and December 1965.

Large numbers of adults begin returning to the island in late February, and they remain until late October. Population size reaches a peak in May and June and then declines to the winter low. Peak populations of 1,700 and 2,200 individuals were estimated in May and July of 1964 and May and June of 1965, respectively (Figure 5). Population estimates were not made for the last half of May or June of 1964. Since this period corresponds with that of estimated peak numbers during 1965, it seems probable that peak numbers in 1964 occurred during this period and that

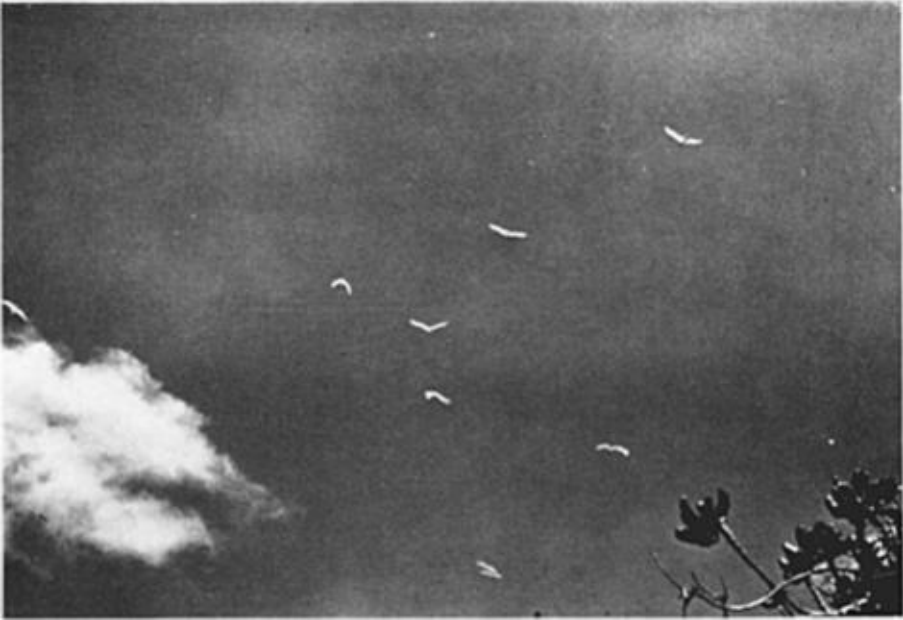


FIGURE 6. Group of Red-tailed Tropicbirds carrying out prebreeding aerial display above the study area.

actual peak numbers of birds in 1964 exceeded 1,700 individuals. My twice-monthly population estimates show that the tropicbird breeding season on Kure is annual (Figure 5).

#### AERIAL DISPLAY

Prebreeding aerial behavior includes nuptial display, soaring and gliding over prospective nest sites, and observation of display patterns of nearby birds. Groups of from 7 to 20 birds carry out a generalized display (Figure 6). Usually in pairs, the birds fly in large vertical circles with one bird above and slightly behind the other. This appears to be the first stage of the nuptial display. The complete display is carried out by single pairs, although individual birds were seen to complete displays with more than one partner.

The complete display is performed with birds facing into the wind. It consists of one to three backward, vertical, interlocking circles executed at 15 to 20 m altitude. A circle is executed in two parts by both birds in turn. The first part is a long shallow glide by the lower bird. The upper bird at this time maintains itself perpendicular to the ground and flies backward and upward. During this backward flight, the bird is also blown backward by the wind, hence this segment of the display flight is much more

rapid than the gliding portion. During the backward flight, the upper bird watches the lower, and as the lower bird pulls up out of its glide and into the vertical stall that precedes the backward flight, the upper bird turns forward and down into the glide position. The long, red, paired, central rectrices may act as a visual stimulus during nuptial display. During the glide the central rectrices typically are held straight out behind the bird, and during the backward flight they are switched from side to side across approximately  $120^\circ$ . When switched to one side they are held there from one to three seconds and then snapped to the other side. In some observations the central rectrices were held to one side during the glide, then switched to the other side during the backward flight. In other instances none, one, two or more, changes in tail position were observed. During nuptial displays guttural croaking calls were given periodically by both birds. The display often ends in a long glide with one bird just over the other.

The large flights of displaying birds took place over areas of scaevola where large concentrations of tropicbirds later nested. At the beginning of the breeding season in 1965, all birds captured within the study area were marked on the breast with blue paint. Never during the ensuing breeding season were blue-marked birds observed displaying any place but over the study area.

Paint markings on breasts of tropicbirds were used to identify the status of the birds carrying out aerial displays. One blue spot was sprayed on birds that nested in the area in 1964 but that had not yet nested in 1965. A second blue spot was applied when the pair produced an egg. A red spot was added to this combination if the nest failed for any reason and a green breast spot was added if the birds renested. A blue cross was painted on the breast of birds present in 1965 that had not bred in the area in 1964. The major drawback of this system was that birds changed their breeding status faster than paint marks could be altered, thus some birds were incorrectly marked at all times. Despite this problem, some patterns and trends concerning the display became obvious on analysis of data gathered using this system.

Seldom were more than half of the birds displaying over the study area paint-marked even after an intensive effort to mark all birds. I believe that these unmarked birds were non-breeders (possibly too young to breed) carrying out only the first part of the breeding display in a manner similar to young albatrosses (C. Robbins, pers. comm.). Young birds evidently in a more physiologically ready state were found sitting on the ground at prospective nest sites, and it was these birds that were marked with a blue cross. In October 1964 I noticed that approximately 80% of displaying tropicbirds had black speckling on the dorsal feathers across the

humerus and in the middle of the back. Such speckling is characteristic of juveniles, and hence these birds were probably young individuals that had not yet acquired fully adult plumage.

Birds marked with one blue spot (*i.e.*, the previous breeders) were commonly seen in display groups, but birds with two blue spots were seldom seen (three or fewer per sighting) and then only after several nests had failed. Birds with a red breast spot (indicating failed nesting attempt) were frequently seen displaying, but birds with a green breast spot (indicating re-nesting attempt) were never seen. Paint-marked birds accounted for up to 50% of those displaying above the study area on any occasion.

Therefore, it appears that tropicbirds display before nesting commences and will return to this stage of the breeding cycle if their nest fails. However, birds with active nests do not display. Parent birds coming in to feed nestlings fly directly to their nest site. Frequently when a parent bird comes to the nest, several birds then displaying in the area will fly to the spot where the parent disappeared into the scaevola and hover over the area calling and displaying. On many occasions parent birds were observed leaving their nest site. These birds circled, gained altitude and flew out to sea without displaying. On several of these occasions displaying birds approached the parent bird and began to display; these overtures were ignored by parent birds. Most displaying birds appear to be non-breeders that fly in to the island only to display, sit on the ground and then return to sea at night.

Unoccupied (non-breeding) birds are on the ground between 09:00 hours and 16:00 hours. Only incubating or brooding birds remain on the island in the evening or at night. The pattern of daily activity of pre-breeding birds seems to include aerial display, followed by a period at a prospective nest site and finally return to sea. Birds frequently detached themselves from aerial display groups and swooped low over the scaevola and landed. When taking flight most birds flew directly out to sea rather than rejoining a display group. In April 1965 I threw seven tropicbirds into the air and recorded their flight paths. None of the seven had yet nested in 1965. Four of these birds had nested in the area in 1964 and all four flew directly out to sea. The other three birds had not nested in 1964 and two of these flew back over the study area and joined a display group. In summary it seems that non-breeders spend more time displaying than prebreeding birds.

Figure 7 indicates the three principal patterns of daily aerial activity of tropicbirds over the island.

At least a few birds were flying over the island during all daylight hours. Very early and late-flying birds were generally those feeding nestlings rather than birds engaged in aerial display. Birds contributing to peak numbers

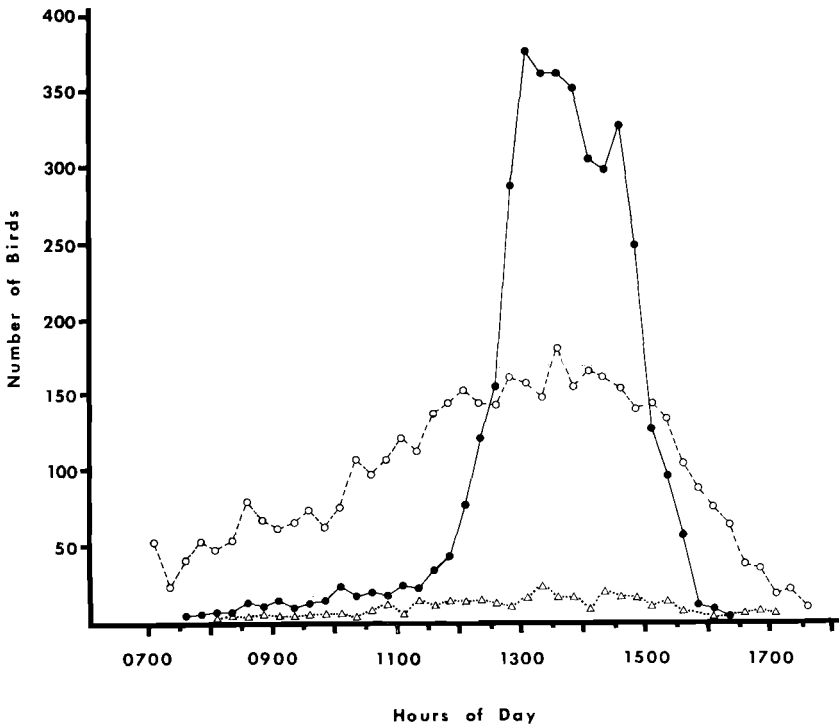


FIGURE 7. Daily activity (counts of birds in flight over Green Island) curves for Red-tailed Tropicbirds on Kure Atoll. Solid line (10 April 1964) indicates the typical daily aerial activity pattern from March through early July. Dashed line (4 September 1964) indicates the typical activity pattern for July, August and September. The large number of birds arriving to feed nestlings which are present at this time tends to obscure the early afternoon peak of displaying birds. Dotted line (30 October 1964) illustrates levels of aerial activity for the beginning and end of the breeding season in February and October-November, respectively.

during the day were not observed to fly in from the sea. These birds were apparently on the ground at prospective nest sites and joined the aerial display flights prior to leaving the island for the night.

Typically small numbers of birds were in flight during the morning and evening hours with a large surge in numbers during mid-day (Figure 7). The beginning of this surge occurred between 11:20 and 13:20 hours. Peak times in 10 samples from 6 March through 6 July ranged from 13:05 to 13:50 hours with a mode of 13:35 hours. The single exception to this was the 14 August cycle, which had a mean peak time of 14:20 hours. The 14 August cycle was exceptional not only because of late peak time but also because it occurred in a month typical of activity cycles in which no definite peaks occurred. Time involved in these daily surges of numbers, from be-



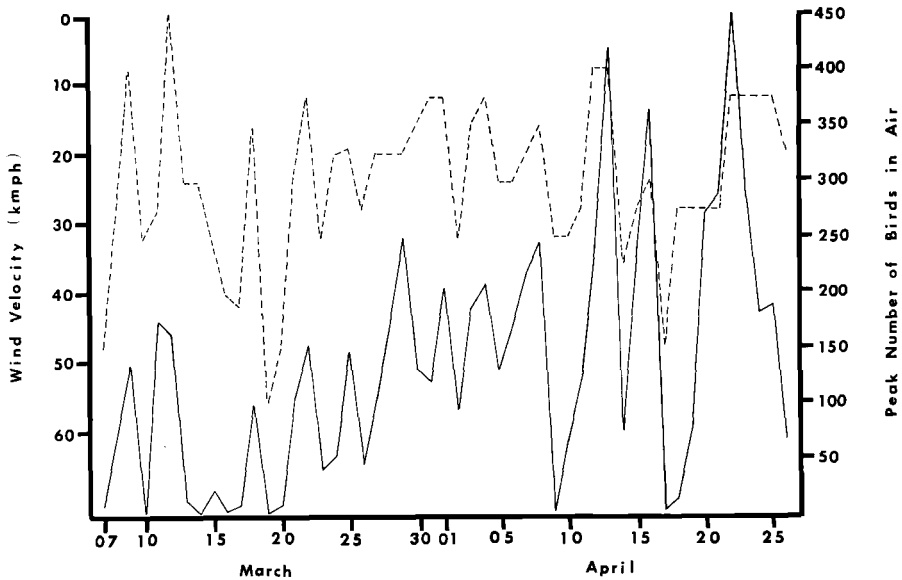


FIGURE 8. Inverse relationship between daily peak tropicbird numbers and wind velocity. Data are from 1965. Dashed line indicates wind velocity and solid line indicates number of birds. Asterisk indicates rain and/or overcast. Note inverted scale for wind velocity.

gining of upswing until end of decrease, ranged from 3.50 to 6.00 hours with a mean for 11 cycles of  $4.36 \pm 0.27$  hours.

Daily cycles showing large numbers of birds but no definite peaks occurred in July, August and September (Figure 7). This type of cycle may result indirectly from the many nestlings present at those times. Parent birds visiting their nestlings throughout the day might have obscured the peak in number of displaying birds.

Aerial activity was at its low ebb (Figure 7) at the beginning and end of the breeding season (*i.e.*, in February and October–November).

Weather conditions determine how many tropicbirds display. Using daily peak numbers and weather data collected during the 1965 tropicbird breeding season, wind velocity is seen to be the primary regulator of peak tropicbird numbers (Figure 8). When wind velocity was 16 kmph or less, peak numbers of tropicbirds were high. Above 16 kmph, tropicbird numbers were depressed. Relative humidity, temperature and wind direction appeared to have no effect on numbers; however, overcast skies depressed numbers. It is difficult to judge the influence of rain and overcast since these conditions were accompanied by high winds. Nevertheless, both 23 March and 2 April had wind velocities of 32 kmph and 23 March with rain and overcast had a peak of 42 tropicbirds whereas 2 April was clear and

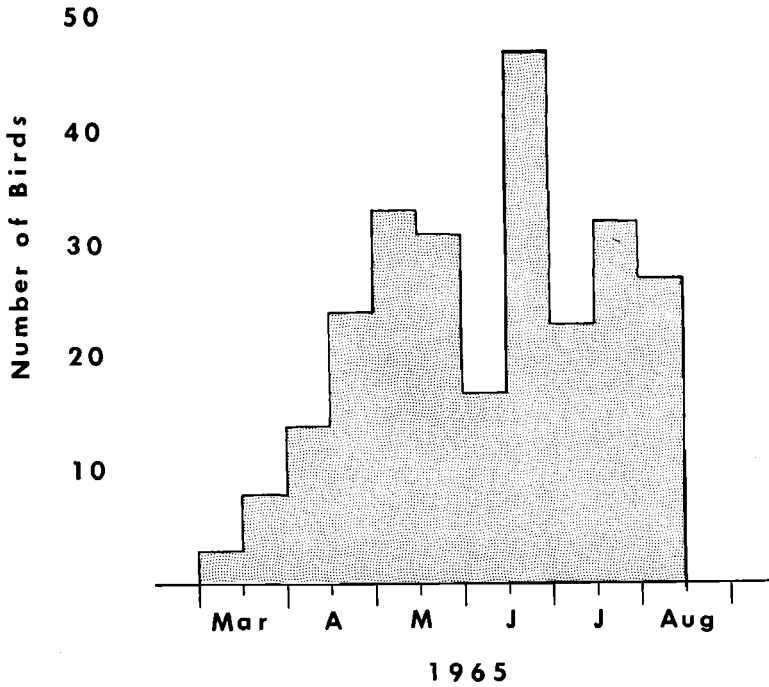


FIGURE 9. Number of unoccupied tropicbirds captured on the study area in 1965. The number of unoccupied birds captured per month changed in proportion to the number of birds using the island, as estimated in Figure 5.

sunny with a peak number of 96. There appear to be two other general rules governing tropicbird display numbers. On days with good display conditions following days with bad display conditions, there will be an increase in peak numbers. Successive days of good display conditions will produce progressively larger peak numbers (Figure 8).

#### ROLE OF NONBREEDING BIRDS ON THE STUDY AREA

In both 1964 and 1965, birds that did not breed in that particular season were found on the ground on the study area. Nonbreeding (= unoccupied) individuals were recorded on the study area in every month of the breeding season of both years. Such individuals were often found several times (up to 5 times in 1964 and 31 times in 1965) throughout the season.

In 1965, numbers of nonbreeding birds increased from March to May, remained steady in June, and decreased in July and August when the study was terminated (Figure 9). The decrease of July and August probably continued apace with the conclusion of the breeding season. Thus the numbers of unoccupied birds recorded on the study area changed in proportion

to the total island population as shown by the population curve for 1965 (Figure 5).

Seventy-two unoccupied individuals were recorded on the study area in 1964 and 90 in 1965. In 1965, 22 of the 72 recorded in 1964 nested, 35 were again nonbreeders, and 15 were not recaptured at all. Of the new nonbreeders recorded in 1965, 18 had nested on the study area in 1964 and the remaining 37 had not been previously recorded.

The 22 unoccupied birds on the study area in 1964 that nested in 1965 were recorded within the study area a total of 49 times in 1964, from one to three times each, at distances up to 100 m from their 1965 nest sites. Individuals were found 11 times on the same sites as their 1965 nests, 27 times 4.6 m away or less and 11 times farther than 4.6 m away. Pairs of birds were found together on seven occasions in 1964. In these cases they were found three times on the same site as their 1965 nest, three times 4.6 m away or less, and only once farther than 4.6 m away. This suggests that nonbreeding birds spend this time choosing a mate and a nest site for the following breeding season.

The reason for not breeding in a particular season may be physiological. Nonbreeding individuals were assumed to be either of nonbreeding age or in poor physical condition from the previous months and unable to breed. It is also possible that some birds failed to breed because they were unable to find a suitable mate. Other factors leading to less than annual breeding are discussed in a later section.

#### MOLT IN RELATION TO BREEDING SEASON

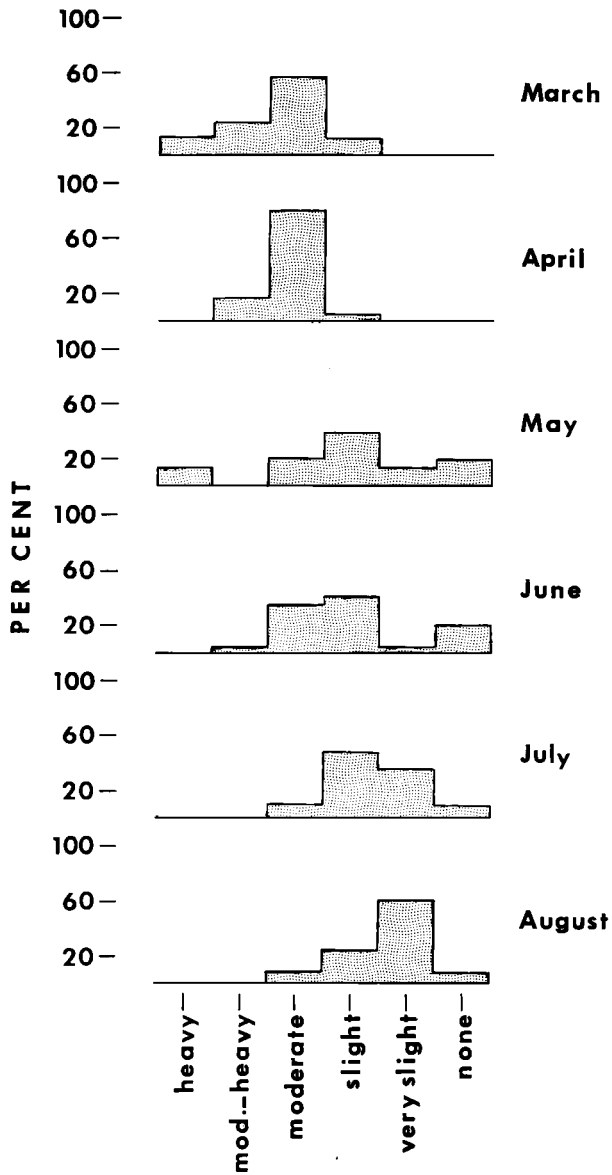
The two major physiological events in a tropicbird's life are breeding and molt, and these do not normally occur at the same time. Schreiber and Ashmole (1970) reported that Red-tailed Tropicbirds on Christmas Island (Pacific Ocean) undergo a complete molt annually. Prospecting (= pre-breeding) birds were completing their molts. Individuals laying replacement eggs did not molt any wing feathers between successive layings within a single breeding period. Stonehouse (1962) found that on Ascension Island molting of primaries stops during breeding in the Yellow-billed Tropicbird.

My limited information on molt generally substantiates the findings of these authors. All 14 birds examined in October and November of 1964 had old and worn plumage. Four of eight birds examined specifically for molt condition during this time were experiencing the beginnings of feather replacement. All 42 birds examined during March and April 1965 had new plumage, and only 11 of 24 (44%) birds examined for molt had feather replacement still in progress; almost all of this feather replacement was breast molt.

The central rectrices, unlike the rest of the plumage, were constantly being replaced. Usually one feather was fully grown while the other was emerging. During the latter part of the breeding season (August), shed central rectrices were often found on the ground near nest sites. These tail plumes are used in nuptial display and seem to require more time to grow to full length than does the rest of the plumage. Molting of central rectrices seems to precede the general molt, beginning late in the breeding season after the need for aerial display and in time to produce a new set for the next breeding season. Schreiber and Ashmole (1970) found most tropicbirds on Christmas Island to have one growing central rectrix. They concluded that at least one central rectrix is molted while the birds are still feeding chicks, and that growth of one normally nears completion at time of laying. Molting of central rectrices was unrelated to molting of the rest of the plumage in two species of tropicbirds on Ascension Island (Stonehouse, 1962).

White feathers of the new plumage of the Red-tailed Tropicbird are suffused with pink. This same pink condition was found in Yellow-billed Tropicbirds of Ascension Island by Stonehouse (1962). He concluded that *Phaethon lepturus* is partially sexually dichromatic with males most commonly having the pink tinge. This dichromatism does not exist in the Red-tailed Tropicbird on Kure. In 1965 all tropicbirds examined within the study area were classified according to amount of rose flush. Six categories were used: heavy, moderately heavy, moderate, slight, very slight, and none. Comparison of degree of rose flush among breeding pairs does not indicate a sexual dichromatism according to plumage tint. Of 30 pairs, males had a deeper rose flush than females in 12 cases, females had greater rose flush in 8 cases, and members of the pair were the same color in 10 cases. The rose flush is apparently a condition of new plumage and gradually fades during the breeding season. Degree of rose flush of nonbreeders found on the study area each month is shown in Figure 10. This shows a decline in degree of rose flush from March through August.

Determining the sex of Red-tailed Tropicbirds was difficult. Wing and culmen lengths from individuals of known sex show that although males average slightly larger, individual birds cannot be separated by these meristic data. Wing length for 14 males ranged from 305 to 333 mm with a mean of  $321.9 \pm 2.3$  mm; 31 females ranged from 301 to 332 mm with a mean of  $318.0 \pm 1.5$  mm. Culmen length for 15 males ranged from 61 to 66 mm with a mean of  $63.0 \pm 0.4$  mm; 31 females ranged from 57 to 67 mm with a mean of  $61.9 \pm 0.4$  mm. Sex could be successfully determined only by palpating a near-term egg in the oviduct or by observation of relaxed muscles and bloodstains about the anus after oviposition.



**DEGREE OF ROSE FLUSH**

FIGURE 10. Monthly distribution of degree of rose flush on unoccupied birds. Note decline in amount of plumage color as breeding season progresses.

### COURTSHIP AND PAIRING

Birds involved in prebreeding aerial display also tend to spend some time on the ground at their prospective nest site. Birds at such sites were found at all times of the day with no particular time being favored. My data indicate that visits lasting one to three hours were most common. When together at the prospective nest site, birds sit side by side, and copulation probably occurs at this time. I never observed copulation in the Red-tailed Tropicbird; however, it was at this stage of the breeding cycle that Stonehouse observed copulation in the Yellow-billed Tropicbird (Stonehouse, 1962).

The time interval between first recorded presence at nest site and onset of egg laying was recorded for all 90 pairs that nested in 1965. This interval ranged from 0 to 91 days with a mean of  $41.3 \pm 2.3$  days. This mean is certainly biased downward in relation to actual courtship period since there was no way of knowing how many visits to the prospective nest site a given pair made before I recorded their presence during my daily rounds. In any event, this interval indicates a considerably longer courtship than the 16 to 35 day period recorded by Stonehouse (1962) for the Yellow-billed Tropicbird.

Among 28 pairs in 1965 in which sex of individuals was determined, males arrived first in 18 pairs, females in 5 pairs, and in 5 pairs the birds were recorded as having arrived together. Chi-square for the ratio of male-female first arrivals (18 to 5) is significant ( $\chi^2 = 5.565$ ;  $.01 < P < .025$ ). Combining data for all 28 nests, prior to oviposition, male tropicbirds were found at nest sites 74 times and females 50 times. Chi-square for this male-female ratio (74 to 50) is not significant ( $\chi^2 = 1.173$ ;  $.50 < P < .75$ ). These data suggest that the male bird tends to initiate courtship and nest site selection and the female is present more often as the season progresses.

### NEST SITE SELECTION AND NEST CONSTRUCTION

The Red-tailed Tropicbird always nests on the ground. It has been reported to nest under the arching stems of a sedge on Rottnest Island (Storr, 1964), under vegetation on Pitcairn Island (Williams, 1960), on the ground under bushes on Christmas Island (Holt, 1958), and in cavities in cliff faces on Lord Howe Island (Hindwood, Keith, and Serventy, 1963).

On the Phoenix and Line Islands, Red-tailed Tropicbirds generally nest under vegetation, upturned coral slabs or abandoned buildings and occasionally within discarded oil drums. In the high Hawaiian Leeward Islands they nest in holes and cracks in volcanic cliff faces. These sites are similar to nest sites of the two species of tropicbirds on Ascension (Boatswain Bird) Island (Stonehouse, 1962). On Kure, the extensive dense growth of *Scaevola taccada* provides abundant cover for nest sites (Figures 11, 12, 13).



FIGURE 11. Stand of *Scaevola taccada* covering the Red-tailed Tropicbird study area on Green Island. Bare stems and branches in the foreground resulted from blowing sand during severe storms in spring of 1965.

Of the more than 2,000 nests that I found and examined on Kure, only one was not beneath scaevola cover. This nest was situated beneath an overhanging tussock of bunch grass, *Eragrostis variabilis*.

Although approximately 40% of the island was covered with dense stands of scaevola, an estimated 90% of tropicbird nests were situated within three m of the edge of the scaevola. Adult birds approach the nest site by hovering above the scaevola, then folding their wings, and plunging through the tangle of leaves and stems to the ground. Leaving the nest site is more complex. The bird's legs are reduced in size so that the bird is incapable of standing and walking (Howell and Bartholomew, 1969). Balancing on its breast, the bird pushes with its feet and pulls with its wings and bill until it reaches an open area suitable for its vertical takeoff. In "crawling" the breast rises slightly as the bird pushes with both feet. The bird moves forward then falls on its breast with wings partly spread to break the fall. The time and energy expended in this process presumably prohibits use of parts of scaevola thickets farther than approximately three m from an open area.

A pair of tropicbirds may prepare or partially prepare several nest scrapes before the egg is laid. One pair prepared four such scrapes. In eight cases in which birds of known sex were seen preparing a nest scrape,



FIGURE 12. Red-tailed Tropicbird nest site beneath tangles of scaevola branches. Paint mark on head of bird was used to facilitate recognition of members of pairs.

seven were males and one was a female. In two cases in which a pair was together at their prospective nest site and the sexes of the individuals were known, the male was preparing the nest scrape. These data suggest that males dominate in constructing nest scrapes.

Completed nest scrapes vary from shallow depressions in the sand, which are cleared of dead scaevola leaves and twigs to more elaborate structures up to 15 cm in diameter and 9 cm deep that are lined with dried scaevola leaves. Five nest scrapes, examined just before or just after oviposition, measured 5, 7.6, 7.6, 9.2 and 9.2 cm in depth and were nearly uniform in width, *i.e.*, approximately 15 cm. Twigs and other obstacles are usually removed from the nest scrape. In 1965, 5 of 11 pairs pulled the 15-cm long nest marker from the ground while preparing nest scrapes on their 1964 nest sites.

On 23 April 1965 one individual was observed while it constructed a nest scrape. Using its feet alternately, the bird threw sand backwards away from the nest site. This process was continued for 10 to 20 strokes per leg, with the bird rotating slowly and continuously in the process. The bird then stopped kicking and picked up a twig from the scrape with its bill. The bird shook its head from side to side throwing the twig away from the nest site. Then it dragged its bill around the base of the nest scrape until another twig





FIGURE. 13. Red-tailed Tropicbird nest site. Egg and nest site marker are visible in foreground.

was encountered and then repeated the head shaking process. Generally, after each twig was removed the bird kicked more sand out of the nest scrape with several strokes of the legs. This bird made a complete circle, turning on its breast and throwing twigs and sand as it turned.

Adult birds maintain the nest scrape while incubating. On one occasion an incubating male turned its head under its body and nudged the egg several times with its bill. Then it wiggled from side to side onto the egg more firmly and began to kick sand from the nest scrape. The bird continued kicking for about 30 seconds.

Nestlings older than 50 days actively maintained their nest scrapes. One 68 day old nestling was observed picking up dried scaevola leaves in its bill and placing them in the nest around its body. Other nestlings were observed maneuvering scaevola twigs around the rim of the nest scrape. On 24 occasions nestlings removed yellow nest markers embedded 15 cm into the ground at the rim of the nest scrapes and arranged them around the edges of the nest scrapes. In some cases nest scrapes of older nestlings acquired a rim of twigs and leaves exceeding 2.5 cm in height and 7.5 cm in width.

When sitting in the nest both adults and nestlings held wings folded against body and head pointing straight ahead and level (Figure 14). On rainy days birds assumed this typical nest posture but with head and neck



FIGURE 14. Normal incubation posture of nesting adult Red-tailed Tropicbird.

pulled back into the body feathers and tilted upward at approximately  $60^\circ$ . In this position the rain ran off instead of penetrating the contour feathers.

When I approached the nest, a characteristic defensive posture (Figure 15) was often assumed by adults and nestlings over 40 days old. In this posture the humeri are raised away from the body and the wrists are held close together at mid-breast; the neck is pulled into the body and the feathers are ruffed making the head look larger. The tail feathers are tilted upward and spread. This position was often accompanied by a guttural screech during which the head was shaken rapidly from side to side. Following this behavior pattern, nestlings usually attempted to crawl away from me. The general effect of the defensive posture was to make the bird appear larger. Defensive behavior known as threatening is found in many birds and includes puffing up of feathers, opening mouths and lifting wings.

Howell and Bartholomew (1969) described the sleeping posture of adult and nestling Red-tailed Tropicbirds, and my observations on nestlings confirm and extend theirs. Nestlings slept in a variety of positions on the nest. In 31 observations of sleeping nestlings, the bill was tucked among scapular feathers of the left wing 11 times, the right wing 9 times. The bill was pointed directly down the middle of the back once. Head and neck were extended and resting on the ground 6 times, and in 2 instances nestlings



FIGURE 15. Defensive posture often assumed by adults and older nestlings. A week-old nestling is visible in foreground.

were in the normal sitting posture. One nestling was observed asleep with head outstretched and rolled to the left, and another was found asleep with its bill pointing upward and resting against a scaevola branch. One nestling was observed once in each of the three sleeping positions: bill under left scapular feathers, bill under right scapular feathers, and bill down the middle of the back. Another nestling observed seven times had its bill under left scapular feathers twice, bill under right scapular feathers three times, head extended and resting on the ground once, and it was observed once sleeping in the normal sitting posture.

#### TERRITORY AND NESTING DENSITY

Tropicbirds on Kure display in large groups over prospective nesting areas. Presumably this group display provides social stimulation (display by neighboring birds accelerating the reproductive cycle) and/or social attraction (tendency of birds in breeding condition to be attracted to areas where birds are already on territory) to aid in synchronization of breeding (Schreiber and Ashmole, 1970). The resulting nests are clumped while areas of apparently equally suitable habitat have few or no nesting pairs. Nesting density within my study area was probably as great as or greater

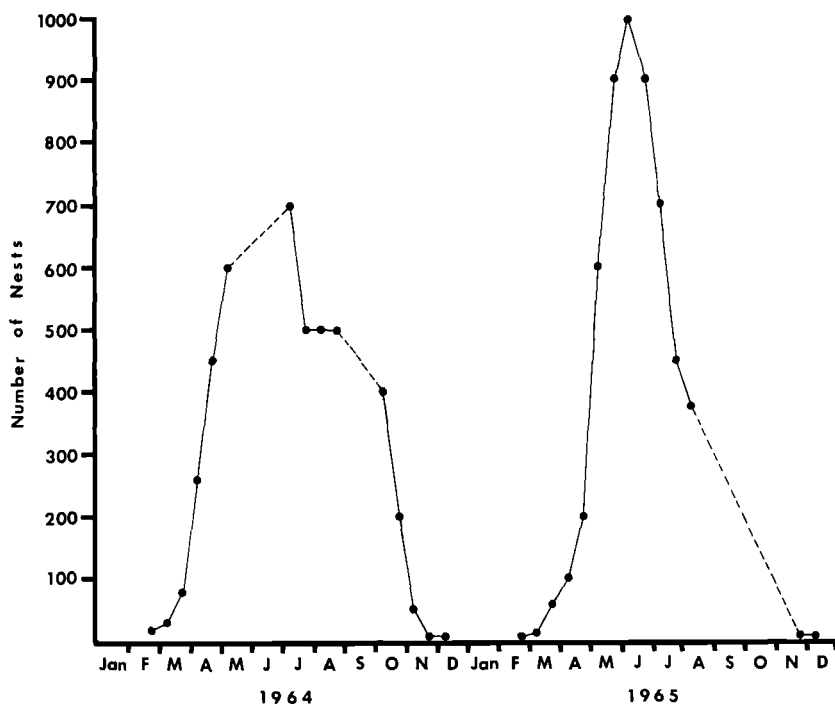


FIGURE 16. Monthly counts of active tropicbird nests on Green Island. The reduction in rate of decrease in July-September 1964 resulted from cessation of rat predation. Dashed line in 1964 indicates a period in which no estimates were made.

than that within any area on the island. In 1965, 90 pairs nested in the approximately 0.57 ha study area or one nest per 64 m<sup>2</sup>. Actual nest density was higher since tropicbirds used only one-third of the study area because nesting was generally confined within three m of the edge of the scaevola thicket and nests were clumped on the windward (beach) side of the area. Thus actual nest density was approximately one nest per 24 m<sup>2</sup>. The average nearest distance between nests was approximately 1.5 m. Nesting birds defended only the area that they were able to reach with their bill from their position on the nest. This territoriality produced two known cases of territorial interaction in two years, resulting in nesting failure. In both cases eggs were destroyed by birds fighting for possession of the nest site. Stonehouse (1962) and Snow (1965) found competition for nest sites to be the primary cause of nesting failure in the species of tropicbirds that they studied. The large areas of potential nesting habitat on Green Island undoubtedly reduces this sort of competition compared to islands where available nest sites are limited to occasional cavities in the coral substrate.

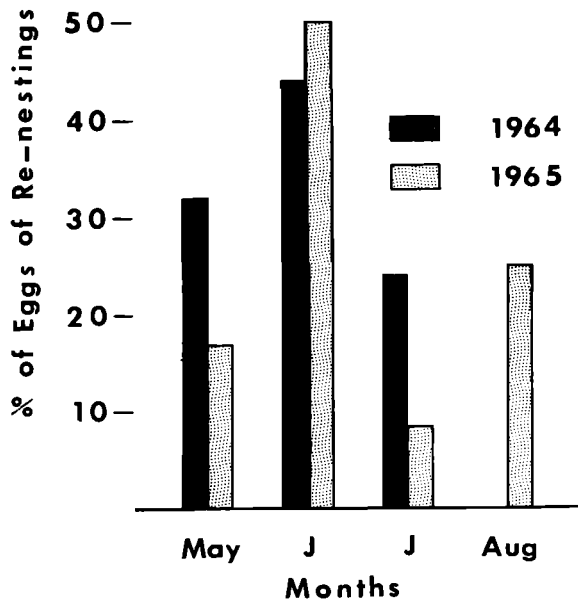


FIGURE 17. Percentages of all re-nest eggs (1964 and 1965) according to months in which they were laid.

#### NESTING CYCLE

At least one nest with an egg or nestling was found on Green Island in every month of the year during my two-year study. Single nests were begun in January and October 1964, and in January 1965; however, egg laying usually begins in late February or early March. In 1964, the number of active nests increased rapidly from March through June, then it decreased rapidly in July as first nestings and re-nestings decreased and as nest predation by rats (*Rattus exulans*) continued. Then the decrease in number of active nests was slowed in late July by cessation of rat predation (Figure 16). In 1965, increases in number of active nests and peak number of nests occurred in the same months as in 1964, but decreases continued steadily after mid-June due to continued predation by *Rattus exulans*. Maximum numbers of active nests were reached in June of 1964 with approximately 750 and in June of 1965 with an estimated 1,000 (Figure 16).

In the study area in 1964, 70.5% of first-nest eggs were laid in March and April, whereas in 1965, 74.2% of first nestings were delayed until May and June due to severe storms in March and April (Fleet, 1972). With regard to re-nesting, these two peaks are quite different. In 1964, re-nestings were restricted to May, June, and July while in 1965 re-nesting peaked in June but continued into August (Figure 17). The coincidence of first nestings and re-nestings in 1965 produced a June peak higher than that of 1964.

TABLE 1  
CHARACTERISTICS OF 104 EGGS OF THE RED-TAILED TROPICBIRD.

Amount of Ground Color	Number of Eggs	%
Egg white	4	3.8
Scattered specks	7	6.7
Medium	81	77.9
Large pigment spots	11	10.6
Solid pigment	1	1.0
Pigment Color		
Red-brown	3	2.9
Red	7	6.7
Purple	93	89.4
Purple-black	1	1.0
Pigment Concentration		
Large pole	75	72.1
Small pole	6	5.8
Both poles	4	3.8
No concentration	19	18.3
Pigment Swirling		
Clockwise from large pole	4	3.8
Clockwise from small pole	2	1.9
Counterclockwise from large pole	2	1.9
No swirling	96	92.4

However, due to the reduced number of renestings in 1965, total number of nesting attempts (and pairs nesting) probably was greater in 1964.

#### EGGS AND EGG LAYING

The female bird occupies the nest for about 24 hours prior to egg laying. At this time the shelled egg can be palpated within the female, and she is docile and reluctant to move from the nest when approached. In four instances, the interval between palpating and egg laying ranged from 20.4 to 24.5 hours.

Clutch size of the Red-tailed Tropicbird is invariably one. The egg is ovate and varies from white to purplish-black depending on amount and arrangement of pigment laid down. Usually the egg has a light purple ground color with a heavier concentration of pigment at one or both ends, but usually at the blunt end. These heavier pigment concentrations are sometimes swirled about the long axis of the egg. The heavier concentration of pigment at the poles of the egg presumably results from reduced friction at these points during the laying process. The swirling that was occasionally observed in the polar pigments probably results from movement of wet pigment as the egg rotates in the oviduct. Table 1 summarizes the intensity and distribution of egg color for 104 eggs examined.

Measurements of length and width were taken from 300 eggs. Length ranged from 56.1 mm to 74.0 mm ( $\bar{x} = 64.18 \pm .16$  mm) and width from 41.2 mm to 56.3 mm ( $\bar{x} = 45.07 \pm .10$  mm). These means are slightly smaller than those given for 36 eggs in various collections by Bent (1922), *i.e.*, 65.5 mm and 46.6 mm, respectively. However, the ranges are quite similar for the two sets of measurements. My egg measurements for the Red-tailed Tropicbird are similar to those of Stonehouse (1962) for the Red-billed Tropicbird, a bird of similar size.

Egg measurements were taken for both eggs of 29 pairs which nested twice during the 1964 breeding season. First eggs were larger in mean length and width than those produced in renesting. The difference in mean lengths was not significant ( $F \bar{c} 28 \text{ df} \ \& \ 28 \text{ df} = 1.81; .05 < P < .10$ ); however, mean widths were significantly different ( $F \bar{c} 28 \text{ df} \ \& \ 28 \text{ df} = 1.96; .01 < P < .05$ ). Approximate volumes were calculated by the formula for an ellipsoid,  $V = \pi/6 \ ab^2$  (Worth, 1940).

Egg volume was less in the second egg in 22 of the 29 cases, and greater in the second egg in 7 cases. Mean volumes of first and second eggs differ by 3.41 cc or 4.79%. Mean volume of second eggs is significantly less than mean volume of first eggs ( $F \bar{c} 28 \text{ df} \ \& \ 28 \text{ df} = 2.13; .01 < P < .05$ ).

Similarly, Stonehouse (1962) found that renest eggs of the Yellow-billed Tropicbird were nearly always smaller than first eggs, with a reduction in volume of 4 to 5%.

#### INCUBATION

After laying, females usually first leave the nest during the same day. Incubation is then taken over by the male. In 27 of 44 instances, the female left on the same day she laid; in 10 cases she left the day after laying; and in the remaining seven cases the female stayed for 2, 2, 2, 3, 3, 5, and 9 days. Records of 36 incubation cycles (*i.e.*, interval from egg laying through incubation watch of adult during which hatching occurred) indicate that males spend slightly more time (not significant) incubating than the females. In 19 cases the male spent more time on the egg, in 15 cycles the female spent more time, and in 2 cycles the time was equally divided. For a total of 1,675 incubation days, males incubated 870 days (51.9% of the time), whereas females incubated 805 days (48.1%). Stonehouse (1962) reported nearly the same difference in the Yellow-billed Tropicbird, with males incubating 52% of the time and females 48%.

Tropicbirds lack a brood patch, and the small feet are placed far back on the body probably playing no role in incubation (Howell and Bartholomew, 1962). The egg is tucked among the breast feathers. Incubating tropicbirds show strong affinity to their eggs. I once pushed a bird off its egg, and the bird immediately returned, nudged the egg several times with



FIGURE 18. Incubation behavior of Red-tailed Tropicbird. Incubating adult is returning to egg after being displaced.

its bill, and then pushed it beneath its breast while moving forward over it. Incubating birds often bend the head beneath the body and nudge the egg (Figures 18, 19). This behavior may function to turn the egg to distribute heat evenly and to prevent adhesions.

Howell and Bartholomew (1969) showed that Red-tailed Tropicbirds possess a strong tendency to retrieve eggs of their own species (one or several) from within 15 cm of the nest scrape. This tendency was found considerably reduced when eggs of other species or egg-like objects were tested.

Periodically during incubation, one parent is relieved by its mate. I observed this substitution twice. In one case the other bird arrived and the pair sat facing each other with heads side by side and breasts touching. The new arrival crowded toward the bird on the egg and eventually displaced it. The other observed instance of this behavior was similar except that the birds sat side by side facing the same direction.

Nest attendance periods of parent birds for 150 incubation periods observed ranged from 4 to 16 days with a mean of  $8.12 \pm .07$  days and mode





FIGURE 19. Incubating Red-tailed Tropicbird bends head beneath body and nudges egg. This behavior also occurs among undisturbed birds. Photographs in Figures 18, 19 were taken on Midway Atoll, 90 km ESE of Kure Atoll.

of 7 days (Figure 20). The skewness to the right which is responsible for the difference between the mean and mode of these records is the result of longer attendance periods (11 through 16 days). These are presumably due to the delay at sea of the relieving bird.

There are from five to eight attendance periods ( $\bar{x} = 6.71 \pm .08$ ) from laying to hatching. The first period, during which the female lays the egg, is usually shorter than the others. In 13 of 39 successful hatchings there was one attendance period beyond hatching, and in 3 cases there were two periods beyond hatching. When records for attendance periods are broken down, it is found there were more attendance periods per incubation during renesting ( $\bar{x} = 7.25 \pm .18$ ) than during first nesting ( $\bar{x} = 6.51 \pm .08$ ) and this difference is significant ( $F_{19 \text{ df} \& \ 54 \text{ df}} = 1.88; .025 < P < .05$ ). Both adults show reduced length of attendance periods (Figure 22). Means of female attendance periods decrease at successive attendances in both first nestings and renestings. Significant differences (computed by a one-way Analysis of Variance) exist within the attendance periods for first nestings

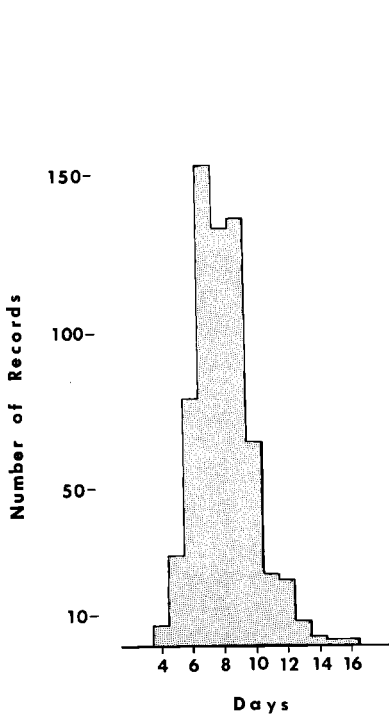


FIGURE 20. (Left) Nest attendance periods of parent birds for 150 incubation periods ranging from 4 to 16 days with a mean of  $8.12 \pm .07$  days and mode of 7 days.

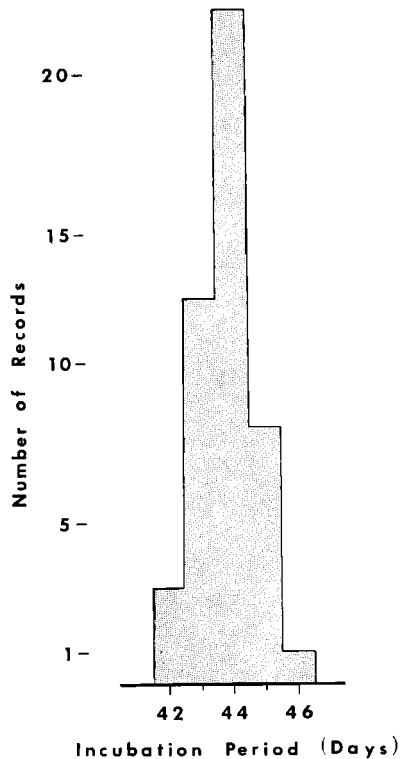


FIGURE 21. (Right) Incubation periods of 45 Red-tailed Tropicbird eggs on Kure Atoll. Mean is  $43.8 \pm .13$  days.

( $F \bar{c} 2 \text{ df} \ \& \ 78 \text{ df} = 16.11; P < .005$ ). Mean values for renesting attendances are smaller than for the first nestings in all successive periods. For males, mean attendance periods for both first nesting and renestings are greater than comparable values for females, with the exception of the first male attendance period of the first nesting compared with the female first attendance period of the first nesting. The only one of these comparisons in which the male attendance period is significantly longer is the second period of the first nesting ( $F \bar{c} 32 \text{ df} \ \& \ 30 \text{ df} = 1.95; .025 < P < .05$ ). The shorter attendance periods of females probably reflect the strain of egg production. During early incubation of the first egg, the female has adequate energy reserves and she remains at sea a relatively short time before returning.

The male's first incubation period is relatively short. His second period is longer than both the first and third, because the female remains at sea

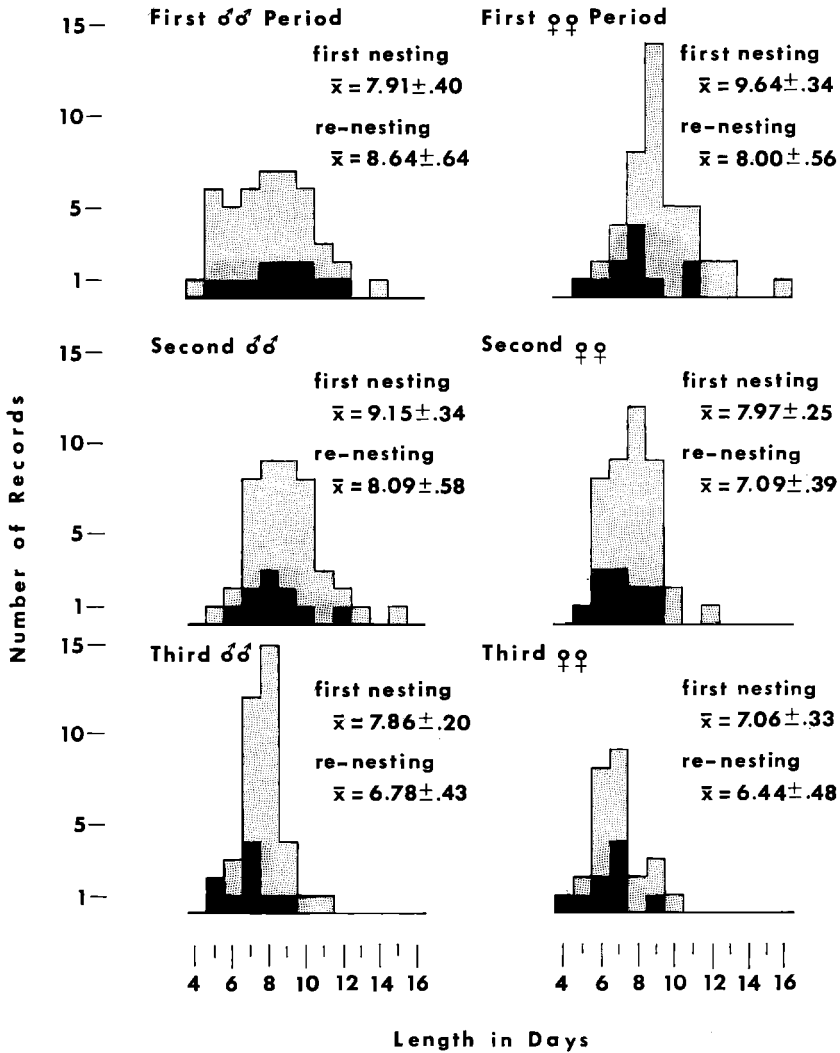


FIGURE 22. Histograms of successive nest attendance periods for both parent birds. Shaded figures indicate the portion of each histogram which is due to attendance periods of re-nestings. With the exception of the second male attendance period of first nestings, there is a progressive decrease in length of attendance periods.

longer. Significant differences (computed by a one-way Analysis of Variance) exist within the male attendance periods for first nestings ( $F \bar{c} 2 \text{ df} \ \& \ 92 \text{ df} = 4.92; .005 < P < .01$ ). The differences are not significant within attendance periods for re-nestings ( $F \bar{c} 2 \text{ df} \ \& \ 28 \text{ df} = 2.61; .05 < P < .10$ ). During re-nesting, however, male attendance periods resemble those of fe-

males during first nestings. The first male attendance period of renesting averages longer than the corresponding male attendance period of the first nesting. This reflects the long time at sea of the female after producing a second egg. The second and third mean attendance periods are progressively shorter as both male and female birds are unable to spend such long periods incubating.

Forty-five incubation periods of Red-tailed Tropicbirds ranged from 42 to 46 days with a mean duration of  $43.8 \pm .13$  days (Figure 21). In two cases, nests were abandoned briefly, but ultimately the eggs hatched. These two records are not included in Figure 21. In 1965 an egg was abandoned for four days (30th through 33rd day) but hatched on the 46th day. In 1964 an egg was abandoned for five days (11th and 30th through 33rd) but hatched on the 48th day. I recorded three cases of unusually long incubation periods on eggs that did not hatch. These were 57, 67, and 77 days long and involved 10, 10, and 11 attendance periods. One of these three eggs was still being incubated when the study ended.

Worth (1940) found that incubation period commonly increases in parallel with the fourth power of the increase in egg volume and that incubation period may be roughly calculated from the formula

$$V = .0063 \frac{(1000 V)^{1.30}}{(T)} \text{ where } V \text{ is volume and } T \text{ is incubation time.}$$

Red-tailed Tropicbird incubation period calculated by this formula is 27.4 days, which is considerably less than the observed mean incubation period of  $43.8 \pm .13$  days. This condition combined with slow growth of nestlings has been pointed out by Lack (1948, 1966) as usually occurring in species whose food supply is limited or erratic. This idea in conjunction with evidence from allometric growth of nestlings and experiments in nestling feeding is developed later.

#### HATCHING

The hatching process, from pipping until the hatchling emerges, requires only a few hours. In one case an egg not pipped at the morning nest check was completely hatched by the same mid-afternoon. Typically a small hole is made in the shell by the chick using its egg tooth. Then the chick enlarges the hole by chewing away the shell with its bill. During this process the chick usually calls unceasingly. These activities may have caused a few incubating birds to leave the nest, because 16 of 128 newly hatched nestlings were seen to be temporarily without an incubating adult. In all 16 instances the hatchling was again being incubated on the following day.

The wet down of hatchlings dries in a few hours and the egg shell is removed from the nest by the following day. In 18 instances where I found

a wet hatchling and an egg shell in a nest on my daily rounds, the hatchling was dry and the shell absent on the next day's round. The new nestling has its eyes closed. The hatchling's balance is poor. When removed from beneath the parent, hatchlings attempted to crawl beneath the adult bird or even beneath the hand of the observer. The fluffy down of nestlings is white with gray tips on the wings, lower back, and in a ring around the neck. It is totally white on the abdomen. Dorsal down is 20 to 30 mm long and that on the abdomen is about 10 mm. The bill is black with a dark brown base (Figure 30). The legs and proximal two-thirds of the feet are pink. Distally the feet are black. In addition to the white down on the abdomen, three individuals had all white down on wings and mid-back. One hatchling had an all white face and another hatchling was completely covered with white down.

The egg tooth persists and becomes light gray whereas the bill turns black. In 42 nestlings the egg tooth remained from 14 to 46 days ( $\bar{x} = 30.1 \pm 1.0$  days) before being shed.

#### ADULT BROODING BEHAVIOR

The adult which was incubating when hatching occurred usually finished its normal attendance period, and in 27 of 58 instances constant brooding continued for one to three further attendance periods (i.e., about 4 to 17 days). The nestling stays beneath the adult for about one week. Beyond this the nestling is more active and alert and generally sits beside or under the wing of the adult bird. Similar wing-brooding behavior was recorded by Howell and Bartholomew (1962). After 10 days to two weeks, adult attendance of the nestling becomes more erratic. When the nestling is about 25 days old, adults come to the nest only to feed the nestling (Figure 23).

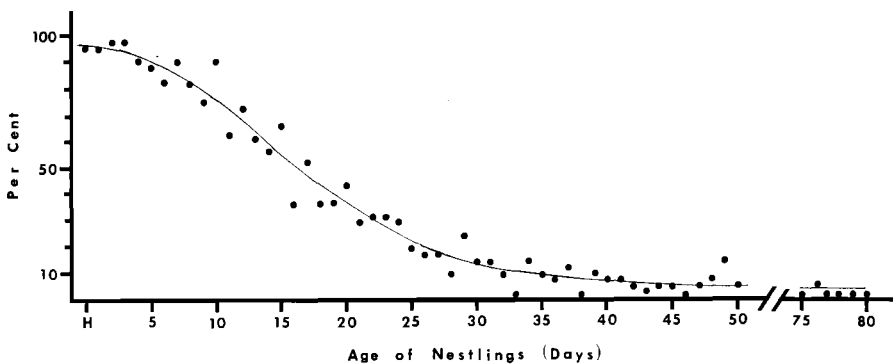


FIGURE 23. Frequency of parent bird at nest versus age of nestling. These records represent daily visits to 41 nestlings. Line is fitted by sight.

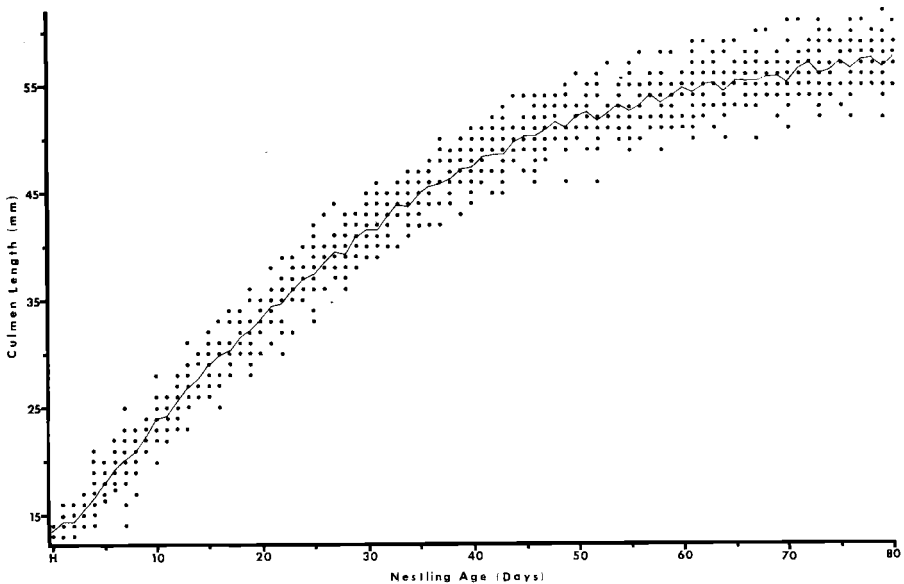


FIGURE 24. Growth of the nestling bill as indicated by the culmen measurement. Dots indicate individual measurements. Duplicate measurements were not plotted. Solid line connects the means.

#### NESTLING GROWTH AND DEVELOPMENT

Nestlings in the study area were weighed and measured every third day. Forty-one nestlings were followed to fledging; two other nestlings were followed for 60 days and 24 nestlings were measured only a few times before succumbing to predation by the Polynesian rat. As a result of these factors, sample size varies from day to day. Sample sizes ranged from 14 to 23 for the first 7 days and from 9 to 17 thereafter.

Growth of the culmen is shown in Figure 24. Approximately two-thirds of the increase in bill size occurs in slightly less than half of the nestlings' pre-fledging growth time. It seems reasonable to assume that this growth pattern is highly adaptive to species in which the nestlings' food supply arrives irregularly, but in large amounts. In species such as the Red-tailed Tropicbird in which food supply may be limited or erratic, allometric growth favoring bill development would allow the nestling to take advantage, at an early age, of occasional large amounts of food presented by the parents. Culmen length at fledging is still short of its full adult size (Table 2).

Growth of tibiotarsus and foot (measured to end of longest toe in this totipalmate species) are shown in Figures 25 and 26, respectively. Both structures show rapid early completion of nearly all growth. Growth of tibiotarsus and foot are essentially complete by the thirty-fifth day. Mea-

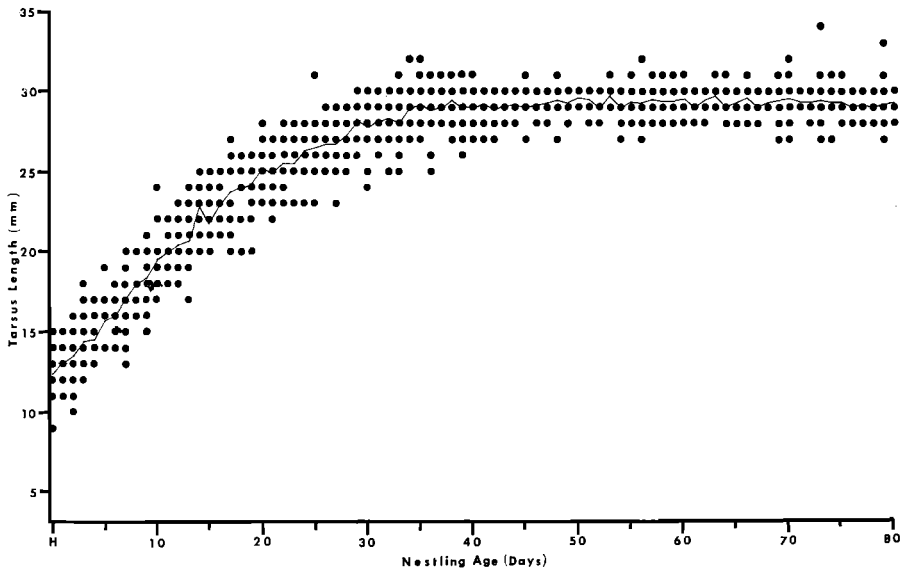


FIGURE 25. Growth of tibiotarsus. See Figure 24 for legend.

surements of tibiotarsus and foot at fledging are essentially the same as those of adults (Table 2). Rapid completion of growth of the unfeathered legs and feet may be advantageous to the nestling with regard to thermoregulation. Howell and Batholomew (1962) suggested that heat is dissipated via the feet to the surrounding air by adults in flight. On Kure I observed behavior that appeared to enhance heat dissipation from the feet by nestlings of the Laysan Albatross, Black-footed Albatross and Blue-faced Boobies.

TABLE 2  
COMPARISON OF ADULT AND FLEDGLING MEASUREMENTS\*

	Range	Mean	Probability
Fledgling Culmen Length	55-63	58.02 ± .32	
Adult Culmen Length	58.5-71	62.69 ± .31	N.S.
Fledgling Tarsus Length	27-31	29.20 ± .14	
Adult Tarsus Length	27-31	29.01 ± .12	N.S.
Fledgling Foot Length	46-53	49.22 ± .28	
Adult Foot Length	47-54	50.43 ± .18	N.S.
Fledgling Wing Length	272-318	300.4 ± 1.6	
Adult Wing Length	311-346	320.1 ± 1.1	N.S.
Fledgling Weight	455-880	680.2 ± 12.9	
Adult Weight	468-710	611.6 ± 7.1	P < .005

\* Measurements are in mm; weights are in grams. Measurements are from 57 adults and 41 fledglings. Differences between means were tested by cumulative F distribution test.

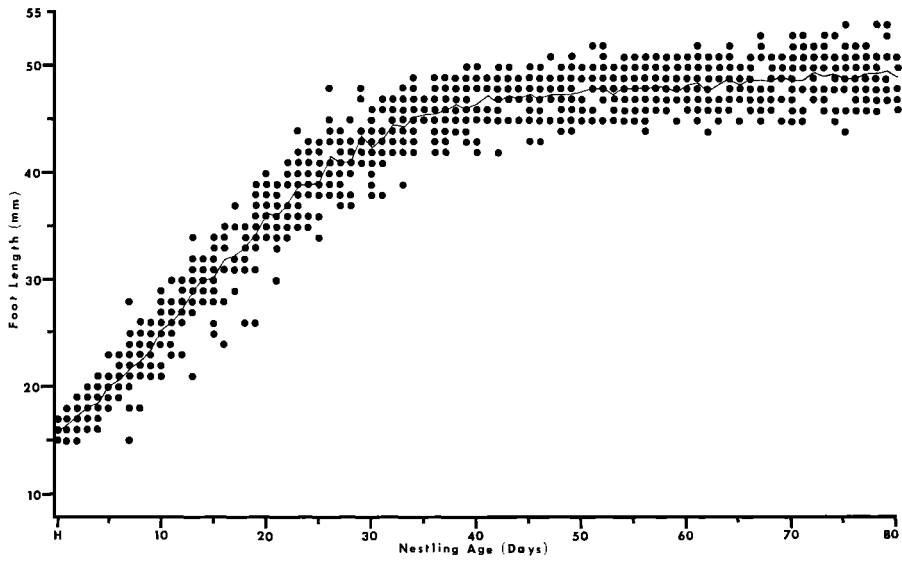


FIGURE 26. Growth of the foot measured to end of longest toe. See Figure 24 for legend.

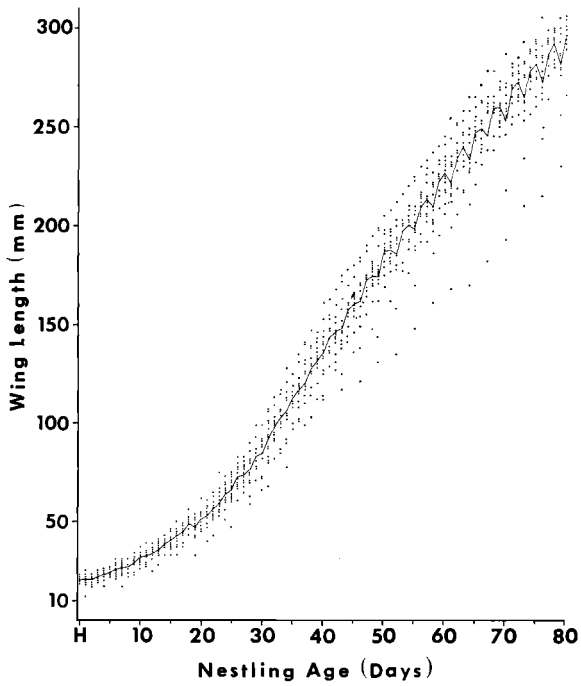


FIGURE 27. Growth of wing (measured from the proximal end of the manus to tip of longest primary feather) feathers of the nestling. See Figure 24 for legend.



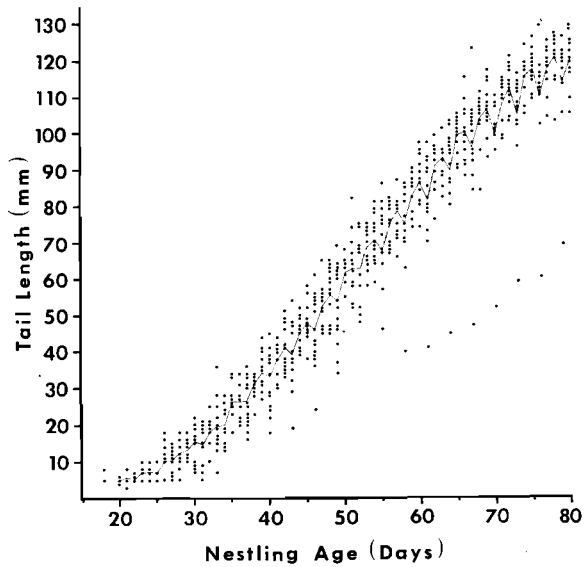


FIGURE 28. Growth of rectrices. See Figure 24 for legend.

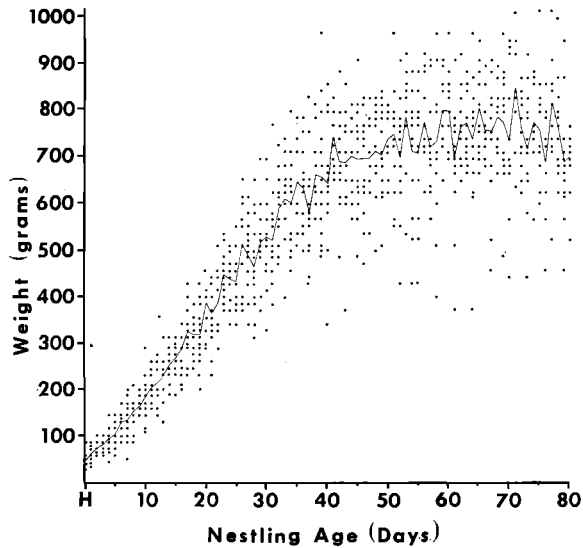
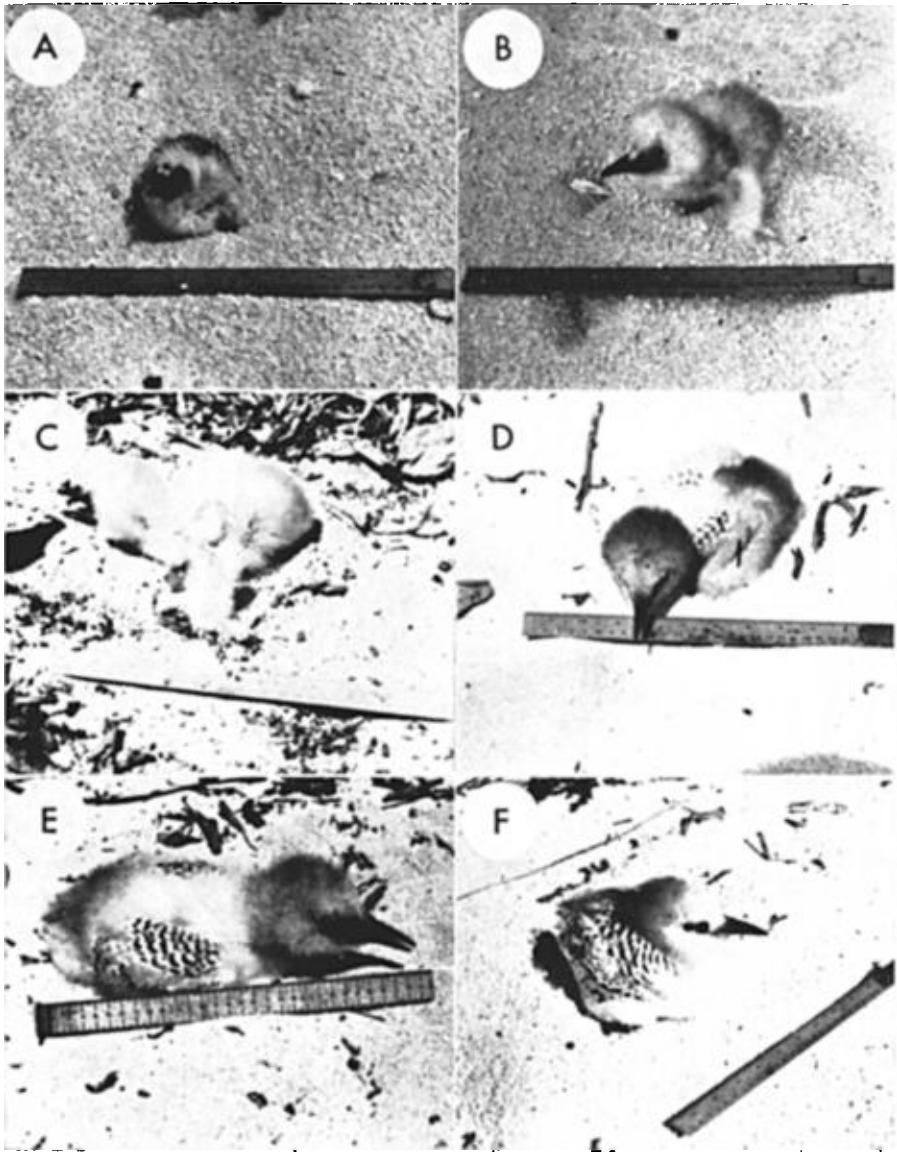


FIGURE 29. Growth in weight (grams) of nestling tropicbirds. Decrease in weight just prior to fledging is typical of other species of tropicbirds on Ascension Island. See Figure 24 for legend.

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 FIGURE 30. A. Newly hatched Red-tailed Tropicbird. Down has almost dried, eyes are still closed, and nestling is unaware of surroundings. It does not react to visual or auditory stimuli. A tap at the base of bill caused the nestling to open its mouth to receive food. Note 30 cm rule in foreground of picture.



- B. Seven-day-old nestling is aware of its surroundings. It will defend itself vigorously by striking with its bill, and it will utter disturbance calls.
- C. Fourteen-day-old nestling striking at shadow of investigator's foot. Nestling is in natal down. At this age the nestling is still highly vulnerable to predation by rats, but it is near maximum size at which attacks normally occur.
- D. Twenty-day-old nestling is beyond susceptibility to predation by rats. The first contour feathers have erupted in scapular region.
- E. Twenty-eight-day-old nestling. Wing and ventral feathers have erupted and egg tooth has dropped off.
- F. Thirty-five-day-old nestling. All contour feathers have erupted.

These birds sat, backs to the sun, with legs and feet outstretched in the shade of their bodies.

Eruption of primary feathers begins at approximately 25 days, and thereafter wing length increases almost exponentially throughout most of the nestlings' growth period (Figure 27). Even with this rapid growth, 35 of 41 nestlings (85%) still had one or more primary quills growing when they left the nest. Wing length of fledged nestlings is considerably less than for adults (Table 2).

Tips of the rectrices appear from the eighteenth to twenty-seventh days (Figure 28). Tail feathers grow rapidly until the seventy-fifth day when growth nearly ceases. Tail length of the fledgling is considerably less than that of the adult but only because fledglings lack the long, red, central tail plumes.

Weight was the most variable of all parameters measured (Figure 29). Weight increased rapidly until about the fortieth day. About five days prior to fledging (and leaving the island) nestling weights seemed to decrease. Similar weight losses occurred in nestlings of *P. aethereus* and *P. lepturus* on Ascension Island (Stonehouse, 1962). Weight loss just prior to fledging apparently results from refusal to feed. Other POBSP workers reported to me that two nestling tropicbirds raised by hand on Johnston Atoll to the south refused proffered food for several days before leaving the island. I had similar results with starving fledglings which I fed back to health in the laboratory on Kure. Prefledging weight loss may be important in reducing wing loading and thereby easing the transition to extended pelagic flight.

#### NESTLING PLUMAGE DEVELOPMENT

Development of nestling plumage was noted. Particular attention was given to the scapular, dorsal and ventral feather tracts and to emergence of primary, secondary and tertiary flight feathers and rectrices. Progressive loss of down in later development was also recorded. Figures 30 and 31 depict nestling plumage development at weekly intervals from hatching to fledging.

From hatching to ninth day, nestlings are covered with down only. Quills of scapular feathers erupted from 9 to 17 days (mode = 13 days); from 15 to 22 days (mode = 18 days) the tips broke and released approximately 6 mm of the growing vanes. The early scapular feathers are easily seen in Figure 30-D. Secondary and tertiary wing feathers generally appear at from 14 to 21 days (mode = 16 days). At 20 to 25 days the ventral tracts come in. Primary feathers and rectrices generally first appear together from 21–27 days (mode = 21 days) and 18–27 days (mode = 23 days), respectively. The dorsal feather tract comes in between 22 and 35 days (mode = 29 days) and is the last major group of contour feathers to appear.

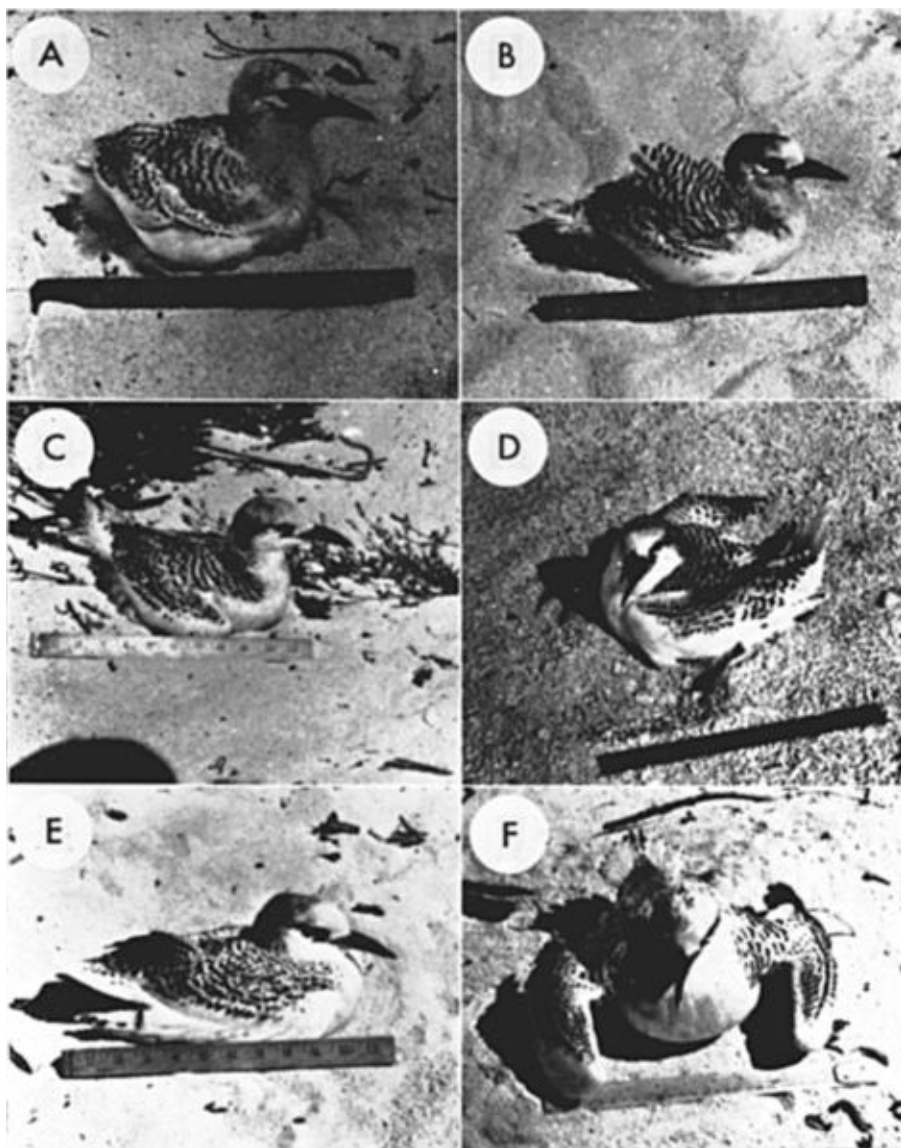


FIGURE 31. A. Forty-two-day-old nestling. Down is restricted to head-neck region and posterior abdomen.

B. Forty-nine-day-old nestling. Down is restricted to neck region. Nestling begins to move out of nest scrape.

C. Fifty-six-day-old nestling. Last of natal down has disappeared.

D. Sixty-three-day-old nestling. At this age the bird is dangerous to handle because the bill has hardened and the jaw muscles are strong.

E. Seventy-day-old nestling. Wing and tail feathers are still growing.

F. Eighty-four-day-old nestling. The bird has entered the pre-fledging starvation period. Immature plumage is complete.

Down loss begins with the first eruption of contour feathers and proceeds apace with development of the juvenal plumage. By the thirty-fifth day, down is gone from the wings, upper back, breast and face; and by the fortieth day down remains only on neck, lower back, and flanks. This remaining down disappears first from flanks, then neck and lastly from lower back. The nestling is free of down between 57 and 76 days after hatching (mode = 67 days).

#### FEEDING OF NESTLINGS

Twenty-seven of 37 (73%) observed feedings of nestlings occurred between 11:00 and 15:00 hours. Tropicbirds are pelagic, diurnal feeders, and the midday peaks in feeding of nestlings and aerial display activity are probably, in part, a function of the flying time between feeding areas and the island.

Adults arriving to feed nestlings fly directly to the area over the nest, fold their wings and drop through the scaevola. A parent moves directly to the nestling and begins the feeding process. When the nestling sees the adult, it begins a guttural chattering call that continues throughout the feeding and until the adult bird has left. Often after the feeding process, the adult sat at the nest site for several minutes before moving out of the scaevola. In 18 observed feedings, total time spent by the adult on the ground ranged from 1 to 10 minutes and averaged  $4.4 \pm .55$  minutes. Time required for actual transfer of food, however, was much less, and in five observations it was completed in 15 to 30 seconds.

Adult birds are specific to their nestling or at least to the nestling in their nest (Howell and Bartholomew, 1969). Nestlings, however, will chatter and attempt to beg food from any adult within sight. In younger nestlings (i.e., < 10 days), gaping response could be evoked by scratching the skin at the base of the bill. Gaping was followed by a gulping response to any object, including my finger, placed in its mouth. Experiments by Howell and Bartholomew (1969) showed that tactile stimulation of the prominent black patch at the base of the bill by the adult is necessary to evoke a gaping response. They also found no indication that adult bill color is important in releasing the gaping response. They suggested that this may be related to the unusual method in which the Red-tailed Tropicbird feeds the nestling. In contrast to the usual pelecaniform pattern in which the young bird feeds from the gular pouch of the adult, in this species (and probably other tropicbirds as well) the adult feeds the nestling by inserting its bill into the gullet of the nestling and disgorging food. (Figure 32, A, B, C).

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FIGURE 32. A. Red-tailed Tropicbird preparing to feed nestling. →  
B. Adult elicits gaping response from nestling.  
C. Adult transfers food to nestling. Note that in contrast to the usual pelecaniform feeding pattern, the adult places its bill within that of the nestling.

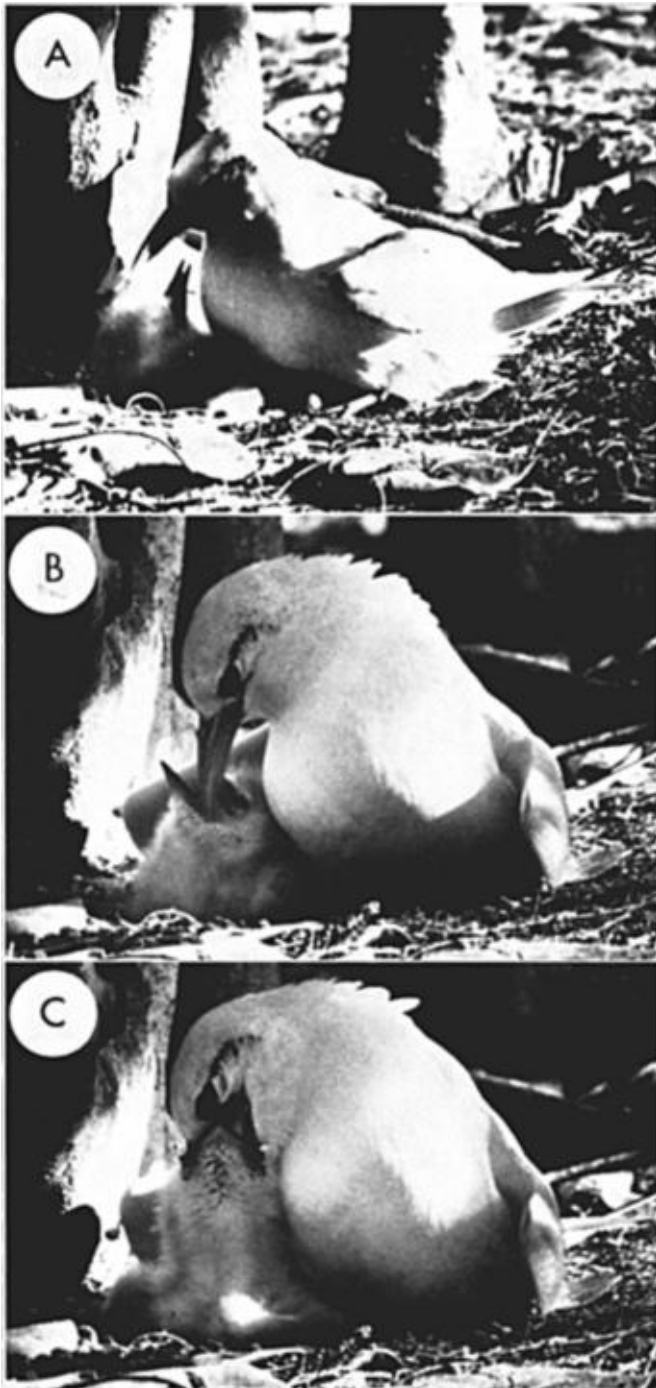


TABLE 3  
AMOUNT AND RATE AT WHICH FOOD WAS SUPPLIED BY PARENTS TO NESTLING  
RED-TAILED TROPICBIRDS.

Age (in days) During Experiment	# Days Fed	Total Wt. of Food Fed to Nestling	Range of Wt. of Food per Weighing Period* †	Mean Wt. of Food/ Feeding	Mean Wt. of Food/ Day	Food/ Gm. bird/ Day
2-4	2	26	3-13	6	13	0.17
10-20	9	222	1-40	17	25	0.08
22-32	9	352	1-112	29	39	0.08
23-33	7	419	1-103	52	60	0.12
23-33	6	250	9-64	36	42	0.09
44-54	7	568	2-136	63	81	0.14
53-63	6	446	6-148	64	74	0.10
53-63	6	393	10-183	66	66	0.08
63-73	7	687	4-174	86	98	0.13
63-73	5	330	3-114	55	66	0.08
66-76	6	363	33-88	60	61	0.09

\* Periods of no feeding not included.

† All weights are in grams.

In feeding, the adult approaches the calling nestling, leans forward and down and places its bill inside the nestling's vertically pointing and gaping bill. The nestling rotates its bill 90° and grasps the sides of the adult's bill. The nestling calls continuously while the adult rocks back and forth and regurgitates food into the nestling. Frequently, the nestling continues to hold the adult by the bill after the food is transferred or the nestling may strike at the adult's bill after releasing it.

I did not key out the kinds of food regurgitated by tropicbirds to their young. However most items were either flying fish (order *Atheriniformes*; family *Exocoetidae*) or squid (class *Cephalopoda*; order *Teuthoidea*). These two groups made up approximately 95% of food items, and this finding is similar to that of Gibson-Hill (1947). In all but one case the other food items were a tuna-like fish generally around 200 mm in length. The single exception was a triggerfish (order *Tetraodontiformes*; family *Balistidae*) regurgitated by a nestling. This was the only reef-dwelling fish found in the diet.

By weighing a series of 11 nestlings twice daily I was able to determine the amount of food received by each nestling during the intervals between weighings (Table 3). Eleven nestlings of various ages were weighed daily at 13:00 and 16:00 hours over a period of 10 days. This procedure divided the day into two periods, and the amount of food taken by a particular nestling was determined for 19 such periods. These data do not indicate whether one or both adults fed a particular nestling. However, other data show that both adults normally participate in feeding the nestling. One nestling went unfed for seven consecutive periods, and four other nestlings

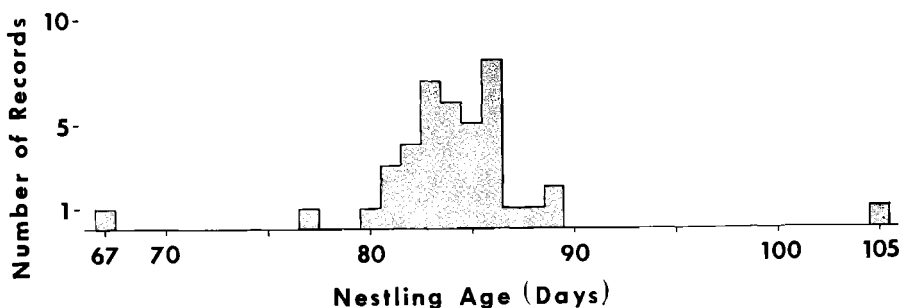


FIGURE 33. Fledging ages of 41 nestlings. Mean is  $84.2 \pm .76$  days.

were not fed for four consecutive periods. Five consecutive periods was the longest that any nestling was fed without missing a period. Younger nestlings are apparently fed every day while in the older nestlings the frequency of feeding is reduced. For the two nestlings under 20 days old, the mean amount of food taken per feeding and per day was substantially less than in older nestlings, probably due to the small size of the younger nestlings. The mean amount of food per feeding and per day increased at 20 days but remained relatively constant thereafter for nestlings of older age groups. The great variation in weight of food transferred to older nestlings per feeding is also of interest. It is my impression that the adult transfers all of its stomach contents to the nestling at a feeding. The small amounts sometimes fed coupled with the fact that total amounts of food given to the nestling stabilize at an early nestling age seem to indicate that the adult birds are procuring food for the nestling to their maximum ability and are unable to collect larger quantities during the time available.

In December 1964 I hand-fed three starving fledglings, which I found on the beach. On successive days, one fledgling accepted 212, 141, 256 and 311 grams of fish. This was the only hand-fed fledgling that was allowed to feed to repletion. This amount of food is considerably more than provided in a comparable period by parents (Table 3). The limiting factor in fledging age may be the rate parent birds can supply food to the nestling.

#### FLEDGING

Fledging age for 41 nestlings ranged from 67 to 105 days and averaged  $84.2 \pm .76$  days (Figure 33). The fledgling which left the island at 67 days flew out to sea after being thrown into the air. Had I not intervened, the bird probably would have remained longer at the nest. The nestling which fledged at 105 days had always been smaller than other nestlings of similar age, and its late fledging is probably due to slow growth resulting from underfeeding.



At about 75 days nestlings begin to exercise their wings. A week prior to fledging, nestlings become more restive and increase their radius of activity. At this time nestlings wander onto the beach for periods of a few hours. Nestlings move back to the nest site at night. From this time on, nestlings may become separated from their parents and starve. Shortly beyond this age (*i.e.*, at about 80 days), nestlings begin the characteristic weight loss just prior to fledging.

One nestling was seen exercising repeatedly in apparent preparation to leave the island. In the morning it moved to the beach, flapped its wings once without lifting off the ground. It repeated this process again about an hour later and then moved back into the scaevola. Twice during the afternoon this nestling moved back out onto the beach. On each occasion it attempted flight several times. On the last attempt it lifted all but its feet off the ground, then it moved back into the scaevola. Fledglings apparently continue this process until achieving flight. Once airborne, fledglings flew directly out over the reef and out to sea. Although unsteady at first, their flight rapidly became proficient. Once having flown, fledglings were not seen again on the island.

#### RENESTING

In 1964, 25 of 46 pairs, (54%) which suffered initial nesting failure nested again. In 1965, however, only 12 of 77 pairs (15.6%) which failed initially nested a second time. Renesting (or relaying) in Yellow-billed Tropicbirds on Ascension Island amounted to 10 to 12% of all layings (Stonehouse, 1962). Stonehouse thought this figure was held down by intense competition for nest sites. Relaying in Red-tailed Tropicbirds in 1964 on Kure, where competition for nest sites was insignificant, amounted to 28.7% of all layings. In 1965, however, relaying amounted to only 11.0% of all layings (Fleet, 1972). The study was ended on 15 August 1965, and it is possible that further relaying occurred after that time. Ashmole (1963) suggested that the extent to which lost eggs are replaced depends primarily on the length of the remaining season favorable for breeding. If the remaining season is sufficiently short, there is no advantage to laying a replacement egg since the chick will hatch too late to fledge. Hence, the decrease in relaying in 1965 may be due to the two month delay in the majority of first nestings of the breeding season.

In relaying, the replacement egg was laid between 21 and 80 days ( $\bar{x} = 41.9 \pm 4.14$  days) after loss of an egg and between 25 and 57 days ( $\bar{x} = 33.9 \pm 1.69$  days) after loss of a nestling. These means are significantly different ( $F_{\bar{c}} 16 \text{ df} \ \& \ 21 \text{ df} = 4.61; P < .005$ ). The cyclic nature of breeding (Figure 5) indicates that on Kure the season favorable to tropicbird breeding is restricted. Therefore, the later in the breeding season that a pair fails,

the less of that season remains for renesting attempts. On the average, loss of a nestling leaves less time for renesting than does loss of an egg. Presumably, pairs that cannot produce an egg within the remaining interval do not renest. The time restriction is less critical to pairs losing an egg, and these pairs can relay even if a longer time is required to produce an egg. In view of the continued energy expenditure from attendance periods and nestling feeding it seems unlikely that the difference in means between egg and nestling loss and relaying (*i.e.*,  $33.9 \pm 1.69$  vs.  $41.9 \pm 4.14$  days) is because birds that lost nestlings have more time to regain energy reserves for egg production.

## NESTING SUCCESS

### CAUSES OF NESTING FAILURE

A significantly higher percentage of eggs produced fledglings in 1964 (37.9%) than in 1965 (17.4%). The difference in nesting success between the 2 years resulted from differences in both the amount of renesting and the degree of renesting success in the two years. The details of nesting success and nesting failure have been treated in depth in a previous paper by Fleet (1972).

### NEST SITE ATTACHMENT

Locations of all nest sites within the study area were mapped in 1964 and 1965. These data make possible computation of mean distances between nest sites for 33 pairs renesting within the same season, 44 pairs remaining together for two breeding seasons, and 12 birds which remated.

Howell and Bartholomew (1969) pointed out that Red-tailed Tropicbirds and other previously studied ground-nesting sea birds show strong nest site attachment. Releasing parent birds equidistant from their egg (or nestling) they found that an empty nest scrape constitutes a stronger attraction for an adult bird than a displaced egg or nearby nestling. Analyses of my records of distances between nest sites of successive breeding attempts substantiates these findings.

The 22 birds that were unoccupied in 1964 and that nested in the area in 1965 tended to nest near the site where they visited in 1964. The 22 individuals were recorded on the study area 41 times in 1964 from 0 to 91.4 m ( $\bar{x} = 9.13 \pm 2.78$  m) from their 1965 nest sites. Of these 41 visits, 11 were to the same location as the 1965 nest site, 5 were within 1.5 m, and 25 were more than 1.5 m distant. In addition, 15 of 18 birds which nested in the area in 1964 but did not nest in 1965 were recorded on the study area 52 times in 1965 from 0 to 91.4 m ( $\bar{x} = 8.6 \pm 2.38$  m) from their 1964 nest sites. Of these 52 visits, 10 were to the same location as the 1964 nest site, 21 were within 1.5 m, and 21 were greater than 1.5 m distant.

Out of 33 tropicbird pairs that renested after failure of their initial attempt, 14 (42.4%) used the same site, 15 (45.5%) used a site within 1.5 m of their first site, and 4 (12.1%) used a site greater than 1.5 m distant. The greatest distance moved was 4.7 m; mean distance moved for these 33 pairs was  $0.7 \pm .18$  m.

Data on 1965 nest sites of pairs that maintained their pair bond of the previous season indicates that nest site attachment is eroded with time. In 44 such pairs, 11 (25%) nested on the same site as in the previous year, 22 (50%) used a site within 1.5 m, and 11 (25%) used a site more than 1.5 m distant. The two greatest distances moved were 39 and 16 m and the mean distance moved was  $2.3 \pm .89$  m. Excluding these two measurements, the next longest distance was 6 m, and the mean for 42 records is  $1.2 \pm .23$  m. Including or excluding these two longest movements, mean movement of nest site over two breeding seasons was greater than mean movement during renesting within the same season. Both mean movements over two breeding seasons were tested against the mean movement during renesting within the same season after all measurements were converted to natural logarithms to increase normality of distribution. Neither mean movement over two seasons was significantly different from mean movement during renesting ( $F \bar{c} 43$  df & 32 df = 1.64;  $.05 < P < .10$ ;  $F \bar{c} 41$  df & 32 df = 1.18;  $P < .10$ ).

In eight nestings in 1965 in which a bird had a different mate than in 1964, mean nest site distance from that of 1964 was  $3.7 \pm 1.74$  m. In four of these rematings, both birds had bred previously in the area with different mates. In these cases the site chosen was much closer to the old site of one member than to that of the other; averages are  $2.5 \pm .82$  m and  $37.7 \pm 14.02$  m. This indicates not a compromise between the pair on an intermediate nest site but rather a re-attachment to a new site by one bird of the pair. In the one pair in which sex of the individuals was known, the nest was nearest the former nest site of the male.

#### PAIR BOND MAINTENANCE

Of 145 individual tropicbirds from 76 pairs nesting in 1964, 40 (27.6%) did not nest or were not present in 1965; 105 (72.4%) nested in both years. Fifty-one of the 76 pairs (67.1%) that bred in 1964 returned intact in 1965, and 47 of these 51 pairs bred in 1965. Birds of the other 25 pairs either were not present on the study area, arrived without their mates, or remated. Table 4 summarizes pair bond maintenance and nesting effort. The pairs that are recorded as successful or unsuccessful in raising a nestling in 1964 in an unknown number of attempts (attempt unknown) probably made two nesting attempts in 1964. These nests were in an area that was added to

TABLE 4  
RELATIONSHIP OF PAIR BOND MAINTENANCE TO NESTING SUCCESS.

1965 Fate of Pairs Unsuccessful in Raising a Nestling in 1964	
Number pairs unsuccessful in raising a nestling in 1964	35
number of pairs maintained	17
number absent or re-mated	18
percent of pairs maintained	48.6%
number unsuccessful, one attempt only	20
number of pairs maintained	7
number absent or re-mated	13
percent of pairs maintained	35.0%
number unsuccessful, two attempts	8
number of pairs maintained	4
number absent or re-mated	4
percent of pairs maintained	50.0%
number unsuccessful, attempt unknown	7
number of pairs maintained	6
number absent or re-mated	1
percent of pairs maintained	85.7%
1965 Fate of Pairs Successful in Raising a Nestling in 1964	
Number pairs successful in raising a nestling in 1964	41
number of pairs maintained	34
number absent or re-mated	7
percent of pairs maintained	82.9%
number successful, first attempt	16
number of pairs maintained	11
number absent or re-mated	5
percent of pairs maintained	68.8%
number successful, second attempt	17
number of pairs maintained	16
number absent or re-mated	1
percent of pairs maintained	94.1%
number successful, attempt not known	8
number of pairs maintained	7
number absent or re-mated	1
percent of pairs maintained	87.5%

the study area in July 1964; however, the nests in that area, at that time, were probably second nestings.

Pair bond maintenance appears related to both nesting success and number of nesting attempts. Of 20 pairs unsuccessful in raising a nestling in one attempt in 1964, only seven (35%) maintained their pair bond in 1965. Of 8 pairs unsuccessful in two attempts, 4 (50%) maintained their pair bond. When these figures are combined with those for pairs unsuccessful in unknown attempts, the number of maintained pairs rises to 10 of 15 (66.7%). Of 16 pairs successful in raising a nestling on the first attempt, 11 (68.8%) maintained their pair bond. Of 17 pairs successful on the second attempt,

TABLE 5  
FATE OF PAIRS THAT NESTED IN 1964 THAT DID NOT REMAIN TOGETHER OR  
DID NOT NEST IN 1965

	Number	Percent
Pair not present	8	27.6
Only one bird present		
did not nest	8	27.6
re-mated	5	17.2
Pair present		
did not nest	4	13.8
re-mated	4	13.8
Total pairs	29	

16 (94.1%) maintained their pair bond. When these figures are combined with those for pairs successful in unknown attempts, the number of maintained pairs is 23 of 25 (92.0%). Thirty-four of 41 pairs (82.9%) successfully raising a nestling in 1964 remained paired in 1965. Of 35 pairs that were unsuccessful in raising a nestling in 1964, only 17 (48.6%) maintained their pair bond. This difference in pair bond maintenance is significant ( $\chi^2 = 10.10$ ;  $P < .005$ ). Also, in both successful and unsuccessful pairs, pair bond is maintained more often in pairs that nest twice in a single season. Pair bond was maintained in 18 of 36 pairs nesting once (50%) and 33 of 40 pairs nesting twice (82.5%), including those pairs probably nesting twice. Comparison of these percentages indicates that they are significantly different ( $\chi^2 = 9.07$ ;  $P < .005$ ).

Seven pairs that successfully raised nestlings in 1964 did not remain paired in 1965 (Table 4). Of six pairs that were followed closely in 1965, both adults were present in only one pair. Of 29 pairs that did not nest in 1965, one or both birds were absent from the island in 21 (72.4%) pairs. In the eight pairs in which both members were present, four remained the same and four pairs remated (Table 5). An unknown number of birds not found in 1965 may have died at sea; the remainder, including those present and mated but not nesting, were possibly energetically unable to nest.

Three of the four rematings occurred between breeding seasons. The single exception occurred in 1965 when a female bird remated after the loss of the egg.

#### SUCCESSIVE BREEDING CYCLES

The interval between successive cycles for pairs breeding in both years was measured from first egg in 1964 to first egg in 1965. Such information is available for 34 pairs that remained paired through both seasons and whose laying dates are known with certainty for both years (Figure 34). Mean

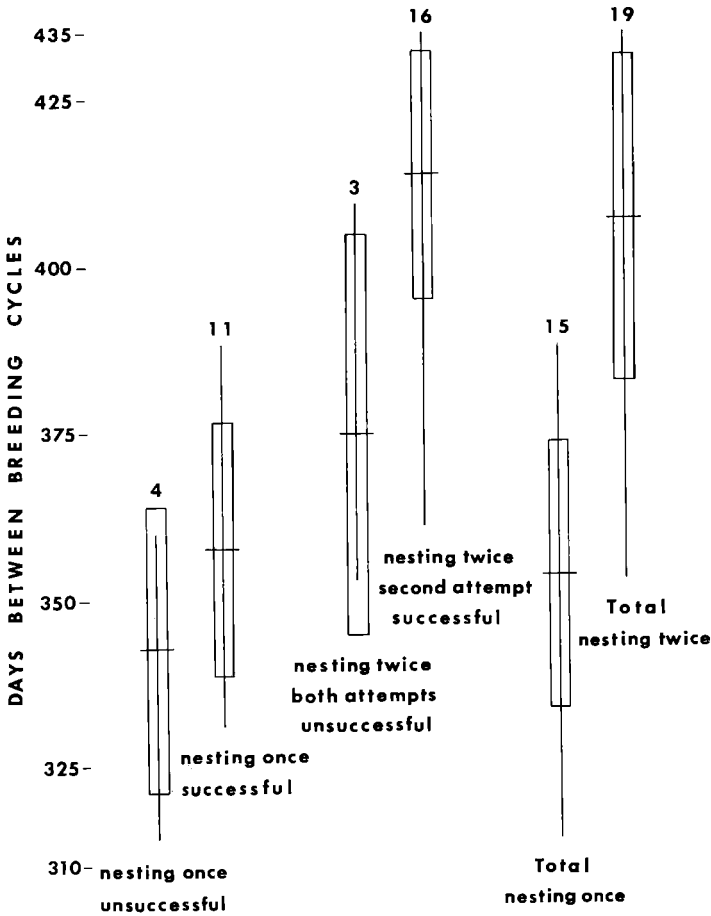


FIGURE 34. Days between successive cycles in pairs remaining together through two breeding seasons. Number of days was measured from first egg date in 1964 to first egg date in 1965. Vertical line indicates range, horizontal line the mean, and the rectangle equals one standard deviation on either side of the mean.

interval between cycles ranged from 343 days in pairs that nested once unsuccessfully to 414 days in pairs that nested twice successfully. Mean time between cycles in all pairs ( $383 \pm 5.99$  days) exceeded one year because unfavorable climatic conditions delayed the 1965 breeding season.

Number of days between cycles is least for pairs that nested once unsuccessfully and greatest in those pairs that nested twice successfully (*i.e.*, fledged a nestling) and the difference between these means is significant ( $t \bar{c} 18 \text{ df} = 6.21; P < .001$ ). Therefore number of days between cycles is directly proportional to energy and time spent by a pair in the breeding effort of the previous cycle.

Time between cycles for nine individual birds which selected new mates in 1965 ranged from 343 to 431 days with a mean of  $396 \pm 9.8$  days. This increased interval is probably due to the time required for formation of a new pair bond.

Further evidence of the energetic costs of the breeding season is seen in data on reneesting. Of the 19 pairs which had to reneest in 1964 and then lost their first egg or nestling in 1965, only 2 (10.5%) reneested. Of 17 pairs that did not reneest in 1964 and then lost their first egg in 1965, 3 (17.6%) reneested. Although these differences are not significant ( $\chi^2 = 0.38$ ), this information seems to indicate that although reneesting helps to maintain the pair bond, the energy requirements are such that pairs have difficulty sustaining this level of breeding activity in successive seasons.

### DISCUSSION

Even in relatively seasonless tropical areas, there are only a few seabird populations which lack seasonality in breeding. Wynne-Edwards (1962) considers that where definite breeding seasons exist, and it is difficult to detect any environmental change that would make one season more favorable for reproduction than another, the adaptive value of synchronization is probably almost entirely social and provides the means of controlling reproductive quotas and output. A much simpler explanation of maintenance of seasonality, and one that does not invoke group selection, is that seasonality of breeding in most populations is maintained by seasonal abundance of food around the breeding islands. Among tropicbirds *Phaethon aethereus* on Daphne (on the equator in the Galapagos Islands) (Snow, 1965) and *Phaethon aethereus* and *Phaethon lepturus* on Ascension Island (8° S latitude) (Stonehouse, 1962) exhibit breeding spread over the entire year. These authors believe obliteration of seasonal breeding in these populations is due to competition for nest sites. Lack of seasonality could hardly occur, however, unless the birds' response to the proximate factors regulating the annual cycle were weak and easily overridden by other pressures. In other words, there is little advantage in nesting at any particular time on these islands and birds with a strong ability to identify the proximate factors timing the season are not strongly selected for and seasonality is progressively eroded.

On Christmas Island (2° N latitude) seasonality of breeding is retained in the Red-tailed Tropicbird (Schreiber and Ashmole, 1970). Lack (1966) suggested that laying in single-brooded species tends to be timed so that young are raised when food is most plentiful. Ultimately the breeding season is adapted to ecological conditions (e.g., food supply) via natural selection. Operationally, this functions by gearing physiological responses of the birds' gonads to some predictable proximate signal.

Schreiber and Ashmole (1970) suggest that the seasonality in Red-tailed Tropicbirds on Christmas Island is caused ultimately by seasonal changes in availability of food, but climatic (and perhaps vegetational) changes at the breeding sites could be significant. It is probably not day length, however, that acts as a proximate timing factor on Christmas Island where day length varies little throughout the year.

Schreiber and Ashmole (1970) interpret Brown (1967) as saying that breeding seasons of many seabirds may be proximally controlled by day length. Proximate timing mechanisms causing sexual development before conditions become favorable are adaptive where optimum conditions for breeding are predictable in time and where temporal changes take place so rapidly that breeding activities must be started before the optimal time if the birds are to take full advantage of a favorable season that is short.

There is generally an enormous flush of marine organisms in spring (Ashmole, 1963). In temperate zones (such as Kure) the breeding season begins about early March. Even when climatic catastrophes occur (*e.g.*, 1965 on Kure), timing of the season is maintained. Lacking other data, one must assume that increasing day length is the proximate factor initiating breeding on Kure, and that seasonal (spring) abundance of marine food is the ultimate factor maintaining seasonality on Kure. Apparently selection maintains the beginning of the breeding season in the climatic "danger zone," because the advantages of being in phase with food abundance outweigh the risks.

Schreiber and Ashmole (1970) use the term "social attraction" (coined by Hailman, 1964) for the attraction which birds in breeding condition exhibit toward areas where birds are already on territory. The term "display interaction" (also coined by Hailman, 1964) refers to acceleration of reproductive cycles as a result of display by neighboring birds. Schreiber and Ashmole prefer to adopt "social stimulation" for the second phenomenon while retaining "social attraction" for the first. In some species, social stimulation may have originated out of selection favoring responsiveness to displays of the mate. Selection favoring social stimulation might also result from the advantages of breeding at precisely the time when environmental conditions are optimal.

On Christmas Island, colonies of *P. rubricauda* show a well-defined breeding season in spring and summer, but synchronization is more precise within than between the various colonies. These facts suggest social stimulation and social attraction within colonies; however, these effects are evidently secondary to the birds' response to seasonal changes in the environment (Schreiber and Ashmole, 1970).

Ashmole (1963) suggests two reasons why choosing a nest site within an existing colony might be selectively advantageous and so be established



as a characteristic of the species. First, he suggests, there may be advantages in breeding among other individuals of the species (*e.g.*, reduced predation in species which have a more or less communal defense against predators). Secondly, for young individuals choosing a place to breed for the first time, the best indication of a suitable location may be the presence of a colony. On Kure large areas of apparently suitable nesting habitat exist but are not used. Instead birds nest in a clumped distribution within areas of *scaevola*. There seems to be little advantage gained from nesting close together on Kure. The major predator, the Polynesian rat, was not deterred by concentrations of nesting tropicbirds. The rats preyed on eggs and nestlings even in the thickest concentrations of tropicbirds on the study area. I never saw the tropicbirds react to the presence of rats nearby and I never saw a dead rat in the area that could have been killed by tropicbirds. Additionally, these same nesting concentrations of tropicbirds occur on other islands where rats are not found. It is possible that there is an advantage from social attraction for young birds nesting for the first time but the greatest advantage, it seems to me, would come from social stimulation derived from the close proximity of other prebreeding birds. Any process such as this, which would speed the completion of breeding season preliminaries, thus leaving more of the optimum season for actual production of offspring, would be selected for.

I did not find differences in synchronization within or among the various clumps of breeding tropicbirds on Kure as did Schreiber and Ashmole. On Christmas Island, eggs were laid in a nine month period, whereas on Kure they were laid in a six month period only. The difference in synchronization between Christmas Island and Kure suggests that with the longer favorable season on Christmas Island due to its greater proximity to the equator there is less selective advantage to early breeding and synchronization.

On Kure displaying groups were composed of prebreeding birds and birds which had failed in a first nesting attempt; therefore a further function of the phenomena of social stimulation and social attraction can be postulated. Ashmole (1963) suggested that in species with long nest attendance periods, infrequent association of mates during incubation could cause difficulty in coordination of the sexual cycles or simply in mate location that would be necessary for relaying after initial failure. In 1964, 25 pairs of tropicbirds remained together and renested after initial nesting failure. Return by these birds to the aerial display portion of the breeding cycle provides, through social attraction, a "meeting place" for the pair, and social stimulation provides a mechanism for coordination of the pair's sexual cycles.

Howell and Bartholomew (1969) suggest that precise fixation on the nest site (ability of parent birds to recognize the nest site) is advantageous for continuity of the reproductive effort within a given season. Egg retrieval by tropicbirds, the sedentary nature of younger nestlings (Howell and Bartholomew, 1969), and starvation of wandering nestlings (Fleet, 1972) are indicative of strong site attachment. Strong nest site attachment in this species may be significant in another way. Selection of a nest site in the season prior to breeding probably facilitates the relocating of each other by birds of a pair and hastens the prebreeding activities thus insuring that maximum physiological and chronological potential for producing an offspring. I suggest that selection favors close linkage of breeding with proximal environmental cues, strong over-winter pair bond maintenance and nest site retention. All of these factors contribute to efficient use of the time and resources available for reproduction.

Maintenance of the pair bond apparently reduces prebreeding time on the island. For nine pairs consisting of newly mated birds, time from first recorded appearance on the study area until laying averaged  $53.0 \pm 8.16$  days (range 24 to 91 days). For 40 pairs that were also paired the previous year, this same time interval averaged  $44.8 \pm 2.57$  days (range 0 to 79 days). The difference between means is significant ( $F \bar{c} 8 \text{ df} \ \& \ 29 \text{ df} = 2.27; .01 < P < .05$ ).

Reproduction is energetically demanding for both parents. Evidence of this energy drain is given in Figure 22 where nest attendance periods of adult birds are seen to shorten as incubation progresses. Increased numbers of attendance periods per incubation in second nesting attempts reflect reduced ability of adult birds to incubate for long periods.

Ashmole (1963) says that Stonehouse's (1962) discovery that replacement eggs in *P. lepturus* are laid 23–30 days after loss suggests that egg production in tropical seabirds requires a considerable period of intensive feeding. Production of replacement eggs in Red-tailed Tropicbirds on Kure required 21 to 80 days ( $\bar{x} = 37.4 \pm 2.1$  days). This second egg of *P. rubricauda* is considerably larger than that of *P. lepturus*; hence more energy is involved in its production. Still, the Red-tailed Tropicbird replacement egg is significantly smaller than its first egg. The reduced volume of the replacement egg probably reflects either the increasingly limited time or resources available for egg production as the breeding season progresses.

Ashmole (1963) hypothesized that the extent to which lost eggs are replaced is related primarily to length of favorable season which remains, and that there is a minimum beyond which there is no advantage in laying a replacement egg, since the chick will not have time to fledge. He further suggested that one expects to find that eggs lost early in incubation are more often replaced than those lost later. Data on renesting by tropicbirds

on Kure substantiates Ashmole's suppositions. The percent of pairs which failed in each month and subsequently renested steadily decreases as the breeding season progresses. In April 1964, 8 of 11 pairs (72.7%) that failed in their first nesting subsequently renested; in May, 12 of 21 (57.1%) renested; in June, 5 of 10 (50%); and for July and August none of the four pairs which failed initially renested. The April ratio is significantly different from that of July and August ( $\chi^2 = 6.23$ ;  $.01 < P < .025$ ).

On Kure less time is required to renest after loss of a nestling than after loss of an egg. I interpret this difference to indicate that pairs losing an egg generally have less time invested in the breeding season than pairs that lose a nestling. Therefore, pairs that have lost eggs have more time remaining to relay. In those pairs that lose a nestling, only the pairs that are able to produce a second egg before the season favorable for breeding becomes too short, do so; the pairs unable to produce a second egg before this deadline do not make a second nesting attempt.

Less than 12 months is required for a successful breeding cycle plus molt in most species of seabirds (Schreiber and Ashmole, 1970). Time required for breeding and molt in Red-tailed Tropicbirds on Kure for those pairs nesting once per season is undoubtedly less than 12 months (Figure 34). The time between cycles for pairs nesting twice, especially those that were successful in raising a nestling, is on the average considerably longer than 12 months (significantly longer than those that nest once unsuccessfully). It seems apparent that the renesting effort strains the 12-month cycle. How fast a pair can recover energetically and how early it can be ready to breed in the next season depends on the amount of time and energy invested in the previous season. Under the conditions existing on Kure, renesting in every season causes birds to fall behind energetically. Although adaptation favors pairs which are most efficient in converting time and resources into viable offspring, limits apparently have been reached in the rates at which energy can be accumulated for breeding. In fact, it appears from the numbers of birds that did not nest in both years (1964, 1965) that the Red-tailed Tropicbird on Kure is not an annual breeder in the usual sense. Many birds are energetically unable to breed in successive seasons.

The factor which probably limits incubation period, fledging age, adult energy input, and the ultimate timing of the breeding season on Kure is availability of food. Ashmole (1963) suggested that sizes of populations of seabirds are controlled by competition for food around colonies during the breeding season. At this time the birds are restricted to a smaller proportion of the total feeding areas or spend much time flying to and from distant feeding areas. While breeding, parents must collect more food if they are to raise young and maintain themselves. The long nest attendance periods probably reflect this difficulty in obtaining sufficient food around

breeding islands and may represent an adaptation that allows the Red-tailed Tropicbird to exploit a greater radius of ocean in search of food during the breeding season.

Ashmole further suggests that if parent birds are only able to collect food slowly, there will be selection (as suggested by Lack, 1948) for physiological characteristics which allow a slow rate of growth and intermittent periods of starvation in order to spread the load of food collection over a longer period. Long periods of incubation and fledging are linked to the uncertainty of food procurement. Pre-hatching and post-hatching development are so closely linked physiologically that it probably would be difficult for selection to change the rate of one without affecting the other (Ashmole, 1963). As mentioned previously, expected incubation period based on egg volume (Worth, 1940) is 27.4 days and far short of the observed mean of 43.8 days. Stonehouse (1962) also found longer incubation periods than expected in the Yellow-billed Tropicbird on Ascension Island.

In species whose food availability is limited or erratic, selection will favor nestlings which have a long post-hatching development period, and can withstand long periods without food and still be capable of assimilating large quantities of food when it is available. The wide range of fledging ages demonstrated by Red-tailed Tropicbirds on Kure (Figure 33) probably reflects different rates of feeding by adults. Limited data (Table 3) indicate that developing nestlings sometimes go unfed for several days at a time. The quantities of food which I hand fed to captive nestlings (up to 311 g at one feeding) greatly exceeded the amounts actually fed to developing nestlings by parent birds (Table 3). This indicates an ability in nestlings to assimilate large quantities of food when it is available.

The most convincing data indicating that food limits nestling growth is the early age of nestlings at which the mean amount of food provided by parents stabilizes. Table 3 indicates that for a wide range of nestling ages (from 23 to 76 days old) and sizes, average food intake remains around 50 g per feeding. This suggests that parent birds are working near the limits of their food collecting capacity. Therefore, selection seems to have favored adaptations in the breeding cycle which increase the amount of favorable breeding time available for feeding the nestling.

#### SUMMARY

The breeding cycle of the Red-tailed Tropicbird (*Phaethon rubricauda*) on Green Island, Kure Atoll, Hawaiian Islands, was studied during 1964 and 1965. Study methods included direct observation of marked nests and of leg-banded and paint-marked birds.

The annual breeding season begins in late February with population build-up and prebreeding aerial display which functions in pair bond for-

mation and synchronization of individual breeding cycles. Pairs nested from 0 to 91 days after first being recorded on the island. Males play the major role in nest site selection and nest construction. Clutch size is one. The egg is incubated by both parents alternately with attendance periods of 4 to 16 days. Due to decreasing energy reserves, adult attendance periods become progressively shorter as incubation progresses. Hatching occurs after 42 to 46 days (mode = 44 days). The nestling is brooded for about one week. After about three weeks, adults come to the nest only to feed the nestling. Nestlings are fed primarily on flying fish (family Exocoetidae) and squid (order Teuthoidea). They complete their growth and leave the island between 67 and 105 days ( $\bar{x} = 84.2 \pm .76$  days) after hatching. Feeding experiments showed that nestlings can assimilate larger quantities of food than are provided by adults. These data suggest that availability of food may determine age at fledging. In cases where failure of initial nesting occurred early in the breeding season, some pairs renested. In cases of renesting, replacement eggs were laid 21 to 80 days after the loss of an egg or nestling. Eggs of renestings were significantly smaller in volume (averaging 4.79% less) than eggs of first nestings. Renesting was carried out by 54.3% of pairs that failed in 1964 and by 15.6% in 1965. Total nesting success was significantly higher in 1964 (37.9%) than in 1965 (17.4%).

Pairs of tropicbirds maintain a strong nest site attachment and tend to renest (and nest in subsequent seasons) at or near the site used previously, especially when pairs remain together. Pair bonds are maintained almost twice as often when a nestling is raised as when the pair is unsuccessful. Also, in both successful and unsuccessful pairs, pair bonds are maintained most often in pairs which nest twice in a single season.

Number of days between successive annual breeding cycles is least for pairs that nested once unsuccessfully and greatest for pairs that nested twice and successfully fledged a nestling. Although renesting helps to maintain the pair bond and adds significantly to total nesting success of the Kure tropicbird population, energy requirements are such that pairs rarely are able to renest in successive seasons.

On Kure day length is probably the proximate factor initiating breeding, and seasonal (spring) abundance of marine food is thought to be the ultimate factor that maintains reproductive seasonality. Apparently selection maintains the beginning of the breeding season in the climatic "danger zone" because reproductive advantages of being in phase with food outweigh the risks. Early breeding has the additional advantage of providing for a longer season favorable to renesting after initial failure.

Prebreeding aerial display improves continuity of reproductive effort within a season. This behavior pattern, along with pair bond maintenance, improves efficiency of time use within the breeding season.

## LITERATURE CITED

- ASHMOLE, N. P. 1963. Regulation of numbers of tropical oceanic birds. *Ibis*, 103b: 458-473.
- BAILEY, A. M. 1956. Birds of Midway and Laysan Islands. Denver Mus. Pictorial, No. 12: 130 pp.
- BENT, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U. S. Natl. Mus. Bull. 121: 190-193.
- BETTS, F. N. 1940. The birds of the Seychelles, II. The Sea-birds. *Ibis*, 14: 489-504.
- BROWN, R. G. B. 1967. Courtship behavior in the Lesser Black-backed Gull, *Larus fuscus*. *Behavior*, 29: 122-153.
- BRYAN, E. H., JR. 1942. American Polynesia and the Hawaiian Chain. Tongg Publ. Co. Honolulu, Hawaii. 253 pp.
- BRYAN, E. H., JR. 1954. The Hawaiian Chain. Bishop Mus. Press IV. Honolulu, Hawaii. 71 pp.
- CLANCEY, P. A. 1955. An occurrence of the Red-tailed Tropic Bird in Natal. *Ostrich*, 26: 38-39.
- CLAPP, R. B. AND P. W. WOODWARD. 1968. New records of birds from the Hawaiian Leeward Islands. *Proc. U. S. Natl. Mus.*, Vol. 124: 39 pp.
- CLAY, H. F. 1961. Narrative report of botanical field work on Kure Island, 3 October 1959 to 9 October 1959. *Atoll Res. Bull.*, 78: 1-6.
- COURTENAY-LATIMER, M. 1955. Red-tailed Tropical Bird in the Eastern Cape and the Orange Free State. *Ostrich*, 26: 38.
- CROWFOOT, W. M. 1885. Notes on the breeding-habits of certain sea-birds frequenting Norfolk Island and the adjoining islets. *Ibis*, 5: 263-270.
- FLEET, R. R. 1972. Nesting success of the Red-tailed Tropicbird (*Phaethon rubricauda*), on Kure Atoll, Hawaiian Islands. *Auk*, 89: 651-659.
- GIBSON-HILL, C. A. 1947. The normal food of tropic-birds (*Phaethon* spp.). *Ibis*, 89: 658-661.
- GIBSON, J. D. AND A. R. SEFTON. 1956. Red-tailed Tropicbird at Port Kembla N. S. W. *Emu*, 56: 198.
- GROSS, A. O. 1912. Observations on the Yellow-billed Tropic-bird (*Phaethon americanus* Grant) at the Bermuda Islands. *Auk*, 29: 49-71.
- HAILMAN, J. P. 1964. Breeding synchrony in the equatorial Swallow-tailed Gull. *Am. Nat.*, 98: 79-83.
- HAYNE, D. W. 1949. Two methods for estimating populations from trapping records. *J. Mammalogy*, 30: 399-411.
- HINDWOOD, K. A. 1947. Occurrence of Red-tailed Tropic-bird in southeastern Australia and Tasmania. *Emu*, 47: 57-58.
- HINDWOOD, K. A. 1955. Red-tailed Tropic-bird in southeastern Australia. *Emu*, 55: 160-161.
- HINDWOOD, K. A., K. KEITH AND D. L. SERVENTY. 1963. Birds of the south-west Coral Sea. Aust. Div. of Wildlife Research, Tech. Paper No. 3: 44 pp.
- HOLT, J. G. V. 1958. The birds of Christmas Island. *The Sea Swallow*, 11: 26-28.
- HOWELL, T. R. AND G. A. BARTHOLOMEW. 1962. Temperature regulation in the Red-tailed Tropicbird and the Red-footed Booby. *Condor*, 64: 6-12.
- HOWELL, T. R. AND G. A. BARTHOLOMEW. 1969. Experiments on nesting behavior of the Red-tailed Tropicbird (*Phaethon rubricauda*). *Condor*, 71: 113-119.
- KEPLER, C. B. 1967. Polynesian rat predation on nesting Laysan Albatrosses and other Pacific seabirds. *Auk*, 84: 426-430.

- LACK, D. 1948. The significance of clutch size. *Ibis*, 90: 25-45.
- LACK, D. 1966. Population studies of birds. Oxford University Press, London.
- LAMOUREUX, C. H. 1961. Botanical observations on Leeward Hawaiian Atolls. *Atoll Res. Bull.*, 79: 1-10.
- LOCKE, L. N., W. O. WIRTZ, JR. AND E. E. BROWN. 1965. Pox infection and a secondary cutaneous mycosis in a Red-tailed Tropicbird (*Phaethon rubricauda*). *Bull. Wildl. Disease Assoc.*, 1: 60-61.
- MATHEWS, G. M. 1915. Birds of Australia, 4: 81-394. Witherby Co., London.
- MAYR, E. 1945. Birds of the Southwest Pacific. Macmillian Co., N. Y.
- McKEAN, J. L. AND K. A. HINDWOOD. 1965. Additional notes on the birds of Lord Howe Island. *Emu*, 64: 79-97.
- MUNRO, G. C. 1944. The birds of Hawaii. Tongg Publ. Co., Honolulu, Hawaii.
- MUNTER, W. H. 1915. Report of destruction of bird life on Laysan Island, Pacific Ocean, pp. 130-140. *In*: Annual report of the Coast Guard for 1915. U. S. Treasury Dept., Wash., D.C.
- MURPHY, R. C., A. M. BAILEY AND R. J. NIEDRACH. 1954. Birds of Canton Island. *Denver Mus. Pictorial*, No. 10: 78 pp.
- OBERHOLSER, H. D. 1919. Notes on North American birds. *Auk*, 36: 556-559.
- OLIVER, W. R. B. 1955. New Zealand birds. (2nd ed.). A. H. and A. W. Reed. Wellington, N. Z.
- PETERS, J. L. 1931. Checklist of birds of the world. Vol. 1. Harvard Univ. Press. Cambridge, Mass.
- READ, G. H. 1912. The last cruise of the *Saginaw*. Houghton Mifflin Co., N. Y.
- ROTHSCHILD, W. 1900. The avifauna of Laysan and the neighboring islands; with a complete history to date of the birds of the Hawaiian possessions, part III. R. H. Porter, London.
- SCHREIBER, R. W. AND N. P. ASHMOLE. 1970. Sea-bird breeding seasons on Christmas Island, Pacific Ocean. *Ibis*, 112: 363-394.
- SCHLATER, W. L. 1927. The Tropic-Bird in South African waters. *Ibis*, 12: 565.
- SIMPSON, G. G., A. ROE AND R. C. LEWONTIN. 1960. Quantitative zoology. Harcourt, Brace and Co., N. Y.
- SNOW, D. W. 1965. The breeding of the Red-billed Tropicbird in the Galapagos Islands. *Condor*, 67: 210-214.
- STONEHOUSE, B. 1962. Tropic birds (genus *Phaethon*) of Ascension Island. *Ibis*, 103b: 124-259.
- STORR, B. M. 1964. The avifauna of Rottnest Island, Western Australia, I. Marine Birds. *Emu*, 62: 53-54.
- THOMSON, A. L. (ed.). 1964. A new dictionary of birds. McGraw-Hill, N. Y.
- WHITTTELL, H. M. AND S. R. WHITE. 1940. The Red-tailed Tropicbird in Western Australia. *Emu*, 40: 95-96.
- WILLIAMS, G. R. 1960. The birds of the Pitcairn Islands. *Ibis*, 102: 65.
- WIRTZ, W. O. 1965. Biological survey of Kure Atoll. (In manuscript.)
- WIRTZ, W. O. 1972. Population ecology of the Polynesian rat, *Rattus exulans*, on Kure Atoll, Hawaii. *Pacific Science*, 26: 433-464.
- WORTH, C. B. 1940. Egg volumes and incubation periods. *Auk*, 57: 44-60.
- WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Hafner Publ. Co., N. Y.

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