NESTING SUCCESS OF THE RED-TAILED TROPICBIRD ON KURE ATOLL

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I studied the breeding cycle of the Red-tailed Tropicbird (*Phaethon rubricauda*) on Kure Atoll, Hawaii, between March 1964 and August 1965. Kure is a low, volcanic-coral atoll at the northwestern end of the Hawaiian Island chain, approximately 1,890 km northwest of Honolulu, at coordinates $28^{\circ} 25'$ N and $178^{\circ} 10'$ W. Green Island, the only stable land mass within the atoll, is situated in the southeastern quadrant of the lagoon, about 400 m inside the reef. The island is crescent-shaped, with the axis of the crescent curving from north to southwest. It is 2.29 km in length along this axis, 0.60 km wide at its widest point, and about 86.67 ha in area. The sand dunes of the western (lagoon) beach have the highest elevation on the island, reaching 7.5 m above sea level.

My study area (approximately 0.58 ha) was the southwesternmost sand dune on Green Island. In this dune, sand has accumulated to a maximum depth of 1 m above the surrounding areas and is capped with *Scaevola taccadae* thickets that sometimes reach 2 m in height.

Methods

All adult Red-tailed Tropicbirds found were banded on the right leg with U. S. Fish and Wildlife Service aluminum leg bands, size 5. Upon egg deposition, each nest site was marked with a yellow, 15-cm garden marker bearing the nest number.

Birds were captured by hand within the dense scaevola thickets that serve as nest sites. As Red-tailed Tropicbirds are sexually isomorphic, to facilitate recognition and to reduce necessity for handling, adult birds of each pair were marked by spraypainting a 5-cm diameter spot in different colors on each bird's head.

The study area was checked daily through two breeding seasons (March 1964 to mid-August 1965). From a fixed beach path I could see far into the tangle of scaevola stems by separating the leafy canopy every few feet. The white plumage of the tropicbirds was conspicuous against the dark leaf litter. This beach path was effective because adult birds need an open space for vertical takeoff, and about 90 percent of the nests were within 2.5 m of the scaevola border.

Results

Breeding cycle of the Red-tailed Tropicbird.—Among the Leeward Hawaiian Islands, Kure Atoll is second only to Midway Atoll in numbers of Red-tailed Tropicbirds. Numbers of the birds using Kure were determined by locating and counting nesting pairs on the island. I then discovered, by paint-marking of nesting pairs within my study area, that these birds never made the aerial displays characteristic of prenesting birds. The sum of nesting birds and birds in aerial display

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was used as a population estimate. The maximum population, estimated throughout two breeding seasons, was 2,500.

On Kure the annual breeding season begins in late February by a population increase and prebreeding aerial displays. Nests are placed under protective vegetation, most commonly scaevola. A shallow nest scrape is prepared and one or both birds frequent the site for several days prior to laying the single egg. Egg-laying begins in early March and continues into August, including the laying of replacement clutches. The egg is incubated by both parents and hatches, based on 45 records, in 42 to 46 days. The nestling is brooded for about 1 week, then the adults sit beside the nestling with decreasing regularity. After about 3 weeks the adults come to the nest site only to feed the nestling. The nestling completes its growth and leaves the island 67 to 105 days after hatching. Based on 37 records, the mean fledging period is 88.7 days. The breeding season ends in late November or early December when virtually all immature birds have left the island, though at least one nest with an egg or nestling was found in every month.

Severe storms in December 1964 and high winds with heavy rains in March 1965 presumably caused a delay in the 1965 tropicbird breeding season. The earliest clutches were deposited the first week of March in 1964 and 1965, but 70.5 percent of the first clutches in 1964 were laid in March and April, while 74.2 percent of the first clutches in 1965 were laid in May and June (Figure 1).

Predation by Polynesian rats.—The breeding cycle of the tropicbird on Kure is profoundly influenced by the Polynesian rat (*Rattus exulans*). The earliest record of *R. exulans* on Kure is in accounts by men from the ship 'Saginaw,' which was wrecked there 29 October 1870 (Read, 1912). On Kure *R. exulans* breeds from March through September and attains a high fall population density. In 1964 the island's rat population increased from an estimated 3,000 individuals in April to an estimated 11,000 individuals in September, according to projections of live-trapping on a 2.81 ha study plot.

The major plant food of these rats was berries of Scaevola taccadae, supplemented to a lesser extent with seeds of Boerhavia diffusa and Eragrostis variabilis. When the rat population reaches an annual maximum, the amount of plant food has decreased and consequently the rats turn to bird prey secondarily. Kepler (1967) documents rat predation on Kure on Laysan Albatrosses (Diomedea immutabilis), Sooty Terns (Sterna fuscata), Noddy Terns (Anous stolidus), and Bonin Petrels (Pterodroma hypoleuca).

Predation on tropicbirds begins with the inception of the birds' breeding season in March and continues until plant food is again plentiful



Figure 1. Percent of total initial clutches laid each month during the breeding seasons of 1964 and 1965. Replacement clutches are not included.

enough to support the rat population. In early May 1964 rats were killing most tropicbird nestlings in the study area, and to obtain a sufficient sample of nestlings for growth studies, I had to trap the rats. Between 6 May and 26 June I trapped and removed 199 rats from the area. In early June I noted that flying fish and squid regurgitated by the Blue-faced Boobies (*Sula dactylatra*) were no longer being taken by rats, and they eventually decomposed along with an occasional dead bird. By this time the rats were feeding on the new crop of seeds and berries and they preyed on the birds only infrequently.

Predation on tropicbirds continued throughout the summer of 1965, probably because severe December storms caused widespread destruction, with slow recovery, of the plants the rats prefer.

Nesting success.—Predation by Rattus exulans accounted for 53.6 percent of total egg loss in 1964 and 64.9 percent of egg loss in 1965 (Table 1). I never saw a rat break a tropicbird egg, although I noted rats running from the vicinity of broken eggs, and once I saw a rat run from beneath an incubating bird. Most commonly eggs found

CAUSES OF EGG AND	NESTLING I	20SS		
	1964		1965	
Total nesting failures	55		83	
Egg loss, all causes (percent of total failures) Number of eggs lost, predation Number of eggs lost, not incubated Number of eggs lost, other causes	15 11 2	(50.9%) (53.6%) (39.3%) (7.1%)	24 8 5	(43.5%) (64.9%) (21.6%) (13.5%)
Nestling loss, all causes (percent of total failures) Number of nestlings lost, predation Number of nestlings lost, other causes	24	(49.1%) (88.9%) (11.1%)	48	(56.5%) (100.0%)

TABLE 1							
USES	OF	EGG	AND	NESTLING	L		

broken were being incubated when previously checked. Occasionally birds were observed near broken eggs. Possibly the incubating adults broke some eggs as they pecked at intruding rats. While the amount of egg breakage by direct rat action is uncertain, most breakage probably resulted from rat activity.

Abandonment of eggs by adults during incubation accounted for 39.3 percent of total egg loss in 1964 and 21.6 percent of egg loss in 1965. Disturbances of adult birds by rats or by my handling probably caused abandonment in most cases. The remaining eggs (7 eggs during 2 years of study) were lost for a variety of reasons. *Rattus exulans* predation was the major cause of nestling loss; it accounted for 88.9 percent of the nestling loss in 1964 and all of it in 1965.

Rats typically attacked a nestling tropicbird from behind, bit through the vertebra and spinal cord, and gnawed, broke, or tore the wings and legs from the body. Rats ate most of the carcass. Remains of some attacked nestlings consisted of no more than feathers, skin, and long bone ends. Nestling remains were found as far as 3 m from their nests.

Predation on young nestlings was heavy (Figure 2). Nestlings become noticeably aware of their surroundings between 5 and 9 days of age. They then become progressively more active and aggressive and will strike and hold any moving object within range. Of nestlings killed by rats, 85 percent were no more than 8 days old, suggesting that rat predation becomes increasingly more difficult as nestlings begin reacting to their environment. The oldest nestling killed by rats was 17 days old; as it was approximately half the average weight for 17-day-old nestlings, its starved condition probably facilitated the successful attack.

In 1964 three nestlings died from causes other than predation by rats. Two of the birds died at ages of 1 day and 6 days, with no



NESTLING AGE, IN DAYS, AT DEATH

Figure 2. Age of nestling Red-tailed Tropicbirds when killed by *Rattus exulans*. Rats killed no nestlings older than 17 days. Deaths of known-age nestlings killed outside the study area are included.

external injuries apparent. The third nestling, which was unattended by an adult from its 3rd day, died at 9 days.

In December 1964 four starving fledglings were found on the beach unable to fly. Ashmole (1963) suggested that food competition among adults in waters around breeding colonies of tropical oceanic birds resulted in mass starvation of nestlings or underweight fledglings. He also noted that food competition might serve, therefore, as a density-dependent control on population size. On Kure no mass starvation occurred, and the small number of losses by starvation may be attributable to the nestlings tendency to wander. If nestlings lose contact with the parent birds before they can fly, they must starve. Nestlings in advanced stages of development (70 days and older) wandered as far as 8 m from their nest sites.

Total nesting success was significantly higher in 1964 than in 1965 (Table 2). Total success in 1964 (37.9 percent) falls within the range of nesting success of *P. lepturus* (30.3 percent) and *P. aethereus* (51.5 percent) on Ascension Island (Stonehouse, 1962). Although removal of many rats from my study area in 1964 may have decreased the per-

	1964		1965		t-test ¹
First nesting:					
Number of pairs	62		97		
Number of eggs lost	21	(33.9%)	34	(35.1%)	P = 0.88
Number of young lost	25	(61.0%)	43	(69.4%)	P = 0.36
Number of young fledged	16		19		
Number of nest results unknown	_		1	(1.0%)	No test
Percent of survival		(25.8%)		(19.6%)	P = 0.36
Renesting:					
Number of pairs renesting	25	(54.3%)	12	(15.6%)	P < 0.02
Number of eggs lost	6	(24.0%)	3	(25.0%)	No test
Number of young lost	2	(10.5%)	5	(100.0%)	No test
Number of young fledged	17		0		
Number of nest results unknown			4	(33.3%)	No test
Percent of survival		(68.0%)		(0.0%)	No test
Totals					
Young fledged	33		19		
Total success (percent of total					
pairs)		(53.2%)		(19.6%)	P < 0.001
Total success (percent of total		(0012/0)		(/+/	• • • • • •
nestings)		(37.9%)		(17.4%)	P < 0.01

TABLE 2 Results of Red-tailed Tropicbird Nesting

 $^{1}P < 0.05$ considered to be significant.

centage of young lost in the first nesting, the 8.4 percent difference in young lost between 1964 and 1965 was not significant (P = 0.36).

Differences in nesting success between seasons were subjected to the Arcsin percentage transformation (Sokal and Rohlf, 1969). Major differences in nesting success between the 2 years result from amount and degree of renesting success. In 1964, 25 pairs (54.3 percent) renested, after having failed in their first nesting attempt. The late start in breeding in 1965 presumably accounted for the reduced number of pairs (12, or 15.6 percent) renesting after initial failure. Replacement clutches in 1964 amounted to 28.7 percent and in 1965 to 11.0 percent of all layings. Ashmole (1963) suggested that extent of replacement of lost eggs is related primarily to length of favorable breeding season. A short season offers no advantage to egg replacement, because chicks probably hatch too late for successful fledging. If this is true, the drastic decrease in replacement clutches by Red-tailed Tropicbirds between 1964 and 1965 might have been due to delayed inception of the breeding season and reduced breeding season length in 1965.

The high degree of renesting success (68.0 percent) in 1964 probably occurred because rat predation essentially stopped in June and thus reduced predation pressure on renesting attempts. In 1965 predation by rats continued throughout the summer and probably no renesting attempts were successful. Results of four renesting attempts and one first nesting in 1965 are unknown. If these attempts succeeded, nestlings would have fledged by late November. Their success and the success of any further nesting attempts in 1965 seems highly unlikely, because the decrease in available plant food for rats occurred by mid-August and probably forced the rats to prey on birds. Even if nestlings fledged successfully from the four nests, the percent success of renesting in 1965 (33.3 percent) would still have been significantly different (P = 0.05) from 1964.

CONCLUSIONS

On Kure Atoll reproductive success of Red-tailed Tropicbirds is intimately connected with the population cycles of R. exulans. In years without the destructive storms of late winter and spring, island vegetation produces adequate food for the rat population by early summer. Hence rat predation on tropicbird eggs and nestlings drops to near zero. Most of the tropicbird initial nesting attempts fail because of predation, but the renesting potential expresses itself during time of minimal predation and results in increased survival of young. This difference is dramatically demonstrated by comparing the percent survival from initial nesting in 1965 to percent survival of renesting attempts in 1964 (Table 2).

In years of destructive storms of late winter and spring, island vegetation produces less food for rats, and rat predation on tropicbirds continues throughout the breeding season. Under such weather conditions the tropicbird breeding season may begin later and thus reduce the number of renesting pairs. This combination of factors causes a substantial reduction in the nesting success for the season.

Stonehouse (1962) reports nest site competition with maximum population densities as the main cause of nest failure in the two tropicbird species nesting on Ascension, and Snow (1965) reports the same for P. *aethereus* on Daphne Island in the Galapagos. On Kure I saw only a single case of nest site competition and, as large tracts of presumably suitable nesting habitat are unused, the island could probably support a larger population of Red-tailed Tropicbirds. I have no evidence of mass starvation of nestlings (cf. Ashmole, 1963) from insufficient food available.

Although Polynesian rats have occurred on Kure for at least 100 years, estimates of tropicbird numbers during this period indicate a gradual population increase, possibly from a low around the turn of the century caused by plume hunters (Table 3). That tropicbird populations on Kure may be maintained by a high colonization rate from nearby islands is unlikely. From the 7,445 Red-tailed Tropicbirds banded in the Lee-

800

400

200

900

1,000

COMPARISONS OF POPU	LATION ESTIMATES	OF RED-TAILED	TROPICBIRDS	ON GREEN	ISLAND
				March	April
Munter (1915)			1915	100	_

1923

1964

1965

TABLE 3

ward Hawaiian Islands since 1963, only two interisland recoveries have been recorded.

Although rat predation is a persistent cause of nesting failure, it varies according to climatic conditions. Population decrease from nesting failure would require at least several years of detrimental climatic factors in addition to rat predation. Apparently variable climatic conditions coupled with the breeding potential of Red-tailed Tropicbirds are steadily increasing the tropicbird population.

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Summary

Nesting success of the Red-tailed Tropicbird on Green Island, Kure Atoll, was studied during the breeding seasons of 1964 and 1965. Total nesting success (percent of total nestings) was 37.9 percent in 1964 and 17.4 percent in 1965.

Predation by the Polynesian rat (*Rattus exulans*) on eggs and nestlings was the main cause of nesting failure. *R. exulans* normally feeds on vegetation and turns to predation on birds only during the shortage of plant food from September through May. Rats did not kill nestlings older than 17 days.

During years without severe spring storms, the Red-tailed Tropicbird's breeding season begins on schedule and renesting occurs during minimal rat predation. In years of destructive late winter and spring storms, island vegetation produces less food for the rat population, predation

Wetmore (MS)

Present study

Present study

on tropicbirds continues throughout the breeding season, the tropicbirds start nesting later, and fewer pairs renest.

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