

THE BREEDING OF THE RED-BILLED TROPIC BIRD IN THE GALAPAGOS ISLANDS

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In the course of field work in the Galápagos Islands from February, 1963, to April, 1964, a limited study was made of the breeding of the Red-billed Tropic Bird (*Phaethon aethereus*). Because visits to the breeding colonies could be made only at fortnightly or monthly intervals, there were many points on which accurate information could not be obtained; but since the visits were at least regular, it was possible to determine the pattern of breeding activity throughout the year.

Two colonies were compared: that of Daphne Island, off the north coast of Santa Cruz Island, which was visited monthly, and the colony on South Plaza Island, an islet off the east coast of Santa Cruz, which being nearer to the Charles Darwin Research Station on the south coast of the same island could be visited every two weeks.

Beebe (1924) has vividly described Daphne Island, a well-known sea-bird breeding station, which members of most of the expeditions to the Galapagos Islands have visited. The island is a crater of pelagonite (tufa) some 500 feet high and about 400 yards in diameter, sparsely vegetated on the outer slopes, where most of the tropic birds nest. Like most such pelagonite cones in the Galapagos Islands, it is stratified like a dome-shaped cake which has been covered with successive layers of thin icing, and subsequent weathering of the steep sides has produced numerous small caves and recesses under the down-sloping strata. The tropic birds nest in these recesses, many of which are quite shallow although a few are so deep that it is difficult or impossible to extract the nesting birds.

South Plaza Island is quite different. It is a low-lying islet of basaltic lava, 700 yards long and about 100 yards wide. On one side, a broken cliff up to 60 feet high runs along most of the length of the island, whereas at the other side the land slopes gently down to the sea. The tropic birds nest in cracks, niches, and shallow recesses in the cliff, a certain number of the nest sites being inaccessible without a rope.

Daphne Island is so large that it was not possible to check the whole island in the few hours available at each visit. Instead, we worked the lower part of the southern slopes systematically, attempting to find all the nests in this limited area. On South Plaza Island we covered the whole length of the cliffs at each visit, but some parts of it were inaccessible. On both islands we made a point of checking all the known sites at each visit.

COMPARISON OF THE TWO COLONIES

Murphy (1936) and Lack (1950) both concluded that in the Galapagos Islands the Red-billed Tropic Bird must nest continuously, as eggs and young had been found in many months of the year. On Daphne Island, whence much of their information was derived, this is certainly so. Table 1 shows the months of laying of 148 eggs in the 116 nest sites that were found. No pattern is apparent, the generally higher numbers in the later months being simply due to the fact that we kept on finding additional nest sites in the course of the year. As we checked all the known sites at each visit, and as old sites are regularly reused, the potential number in use increased slightly month by month.

On South Plaza Island the pattern was entirely different. When we started, in February, 1963, the breeding season was evidently nearly over. We found four nests, all with young which fledged in March and April. There was then no more nesting for several months, and then there was another well-defined breeding period with its peak in October and November, apparently at the same time as in the previous year (table 1). All four of the nest sites found the season before were reused, three in October and one in November—almost exactly the same months as the year before.

TABLE 1
THE BREEDING SEASONS OF RED-BILLED TROPIC
BIRDS AT DAPHNE AND SOUTH PLAZA ISLANDS,
GALÁPAGOS ISLANDS

	Number of nests started in each month ¹	
	Daphne	South Plaza
1962 October	—	2
November	—	1
December	—	1
1963 January	—	0
February	10	0
March	5	0
April	12	0
May	7	0
June	15	0
July	18	0
August	13	1
September	10	2
October	18	9
November	18	8
December	14	4
1964 January	8	1
February	—	0
March	—	0
April	—	0

¹ Nests are dated by the month in which the egg was laid. Visits to Daphne covered only the year from February, 1963, to January, 1964.

Apart from the obvious structural differences between the two islands and the type of nest hole available, there are other striking differences between these two breeding populations. The South Plaza breeding population is small, probably less than 50 pairs (in the second breeding season we probably found well over half of the nests). The nest sites were well separated and we saw no evidence of a shortage of sites. Nesting success was fairly high: in the second breeding season, 55 per cent of the nests found at an early stage were successful (including three of the four nests used successfully the year before).

The breeding population of Daphne Island, on the other hand, must number many hundreds of birds and many of the nests are close together. There are more pairs of birds than there are nest sites, and intense competition for the nest holes

appears to be the rule. Nesting success in consequence is low. It is apparently also as a consequence of overcrowding that breeding activity is continuous throughout the year. The data on which these conclusions are based are set out in the following section.

BREEDING POPULATION OF DAPHNE ISLAND

At each visit to Daphne Island, every adult tropic bird that could be reached, in the holes that were being checked, was taken out and banded, or if it was already banded its number was noted, and it was then replaced in its hole. This procedure does not deter the bird from settling back on its egg again immediately. After several visits it became obvious that competition for nest holes was intense, changes of occupancy between successive layings in the same hole being the rule rather than the exception. One might, for example, find an adult on an egg or young bird, then a month or two later a different adult would be found in the hole, the egg or nestling having meanwhile disappeared. The next month another adult would be in the hole; and a month or two later yet another adult on a new egg would be found in the same hole.

An analysis of the records of banded adults gives a more precise idea of the situation. First, a rough calculation may be made of the number of different adults using the 116 nest holes that were found. By December, 1963, 165 adults had been banded in the holes. On subsequent visits 52 adults were found in them, of which 19 were unbanded and 33 banded. This suggests that about 37 per cent of the adult population using these holes was banded, from which a total population of about 450 tropic birds may be calculated. Even allowing for considerable error, for the conditions clearly were not suitable for such a simple capture/recapture analysis, there still seems little doubt that far more birds were competing for these holes than the 232 that could be accommodated. Competition must have been even more intense than these figures suggest, since many of the holes seemed to be barely suitable and were much less sought after than the good holes.

Banding showed that different adults were usually involved in successive nesting attempts in the same hole. Thus there were 15 instances in which both the adults of one nesting were banded, as was also one adult of the nesting immediately preceding or following this one; and in only one of these instances was the same banded bird involved in both nestings. There were 14 instances in which only one member of the pair was banded in two successive nestings in the same hole, and in only three of these cases was the same bird involved. Thus a change of occupancy was proved in 14 out of 15 cases, and a probable change of occupancy occurred in a majority of 14 other cases.

There were not enough records to show how often adults changed their nest holes. Only five banded individuals were found nesting a second time during the period of observation; four were in the same hole as before and one had moved to another hole. But changes of nest holes are probably more common than these figures suggest, as of 19 nesting adults banded on the first two visits only one was found nesting again in the same hole as before, although the nests were all checked regularly and ten other adults were later found nesting in them.

On all visits, a good proportion of the nest holes were empty. At first sight this is rather puzzling in view of the evidence for competition for nest sites; but our visits were for only a few hours on one morning a month, and many more birds must have been visiting the holes than we could record. Also, as stated

previously, a high proportion of the nest holes were probably barely suitable, whereas others were apparently much more sought after. Thus of the 41 nest holes found on the first two visits and checked on all subsequent visits, 18 were not used again (unless eggs were laid in the holes and lost between visits), while two were used four times, one three times, and the rest twice.

With such widely spaced and brief visits it was of course impossible to determine the causes of nest failure, but the high proportion of nests that failed at an early stage (that is, nests that were found with an egg, and then were empty or deserted at the second visit), amounting to 34 per cent of all nests started, suggests intraspecific strife. There are no other competitors for nest holes on Daphne Island, and the only known predator is the Galápagos Owl (*Asio galapagoensis*), which was found to take occasional half-grown, young birds.

In the five cases where a banded bird was found nesting for a second time, the previous nesting had been successful in one case, the interval between laying dates being 10 months (February–December). In the other four cases, the first nest had failed, and the intervals between laying dates were three or four months. On South Plaza Island there was a repeat laying in one of the nests that failed, and in this case too the interval between laying dates was three months. This repeat laying was the single January record shown in table 1.

DISCUSSION

It seems unlikely that the tropic bird population of Daphne Island is physiologically different from that of South Plaza Island, only 16 miles away, a very short distance for a tropic bird to traverse. Both islands are centrally situated within the breeding range of the species in the Galápagos Islands. Hence it would be supposed that under less crowded conditions the birds from Daphne Island would show a distinct breeding season with a peak in October and November. The most likely explanation of the continuous breeding of the tropic birds and the lack of any obvious pattern is that it is due to competition. Many birds, for lack of a good site, are unable to nest at the normal time and eventually nest late, either taking over a nest hole from another pair or else making do with a somewhat unsuitable site. The high rate of nest failure, itself due partly to competition for sites and partly to the use of poor sites, leads to a large number of repeat nestings (after intervals of 3 to 4 months). A combination of these factors, it seems, has spread breeding more or less evenly through the year, obliterating what would otherwise be a well-marked seasonal pattern.

This could hardly be possible unless the birds' response to the proximate factors regulating the annual cycle were weak and easily overridden by other pressures. The limited data on breeding success are suggestive in this connection. Of the 88 nests on Daphne Island that could be tested for success, the success of the 52 that were started in the months April through August, the off-season of the breeding population of South Plaza Island, equaled that of the 36 nests started in the months of September through November, the peak of the breeding season on South Plaza Island. This represents a nesting success of 33 and 31 per cent, respectively. It may be suggested that the advantage of nesting at one season rather than another in the Galápagos Islands is slight, and that the birds' response to the proximate factors timing their breeding season is correspondingly weak. A very small selective pressure, resulting from the advantage of avoiding intraspecific competition, could lead to the

complete breakdown of a fixed annual cycle. The tropic bird population on the Galápagos Islands may be at just such a transitional stage.

The present data are unfortunately not complete enough to warrant a very detailed comparison with the Red-billed Tropic Bird of Ascension Island, where the much more intensive study by Stonehouse (1962) revealed a situation in some respects similar to that reported here but in others significantly different. On Ascension Island, competition for nest sites was intense, not only within the species but also with the smaller Yellow-billed Tropic Bird (*P. lepturus*). Nest losses due to this competition were heavy and nest holes often changed ownership. There was, however, no evidence of an annual cycle, the intervals between nesting attempts, whether after a previous success or failure, being apparently independent of environmental influences. Further complications were introduced by competition between the two species, whose cycles were of different lengths. There is no doubt that a more thorough investigation of the population of the Galápagos Islands, with a detailed comparison with the situation on Ascension Island, would be of the highest interest.

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LITERATURE CITED

- Beebe, W.
1924. Galapagos: world's end (Putnam, New York).
Lack, D.
1950. Breeding seasons in the Galapagos. *Ibis*, 92:268-278.
Murphy, R. C.
1936. Oceanic birds of South America. Vol. 2 (Amer. Mus. Nat. Hist., New York).
Stonehouse, B.
1962. The tropic birds (genus *Phaethon*) of Ascension Island. *Ibis*, 103b:124-161.

British Trust for Ornithology, Beech Grove, Tring, Hertfordshire, England, September 12, 1964.