EXPERIMENTS ON NESTING BEHAVIOR OF THE RED-TAILED TROPICBIRD, *PHAETHON RUBRICAUDA*

THOMAS R. HOWELL AND GEORGE A. BARTHOLOMEW

Department of Zoology
University of California
Los Angeles, California 90024

This study was undertaken in the course of more extensive investigations of the thermoregulatory adaptations of sea birds nesting on Midway Island, a coral atoll at 28°13′ N, 177°23′ W in the leeward chain of the Hawaiian Islands. The Red-tailed Tropicbird (*Phaethon rubricauda*) is an abundant breeding bird on Midway. Some of its physiological and behavioral adaptations to environmental conditions on this island have previously been discussed (Howell and Bartholomew 1962). Our limited time was devoted primarily to the studies on thermoregulation, but the opportunities for behavioral research were so great that we undertook simple field experiments on some obvious features of nesting behavior in this and in other breeding species (Bartholomew and Howell 1964).

The tropicbirds on Midway are especially well-suited for field experiments. They nest on the ground in large numbers, and many replications of a given experiment may easily be performed using different birds each time. With care, adult birds can be removed from the nest while experimental procedures are carried out; when released, the birds usually return to the nest within a few minutes if not immediately. On Midway during the summer months, tropicbirds can be found at most stages of their breeding cycle so that eggs, newly-hatched chicks, and well-grown young are all readily available to the investigator. We saw no evidence of predation on eggs or chicks (*Fregata minor*, the only potential avian predator, was not common), and exposure of eggs or chicks during the experiments never caused losses.

The Red-tailed Tropicbird nests only on remote islands and never comes to land except to breed. On Midway, pairs of these birds may nest in relative isolation or sufficiently close together as to form loose aggregations in which the incubating birds are spaced at least 0.5 m apart. Occasionally nests are much closer together if located on opposite sides of a piece of driftwood or some similar barrier that blocks visual and physical contact. Only nest sites in full or partial shade seem to be successful, and nests are most numerous in groves of introduced *Casuarina* trees, under *Scaevola* bushes, and around abandoned buildings. The nest is a simple scrape in the sand. The clutch is invariably a single egg, the color of which varies from almost pure white (rarely) to a purplish-brown hue resulting from varying densities of superficial pigmentation. Both parents participate in incubation and care of the young, but we were unable to distinguish the sexes externally. Tropic birds lack an incubation- or brood-patch, and the very small feet do not seem to play any role in incubation or brooding except, possibly, as tactile or thermal receptors (Howell and Bartholomew 1962).

We did not determine the incubation period, but Stonehouse (1962) reported 40–42 days for *P. lepturus* on Ascension Island, and that of *P. rubricauda* is presumably similar. The chick at hatching is covered with a dense coat of long, fine down and is brooded under the body of the parent for the first three or four days; thereafter, it is brooded under one wing (Howell and Bartholomew 1962). The parent feeds the young bird by regurgitation, with the bill of the adult inserted into the gullet of the chick, which makes pronounced gulping motions. Larger juveniles almost completely engulf the head of the feeding parent (see also Gibson-Hill 1949:232). The type of feeding behavior we observed in *P. rubricauda* was not reported by Stonehouse (1962) in his study of *P. lepturus* and *P. aethereus*, but he informs us (in litt.) that he is uncertain of the exact method of parent-young food transfer in those species, as his study was concerned with other aspects of tropicbird biology.

The tropicbirds on Midway showed no fleeing response when approached at the nest and did not leave it unless forcibly removed. If picked up and carried a few meters away and then released on the ground, they usually started to return to the nest immediately and rarely remained away from it for more than 10 min. The reduced hind limbs of tropicbirds render them incapable of standing and walking, and they move by a series of lurches when on land. Despite this awkward locomotion

The Condor, 71:113–119, 1969

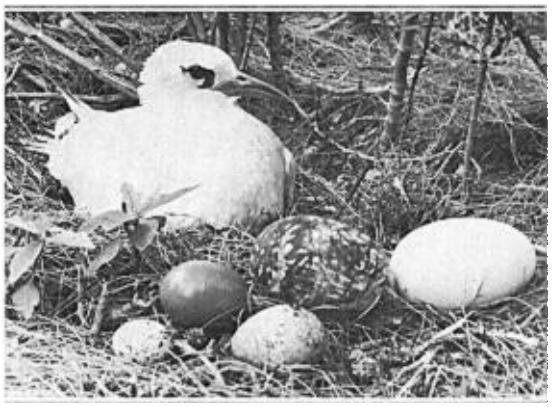

FIGURE 1. Adult Red-tailed Tropicbird on nest, with eggs used in tests (l. to r.): Brown Noddy; red plastic; tropicbird; albatross, artificially blotched; albatross, unmodified.

they manage to settle on the egg or newly-hatched chick without damage or injury to either.

EXPERIMENTS ON NESTING BEHAVIOR

By experimental manipulations at the nest we tested the responses of tropicbirds to a variety of situations involving eggs and nestlings. Preliminary observations showed that most birds responded to a test situation within 10 min. Therefore, unless otherwise mentioned, all tests were scored according to the birds' responses within a 10-min interval. Some of the test objects used are shown in figure 1. Results of responses to the test situations are summarized in tables 1 and 2, and the experimental procedures are described in the following sections.

Retrieval of own egg. In the first series of tests we removed the eggs from beneath incubating birds, restraining the birds if necessary. We placed each egg in full view, about 15 cm in front of a bird sitting on its empty nest. Of 16 birds tested, all but one retrieved the egg. The one bird that did not retrieve was highly disturbed by our handling and, when released, turned itself away from the egg to lunge at a Laysan Albatross (*Diomedea immutabilis*) that happened to walk by. After 55 min the tropicbird was still facing away from its nest and we then replaced the egg. Later observations showed that the bird eventually resumed incubation.

TABLE 1. Retrieval experiments on Red-tailed Tropicbirds.

Test object*	Number retrieving	Number not retrieving
Own egg	15	1
Unmodified egg of *Diomedea* sp.	8	7
Blotched egg of *Diomedea* sp.	2	8
Egg of *Anous stolidus*	0	10
Egg of *Gygis alba*	1	2
Red plastic egg	0	10
Own egg; egg of *Puffinus pacificus* under bird on nest	7	3
Tropicbird egg; adult brooding chick in nest	5	5

* Except in the test involving brooded chicks, the bird's own egg was removed from the nest at start of experiment. All test objects were placed 15 cm in front of the nest. See text for details.

Tropicbirds retrieved in the usual avian manner, placing the tip of the bill over the far side of the egg and then drawing it toward the body; manipulation of the egg was skillful and retrieval was completed quickly once begun. No vocalization was heard at any time during the process of retrieving, tucking under, and settling.

Effect of egg size and pattern on retrieval. Following the procedure outlined above, we removed an incubating bird's own egg and placed a test egg 10 to 15 cm in front of the bird sitting on its empty nest and scored responses. An unmodified albatross egg was used for one series, and the tests were then repeated using another albatross egg that we marked heavily with brownish ink (fig. 1) to provide a less extensively white object. Additional tests were made with Brown Noddy (*Anous stolidus*) and White Tern (*Gygis alba*) eggs; as these are naturally blotched we did not attempt to modify them.

The reactions to the unmodified albatross egg indicate that this large egg is decidedly less likely to evoke a retrieval response than is a tropicbird egg. Only 50 per cent of the birds tested retrieved the big egg, and most of the non-retrievers showed no visible reaction to it. When, after 10 min, the non-retrievers of the large egg were offered their own egg instead, they promptly retrieved it. The artificially blotched albatross egg was even less effective than the unmarked one. Out of 10 birds, only two retrieved it; one showed interest but did not follow through; one pecked hesitantly at it; another pecked strongly at it in an apparently definite rejection response; and the other five did not respond. Non-retrievers of the blotched albatross egg promptly retrieved their own egg when it was substituted for the larger one.

The small eggs of the terns evoked even less of a retrieval response, with only one tropicbird of 13 tested reacting positively. The others often fidgeted and turned and looked into their empty nests as though seeking their own missing egg but showed no reaction to the tern egg. One bird even lurched out of

its nest and lunged back right over the tern egg without seeming to notice it.

Response to a red plastic egg. This artificial egg was the size of that of a domestic hen and thus slightly smaller than that of a tropicbird. We partly filled the plastic egg with sand so as to approximate the weight of a tropicbird's egg. Red was chosen as the color most likely to evoke some response as the bird's own bright red bill and tail-streamers presumably have some signal function. The red egg was positioned in front of an incubating bird whose own egg had been removed as described previously. The responses were negative with one partial exception. One bird retrieved the red egg after 2 min, experiencing some difficulty because of the slick surface. At first it tucked the egg under its abdomen, but after a few seconds it rejected the red egg by pushing it out of the nest. Then, lurching out of the nest and using its bill, it rolled the egg away about 0.5 m. When the bird's own egg was placed beside the now empty nest, the bird returned at once and retrieved it.

Red egg in nest. In these tests an incubating bird was removed from its nest, a red plastic egg substituted for the normal egg, and the bird placed on the ground facing the nest at a distance of about 15 cm. Of 22 birds tested, 14 returned and settled on the red artificial egg. Ten of these birds appeared to settle on the red egg as readily as they would on their own; four seemed agitated but finally settled on the red egg. Of the other eight birds, three got on the nest but crowded the red egg to one side; one returned, inspected the nest and egg, and then withdrew. Four birds did not return to the nest during the 10-min interval and these were scored as "no response."

Retrieval while brooding egg or chick. As the tropicbird's clutch is invariably only one egg, we tested to see if the presence of an egg or newly-hatched chick under an adult bird on its nest would block the retrieval response. In the first series of tests, the egg was removed from beneath an incubating bird and placed 10 to 15 cm in front of it and in full view. At the same time, a substitute egg was placed under the bird on its nest. The substitute egg, taken from the nest of a Wedge-tailed Shearwater (*Puffinus pacificus*), was pure white and slightly smaller than a tropicbird egg. There was no indication that the shearwater egg was disturbing to the tropicbirds despite the slight differences in color, texture, and size. Most of the tropicbirds retrieved their own displaced egg even though the substitute was present in the nest.

TABLE 2. Egg or chick versus empty nest.

Experimental conditions	Choice			
	Empty nest	Egg or chick	Egg or chick, then to nest	No choice
Own egg beside nest	7	1	1	1
Own chick less than 4 days old beside nest	7	1	1	1

Several of the tropicbirds showed an unusually strong tendency to retrieve, and three of these were presented with additional eggs. Each of the three birds retrieved four eggs that were presented one at a time, even though unable to cover them, and eggs protruded from all sides of the sitting bird. One insatiable retriever tucked five tropicbird eggs under itself in sequence, and then repeatedly attempted to retrieve the blotched albatross egg when this was placed before it.

Birds brooding recently-hatched chicks showed a somewhat reduced tendency to retrieve, with only 5 out of 10 birds tested retrieving an egg placed before them.

Egg or chick vs. empty nest. We investigated the relative attractiveness of egg, chick, and empty nest by testing a series of birds in the following manner. We lifted a bird from its nest, moved the egg or chick 10–15 cm away, and released the parent bird on the ground about 1 m from the nest and facing it. The egg (or chick) was always in full view and slightly to one side of the nest so that the bird had to move in the same general direction to reach either one. The results showed a pronounced tendency by the adult bird to settle on the empty nest during the 10-min test interval (table 2). Five of the seven birds that had eggs but chose the empty nest retrieved the egg within 5 min, but none attempted to retrieve chicks. However, even chicks less than four days old (still being brooded under body) crawled to the parent on the nest when the adult bird returned, and were promptly taken under the wing. No chick returned to the nest while the parent was absent.

Chick exchange. The single chick of the tropicbird stays at or very near the nest site until fully fledged. We tested a series of adult birds to see if they would discriminate between their own and another chick when the latter was placed in the nest site. The brooding adult was picked up, its own chick removed, a new chick placed in the nest, and the adult released on the ground beside it. To our surprise, brooding adult birds immediately accepted a substitute chick even though

TABLE 3. Chick substitution.

Characteristics of own chick		Characteristics of substituted chick		
Approx. age in days	Plumage	Approx. age in days	Plumage	Results
<1	Gray down	14	Gray down	Broods under wing
1–2	Gray down	7	White down	Broods under wing
5	Gray down	5	White down	Broods under wing
7	White down	1–2	Gray down	Broods under wing
4	Downy	Juv.	Barred wing coverts	Juv. settles beside adult
14	Gray down	<1	Gray down	Broods under body
Juv.	Barred wing coverts	4	Downy	Broods under wing
Juv.	Barred wing coverts	3	Downy	Broods under wing
1–2	Downy	Juv.	Barred wing coverts	Feeds within 3 min
3	Downy	Juv.	Barred wing coverts	Feeds twice within 5 min

it might differ considerably in size or color from their own (table 3). Even more surprising was the fact that in two instances adults fed the substitute chick only a few minutes after the latter was deposited in the nest. In these two instances a juvenile bird was substituted for a small chick. In each case, the juvenile gave a low-pitched trilling or purring sound. This was followed by brief contact between the bills of the adult and the juvenile, and then the feeding took place.

Stonehouse (1962), discussing *P. aethereus*, reported that "chicks placed experimentally in nests other than their own were usually attacked by the resident chick and also by returning parents." However, Stonehouse twice found that a *P. lepturus* egg placed in an empty *aethereus* nest was hatched and raised successfully, and that an *aethereus* chick that accidentally tumbled into another *aethereus* nest containing a much older chick was accepted and both birds successfully reared. Our experiments differed in that we replaced one chick with another, and it may be that aggressive responses at the nest site are not released unless more than one chick is present (although not necessarily even then). The varied results point up the need for further investigation.

Gaping response of chicks. In all pelecaniform families other than the Phaethontidae, the nestling feeds by thrusting its beak into the gullet of the adult. However, the parent Red-tailed Tropicbird feeds the nestling by thrusting its beak deeply into the gullet of the gaping chick and disgorging food. There is first a brief period of bill-contact between the two birds and then the young bird gapes widely and gulps at the bill of the adult. Since this manner of feeding is unique within the order Pelecaniformes, we attempted to determine the stimuli that evoke the gaping response of the young birds.

We heard no vocalizations by the adults in connection with feeding and therefore made no attempt to test for effects of sound stimuli. The bright color of the bill in adult tropicbirds and the bill contact just prior to feeding prompted us to test the relative importance of color and of tactile stimuli in evoking the gaping response of the chick. The bill of young Red-tailed Tropicbirds is dark gray, and at its base there is a small area of bare blackish skin that contrasts conspicuously with the light-colored down that covers the rest of the head. The initial tests were carried out on two age groups of 10 birds each. Group 1 consisted of downy young birds, from newly-hatched and still-damp chicks to those of an estimated age of 10–12 days, still downy and not yet showing barred wing coverts. Group 2 consisted of juveniles, from those still with down and barely showing barred wing coverts to those without down and fully covered with contour feathers (fig. 2). The first test objects used were (1) an adult tropicbird skull with the color of the beak restored with red ink, and (2) the investigator's index finger. Three patterns of potential stimulation were presented. In sequence, the test object was moved slowly back and forth 1–2 cm on either side of the chick's

FIGURE 2. Young Red-tailed Tropicbirds representing the two age groups used in experiments on gaping response and substitutions in nest (see text).

FIGURE 3. Red-tailed Tropicbird chick with objects used in tests on gaping response (l. to r.): tropicbird skull with red beak; green simulated beak; yellow simulated beak.

bill without touching it; then the ramphotheca of the chick's bill was gently tapped; and finally, the bare skin at the base of the bill was gently tapped. Although a few young chicks in Group 1 moved the head from side to side as the test object was passed before them, none gave a gaping response. No gaping response was evoked by tapping the ramphotheca, although the birds reacted by head movements to the contact. However, all 10 birds gaped readily in response to tapping of the bare skin at the base of the bill. If the birds were allowed to take the test object into the mouth they gulped and swallowed vigorously. Only the oldest of the 10 birds showed a slightly equivocal response. It gave a few harsh scolding notes when approached, gaped in response to tapping at the bare skin area, but did not seize and gulp strongly at the test object unless it was thrust into the mouth.

All of the birds in Group 2 except the youngest bird reacted to the experiment with hostility. They usually gave harsh, snarling cries when approached or touched, and bit and shook the test object fiercely. The youngest bird, barely showing barred wing-coverts, scolded slightly when approached, gaped slightly when touched on the bare skin at the base of the bill, and gulped weakly at the test beak when this was put into its open mouth. This bird did not gape in response to the investigator's finger.

We carried out further tests with simulated beaks of different colors. These were shaped from flat pieces of wood to resemble an adult's beak in profile and were colored yellow and green, respectively (fig. 3). These and the previous test objects were then tried on a new group of 10 chicks. Six of these were similar in age to those of Group 1, and four were older, as in Group 2.

All six of the younger birds gaped and gulped in response to any of the four test objects when these were touched to the bare skin at the base of the bill.

The four older birds were less sterotyped in their reactions and less inclined than the younger ones to respond to the artificial situation with which they were presented. The smallest of these birds gaped only slightly in response to tactile stimulation at the base of the bill but gulped vigorously at each of the four test objects when these were placed inside its mouth. One bird thrust its bill toward the yellow simulated-beak when it was presented; no contact was made and only the one thrust was attempted. The same bird immediately responded to tactile stimulation by each of the four test objects. One of the other birds accepted the yellow simulated-beak (the first one offered) when used in tactile stimulation, but did not accept the others. The responses of the remaining two birds were entirely negative; they appeared annoyed by the stimuli and reacted aggressively. We conclude that younger birds will respond to tactile stimulation alone, but older birds require a closer approximation to the total stimulus pattern presented by the feeding parent if they are to respond positively.

Gross (1912) reported somewhat different responses in his study of *P. lepturus* in Bermuda. He stated that downy chicks of this species gaped readily in response to "a mere touch, or even the click of the camera . . . Often when I placed my hand near them they would pick at my fingers . . . ." Stonehouse (1962), writing about the same species on Ascension Island, said that "Feeding was accompanied and punctuated by persistent begging calls from the chicks, to which the parents responded with guttural clicks and 'chucks.'"

Our data suggest that the feeding behavior of *rubricauda* differs somewhat from that of *lepturus*, but more observations of natural feedings are needed to substantiate this. Gross (1912) mentioned that the downy chick of *lepturus* has a conspicuous area of blackish bare skin at the base of the mandible, and it seems likely that (as in *rubricauda*) tactile stimulation of this area would elicit a gaping response.

MISCELLANEOUS BEHAVIOR

Sleeping. The adult Red-tailed Tropicbird has a variety of sleeping postures. Some sleep in the sitting posture used during incubation (fig. 1) with the head drawn back slightly and the bill pointing anteriorly. Others sleep with the head and neck extended and resting flat on the sand. Still others sleep with the head turned posteriorly and the bill tucked in among the scapular feathers. Large juveniles as well as adults may assume this posture. Some smaller juveniles and chicks may sleep in a rather curled-up position, with the head resting to one side on the sand.

Shearwater-tropicbird chick interaction. While we were watching nesting tropicbirds in the sand under a *Scaevola* thicket, an adult Wedge-tailed Shearwater started to walk across the nesting area and by chance came close to a 4- or 5-day-old tropicbird chick. The chick at once nibbled gently at the shearwater's beak and then attempted to get under its wing, alternating several times between these two actions. The shearwater halted beside the chick and repeatedly nibbled gently at the latter's down, as though trying to preen it, and several times tried vigorously but unsuccessfully to tuck the chick under its abdomen by using its bill in the usual "retrieving" manner. The interaction lasted for about 30 min, after which the shearwater moved on.

DISCUSSION

The Red-tailed Tropicbird, like other ground-nesting sea birds that have been investigated, is markedly attached to its nest site. Even an empty nest scrape constitutes a stronger attraction for an adult bird than a displaced egg or chick close by. As the nest is no more than a slight depression in the sand in a location that usually lacks conspicuous distinguishing features, a persistent precise fixation on the nest site (once chosen) would be advantageous for continuity of the reproductive effort in a given season. Site-attachment necessarily precedes egg-laying, and, as the egg normally remains in the nest, there would be no obvious selective advantage in having the egg, an object-stimulus, replace the nest site, a specific locality-stimulus, in the orientation behavior of the adult bird.

Although under natural conditions the egg is unlikely to be displaced for any great distance, the awkward, lurching terrestrial locomotion of tropicbirds may easily cause some displacement of the egg, especially during the change-over by the incubating parents, and selection would favor ready and skillful retrieving behavior. Tropicbirds often nest in close association with other species of ground nesters. On Midway, their nests may be close by those of albatrosses, shearwaters (nesting on the surface of the sand in this locality), boobies, and terns. This association may have some relation to the tropicbirds' pronounced tendency to retrieve an egg of their own species and the much weaker tendency to retrieve an egg that is larger or smaller or differently colored. As tropicbirds have a clutch of one and are normally never faced with more than one egg (or chick) in the immediate vicinity of their nest, there may have been no selection for a "stop retrieving" response; hence, their tendency to keep retrieving eggs (when experimentally provided) despite the presence of an egg or chick already in the nest. Also, the lack of an incubation patch may result in an inability to distinguish tactilely between one or several objects in the nest.

Even young chicks are capable of some terrestrial locomotion, but the young birds seldom if ever leave the immediate vicinity of the nest site. Thus, strong site-attachment by adults would be sufficient to insure continual parent-offspring contact, and recognition of individual chicks might not provide much if any additional advantage. Nevertheless, the immediate acceptance by adults of a substitute young bird of very different age from their own is surprising and is worthy of further investigation.

We found no indication that bill color in adults is important in releasing the gaping response of young birds. This may be related to the fact that these tropicbirds feed their chicks by inserting the bill into the gullet of the young bird instead of following the typical pelecaniform pattern in which the young bird goes into the gular pouch or gullet of the parent for food. In those birds, such as various gulls (*Larus* sp.), in which bill color has proved important in feeding behavior, the chick stimulates the adult to open its beak, and the color provides a target-stimulus for pecking or nibbling by the young bird. In the Red-tailed Tropicbird the adult tactilely stimulates the young bird to gape, and there does not appear to be a specific visual target for actions by the chick expressing hunger. The young tropicbirds may solicit feeding by their vocalizations, and this too invites further study. Possibly the bill color of adults plays a role in species recognition or in intraspecific display, but we have no data on these points.

The method of parent-young food transfer in tropicbirds is one of many ways in which

the Phaethontidae differ from the pelecaniform families with which they are traditionally placed. Except for the totipalmate feet and the absence of an incubation patch, there is little structural resemblance between these groups. Tropicbirds have well-developed external nostrils, and there is no definable gular pouch. The chicks are fully covered with long, dense down at hatching and are capable of effective thermoregulation. After the first few days, the chicks are brooded only under the wing of the parent; this unusual trait is probably related to the striking reduction of the hind limbs and entire synsacral region, which makes both perching and upright walking impossible and constitutes a unique characteristic among all families of birds.

Although the relationship of the tropicbirds to the Pelecaniformes must be considered uncertain, it is at least equally difficult to recognize a closer affinity with any other order. The Phaethontidae appear to be an aberrant group, incapable of survival in any habitat except the tropical seas and remote islands that they presently inhabit. However, they possess a constellation of adaptations that has proved highly successful within this vast environment.

SUMMARY

The nesting behavior of the Red-tailed Tropicbird on Midway Island was investigated through experiments involving the following activities: (1) retrieval or non-retrieval of a bird's own egg; or an egg of different size, color, or pattern; or an additional egg or chick by an adult brooding one or the other; (2) acceptance or non-acceptance of a differently-colored egg substituted for a bird's own in the nest; or a chick of different color and/or size substituted for a bird's own chick; or the relative attractiveness of a displaced egg or chick vs. an empty nest; (3) gaping response of chicks in relation to visual and tactile stimuli. Tropicbirds almost always retrieved their own egg when it was displaced. Much larger eggs were less frequently retrieved. An artificial red egg was not retrieved but was usually incubated if substituted in the nest for the bird's own egg. An egg was less frequently retrieved if the adult bird on the nest was already sitting on an egg or chick; chicks were not retrieved but usually crawled back to the parent on the nest. Adult birds usually returned to their empty nest rather than to a displaced egg or chick beside the nest. Chicks of very different size and/or color were readily accepted by adults, at least during our observation periods, when substituted for the latter's own chick. Only tactile stimuli applied to the bare skin at the base of the chick's bill were effective in evoking the gaping response.

LITERATURE CITED

BARTHOLOMEW, G. A., AND T. R. HOWELL. 1964. Experiments on nesting behaviour of Laysan and Black-footed Albatrosses. Anim. Behav. 12:549–559.

GIBSON-HILL, C. A. 1949. Notes on the nesting habits of seven representative tropical sea birds. J. Bombay Nat. Hist. Soc. 48:214–235.

GROSS, A. O. 1912. Observations on the Yellow-billed Tropic-bird (*Phaëthon americanus* Grant) at the Bermuda Islands. Auk 39:49–71.

HOWELL, T. R., AND G. A. BARTHOLOMEW. 1962. Temperature regulation in the Red-tailed Tropic Bird and the Red-footed Booby. Condor 64:6–18.

STONEHOUSE, B. 1962. The tropic birds (Genus *Phaethon*) of Ascension Island. Ibis 103b:124–161.