

NESTING ACTIVITIES OF THE RED-FOOTED
BOOBY IN BRITISH HONDURAS

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FROM 14 February to 9 May 1958 I conducted an intensive investigation of the breeding activities of the Red-footed Booby (*Sula sula sula* Linnaeus) on Half Moon Cay, 80 km east of Belize, British Honduras. The detailed results of the study appear in my thesis for the degree of Master of Science (Verner, thesis submitted 1959).

Half Moon Cay (Figure 1) is a tiny coral island, 1.16 km in length, supporting mainly coconut palms (*Cocos nucifera*). The floor of the narrow eastern half of the cay has been cleared, and the palms there are planted in rows. On the western portion, exclusive of the booby colony, the palms are distributed naturally, the floor beneath being covered with lush, mat-forming herbs. Within the booby colony very few palms are present; instead, eight species of broadleaf trees form a nearly continuous overhead canopy from about six to 15 meters above the ground. The number of booby nests in each species of tree fairly well indicated the relative abundance of each species (Table 1). The floor of the colony is composed of coral stones, which permit potential humus to percolate away with the rains. As a result, there is little in the way of an herbaceous understory.

The only undomesticated mammal on the cay is *Rattus rattus*. Ninety-eight species of birds were recorded during the course of the study. At least 77 of these were migratory forms, and, of these, only 17 were recorded regularly enough to indicate that they winter on or near the island. Two species, the Red-footed Booby and the Magnificent Frigate-bird (*Fregata magnificens*), were nesting at the time of the study; and probably both the White-crowned Pigeon (*Columba leucocephala*) and the Groove-billed Ani (*Crotophaga sulcirostris*) nested there later in the year. A number of small lizards and two larger ones, the False Iguana (*Ctenosaura similis*) and the Iguana (*Iguana iguana*), were abundant. Nothing was observed to substantiate the many reports that these larger lizards harm nests, eggs, and young of the Red-footed Booby.

The climate at Half Moon Cay is generally mild, although the high humidity makes even slight temperature differences more noticeable. Temperatures were recorded three times daily—morning, noon, and night—between 20 March and 7 May and the range was from 23°C (73°F) to 32°C (90°F). With the exception of the early morning average of 26°C (79°F) in March, all three daily averages for March,

April, and May were above 27°C. During the three-month study period, which was in the dry season, it rained hard on one day and showered on four. Average annual precipitation at Belize since 1919 is 1,861 mm (73.26 inches), with a range of 1,068 to 2,779 mm (42.03 to 113.33 inches). March, with an average rainfall of 38.9 mm (1.53 inches), is the driest month; October, with an average of 309 mm (12.15 inches), is the wettest. There is nearly always a moderate easterly breeze across Half Moon Cay. This not only mitigates the effects of the high humidity but also keeps the entire island practically free of small flying insects.

Most of the observations on nesting behavior were conducted from a three-meter-high platform in a *Ficus* sp., from which over 100 occupied booby nests could be seen. The birds' indifference to all my activities made it unnecessary to place a blind on the platform. All the nests in the colony were systematically counted between 16 February and 3 March. Considering the number of nests (1,389) and the large number of non-nesting individuals present, I estimated that there were approximately 3,500 Red-footed Boobies (not counting nestlings) on the island at the time. Of that number probably 500 were immature birds that roosted in groups in various sections of the colony.

FORMATION AND MAINTENANCE OF PAIR BOND

Although pair formation was incompletely observed, two incidents provide a clue to the method employed. When a pair had its nest



Figure 1. Half Moon Cay. The booby colony occupies 4.38 hectares (10.96 acres); the western section, where trails are concentrated, was the principal study area. The large white dot marks the location of the observation platform.

destroyed, the birds continued to maintain a territory (either the same or a new one), even if they did not attempt to reneest. Several of these "nestless pairs" were observed throughout the study period, and it was from two of these that I obtained data on pair formation.

The female of nestless Pair 75 died, and the male was observed closely on the following days. Two days after the loss of his mate, the male was performing what I called the "four-point" display (Figure 2) at passing birds. The following day he was four-pointing actively to another bird that was perched on his territory about 60 cm in front of him and that occasionally responded to his four-points with a bow in his direction. Apparently the pair bond had just recently been formed between these two birds, or it was being effected at that time, since they remained paired thereafter.

In the second case Male 64 was apparently on the verge of changing mates. The pair had been without a nest for 35 days when the male, while standing beside his own mate, was seen four-pointing to a third bird (presumably a female) on a perch about five meters from his own. The second female bowed in response. During the next hour the male shifted back and forth between the two females. Both females, as well as the male, engaged in four-pointing; and the male brought twigs to both females. No other bird was observed with the second female, and the male was roosting with her at dark. The following morning, however, he was back on his own territory with his own mate, and nothing further developed. The second female was not seen again.

The "four-point" and its variations were the most frequently observed displays. In a full four-point the bill, tail, and both wing tips were directed skyward as illustrated in Figure 2C. The posture was accompanied by a single, rattling, drawn-out note (*walk*, or better, *waaalk*), usually on a low pitch and with only a slight inflection at the end, or by no call at all. The posture began with the booby extending its head and bill upward until the bill was nearly vertical, thus exposing the throat area (Figure 2A). Before this action was completed, the tail began to rise toward a vertical position (Figure 2B), and the wing tips began to rise before the head and tail were fully erected. The wings were not extended from the body, however. Instead the carpal joints were depressed and the remiges spread so the primaries were pointed nearly vertically. All the actions were slow and deliberate, and the full posture just described was not always attained. Rarely a four-pointing bird that was standing on a perch terminated the display by bowing very low (Figure 2D). Every gradation between the full pose and simply raising the head and bill slightly was observed.

The following case typifies the complete four-point display as performed only by nestless pairs but never completely by nesting pairs. The male stood on a perch facing his mate, who stood on another perch about 60 cm away. The female seemingly paid little attention to the male; but he never moved his gaze from her. He tried to command

her attention by extending his neck fully in order to thrust his bill in her direction. If she turned toward him, he began a four-point. But if she turned away before he reached the full pose, he relaxed and again thrust for her attention. Only when the female gave the male her full attention did he complete the four-point. No bird was ever seen to expand, or in any way enlarge, its gular sac during any such display.

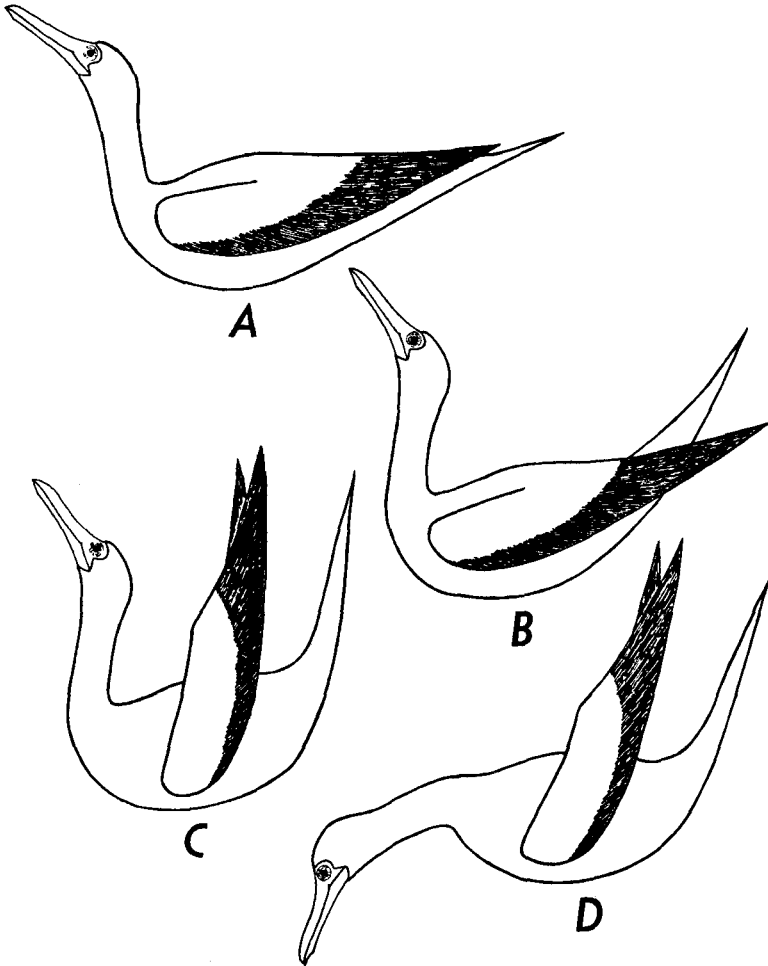


Figure 2. Stages of the "four-point" display. A, B, and C illustrate typical stages of the display with C being the usual climax position. D illustrates the "bow," which infrequently followed stage C.

The female frequently acknowledged the male's display with a bow or bill thrust in his direction, and occasionally she assumed a four-point herself, rarely attaining the full posture. During one such ritual, however, a female was initiating every four-point, and the male was responding with the same, so that both reached the full pose at nearly the same instant.

Although this display was used, especially in its incomplete stages, as a warning to trespassers, its chief importance was in courtship and maintenance of the pair bond. Since nesting males four-pointed only occasionally, it was probable that their domestic responsibilities were sufficient to maintain their pair bond. The "stick-shake" display was observed more among the nesting pairs, and perhaps served the same function as did four-pointing during the nestless period.

When a stick was brought to the territory by one partner, a "stick-wave" display followed. In performing the stick-wave, the bird stood on a perch (or the edge of the nest) with a stick in its bill, waving its head about while holding the stick and uttering a series of guttural squawks indistinguishable, or practically so, from the call given by all Red-footed Boobies when landing. The stick-wave was usually followed by the stick-shake display by both members of the pair. The stick was passed from one bird to the other, but frequently both birds held the stick and shook it mildly. Then they arched their necks forward and down together to place the stick at their feet. Without exception, when either sex or both together held the stick down at foot level to place it on their nest or perch, it was trembled or quivered into place. The stick often became quite a toy for the birds as they passed it back and forth between them. Only the males of nesting pairs gathered sticks, while both sexes of the nestless pairs did so; but the antics of the birds were the same after the stick was secured. It was finally dropped to the ground by the nestless birds, however, since they had no nest to which to add the stick.

Unlike nesting pairs, both birds of the nestless pairs were absent from the territory most of the day, invariably returning separately in the evening. Their evening behavior assumed different forms, with each pair tending to emphasize one or another feature of the general pattern of activity. For example, Pair 64 stressed the four-point and the stick-shake displays; Pair 70 usually sat quietly, while the female preened the nape and back feathers of the male, and were more active at "billing" than the others (billing by the Red-footed Booby seems to be an argumentative gesture, with one bird actually snapping suddenly at another's bill); and Pair 75 concentrated on the four-point and

actual copulation. Pair 75 was the only nestless pair that I saw copulating, although Pair 74 made several unsuccessful attempts to do so. It seems unusual that Pair 75 copulated regularly for a full month, but never attempted to build a nest. An examination of Female 75's ovary revealed no enlarged follicle, and the significance of their activity was not determined. The other activities mentioned were common to all pairs.

Several things suggest that the monogamous pair bond of this species is at least sustained, if not life-long. First, at least 10 of the nestless pairs were holding territories within view of the observation platform, and most of these pairs were first noticed about two months before I left Half Moon Cay. All remained paired and on the same territories for the remainder of the study. Second, the nesting season for the colony as a whole takes most of the year, so there would be very little, if any, time between successive seasons for a period of general courtship and pairing. Third, the fact that Male 75 remated late in the nesting season shortly after the loss of his original mate indicates an absence of a general courting period. It is of interest, too, that the newly formed pair did not change territories. This same evidence also suggests that at least some pairs maintain their territory throughout the year.

TERRITORY

The territory of the Red-footed Booby is used for nesting, copulation, and occasionally for roosting by the nonincubating mate. Usually, however, the nonincubating bird roosts on a perch that is often shared with other birds and that is removed from all territories. Each territory, therefore, is small, probably not exceeding 0.6 square meters and includes only the nest and the adjoining three or four perches used for landing and take-off. In most cases neighboring territories were not contiguous; in fact by far the largest portion of the colony was not defended by any pair.

The stick-wave display was apparently used to denote territorial ownership and probably also helped to maintain the pair bond of both nestless and nesting pairs. In most cases where the sex was known, this display was performed by males; however, on a few occasions nestless, paired, territorial females were observed gathering nest materials, and they were also seen stick-waving. Therefore, it seems that stick-waving normally follows the return to the territory with nest materials and is common to both sexes. The infrequency of stick-waving by females is probably attributable to the fact that they gather nest materials only for a brief period prior to nest construction. On several

occasions, immature birds that had nearly attained adult plumage were observed giving the stick-wave. One such bird occasionally gave the display, always from the same perch, for a period of at least two months. It not only waved the stick about and squawked loudly but also made several motions as though to place the stick on its perch. The bird was present at its perch every evening, and frequently it engaged in lively battles with nesting adults whose territories were nearby. In several cases the immature seemed to be deliberately challenging the other birds to dispute his right to that spot. To me these activities were suggestive of territorial selection.

On the basis of indirect evidence, I suspect that the male selects the territory. The male of a nestless pair that was maintaining a territory was killed; the female was marked and her movements traced after the death of the male. In two days she had deserted the territory and was roosting in the evenings near the observation platform. In a second case, mentioned earlier, the female of a nestless pair died and the male soon acquired a new mate while remaining on his original territory. This was on 26 April, when most pairs already had young well advanced. The pair remained on the territory but never attempted to nest.

Territorial defense was at times quite fierce. Boobies were frequently seen biting and jabbing each other, and occasionally one gripped another around the neck so tightly the victim was unable to free itself. Such encounters sometimes lasted for several minutes. As a rule, however, threat displays sufficed for territorial defense. Adults and moderate-sized young alike were active in defending the territory against all intruders, including other boobies, frigate-birds, iguanas, and humans. Although the degree of resistance to me varied considerably among individuals, nearly every adult booby stood its ground at the nest until it was removed bodily. The first few times that I disturbed them, the birds were very active in resisting me, squawking loudly while biting and stabbing at my hand and a stick I used to force them off the nest. But gradually they became accustomed to my intrusions and tried only to bite me, paying little attention to the stick and not squawking. They reacted similarly to a mirror on a long pole that was used to examine the contents of nests high in the trees. Adults would not attack a strange downy young if one was moved from its nest to a strange nest, but nestlings fiercely resisted intrusion by other young. Smaller young on their own nest invariably subdued larger young introduced from other nests. After the young birds had begun to darken through acquisition of the juvenal plumage, they were forcefully driven off by adults when they strayed or were placed on the wrong territory.

I called the principal threat display the "one-point." Both sexes gave the display, but males were generally more aggressive. In a typical, exaggerated one-point, a booby thrust its bill forward toward the intruder and waved its head slowly and methodically from side to side. Usually, though not invariably, this action was accompanied by a series of loud squawks, normally with a screeching quality. Ordinarily, the threat was given from a sitting position by an incubating bird; however, birds also one-pointed while perched. In its mildest form, the one-point involved only the forward thrust of the bill without the head waving or calling, and all gradations between the two extremes were observed. I was frequently unable to distinguish between a weak one-point and the very early stage of a four-point.

NEST

Since only the males of nesting pairs, and both males and females of nestless pairs, were observed gathering nest materials, and since the females of the nestless pairs were invariably the first noted and the most active at gathering materials, it is likely that female Red-footed Boobies initiate nest construction. The males then assume the gathering responsibilities, while the females carry on most of the actual construction.

The only nest for which the complete construction was observed was a second attempt by Pair 22, which had their territory six meters in front of the observation platform. These birds lost their egg on 15 February but clung to their original territory after the loss. However, they both left the territory during midday, and neighboring boobies and frigate-birds took all the material from their nest. This common practice in the booby colony dictated that at least one member of a pair be on guard at all times to protect the nest even before the egg was laid. I saw nests completely stripped and added piece by piece to other nests in half an hour! On 4 March Pair 22 had definitely begun to build a new nest in the same position as their first. At 1747 they copulated at the nest site; then the male flew off while the female guarded the new nest, which consisted of a very few sticks at that time. At 1803 the male returned with a twig bearing dying leaves that was probably taken from a nest recently deserted by another pair.

The male guarded their nest all the following day. At 1622 his mate returned, and the two birds immediately began to adjust nest materials. Between 1627 and 1757 the male brought 41 separate sticks for the female to add to their nest; all but two were taken from a vacant nest 3.8 meters away. Each time the male returned to the nest with a stick he squawked loudly just before alighting. After landing he performed the stick-wave display so that the call and actions of landing were continuous with the call and actions of the stick-wave. Occasionally the female responded with a soft, squawking chatter. She invariably made the final placement of each stick on the nest, although the male often helped her move the stick toward the nest. All the sticks collected that day were added to the rim of the nest, with the female working all of them in about her and

occasionally turning around and around in the bottom of the nest. Without fail each stick was quivered or trembled into place. Just before dark the birds copulated and then settled down to roost.

For the next few days, one or the other of the birds guarded their nest, and construction continued more slowly. At 1112 on 12 March, just eight days after their nest was begun and 25 days after the loss of their first egg, Female 22 laid another egg.

The birds continued to add to their nest occasionally throughout incubation and even after the young was hatched. Other pairs were also observed adding to their nests after they had young; in fact, one male was seen collecting nest material a month after the egg had hatched. Twigs, freshly broken and bearing fresh leaves, were added to the lining of the nest before the egg was laid and *throughout incubation*, and dry leaves were occasionally removed from the lining. Fisher (1903) wrote that at Laysan Island he found leaves scattered under the eggs in newer nests. He used these leaves as a crude index to the incubation stage of an egg, assuming that the drier they were the longer the egg had been incubated. However, since fresh leaves were added to the nest lining throughout incubation at Half Moon Cay and incubation takes about 45 days, this sort of index is invalid.

Below the nests at Christmas Island, in the mid-Pacific, Streets (1877) noted mounds of twigs that were sometimes cemented together with excrement. "It probably afforded them diversion during the monotonous period of incubation to break off all the twigs within reach of their bill, and to drop them under their nests. These mounds furnish evidence of the nests being occupied for several successive years; for the lean bushes could not furnish a sufficient amount of twigs to build them up in a single breeding-season." A possible and more reasonable explanation of the mounds is that pairs utilize the same *site* in successive years but probably not the same nest; the mounds, then, represent an accumulation of the nests of previous years. This explanation lends support to my belief that at least some pairs maintain territories throughout the year and that the pair bond is sustained or life long. I doubt that many nests at Half Moon Cay could survive the stormy season. Even by the end of my stay a few of the recently abandoned nests had nearly collapsed. Also the young birds usually left their nests to stand on perches long before they were fledged and, from there, tore their nests apart, piece by piece, until nothing was left of them. Eighty-one of 221 nests that were checked weekly had flying young by 9 May, and 74 per cent of these had removed their nests.

Nests were composed of small sticks, twigs, and coarse herb stems that were plucked with the leaves still attached. Thus nests frequently

had streamers of sticks with dry leaves hanging down from their rims as far as 500 mm. Of 27 nests, 24 were circular and three were slightly oval. The diameters of the circular nests ranged from 260 to 420 mm and averaged 306 mm. The diameters of the three oval nests were 480 x 340, 380 x 300, and 340 x 190. The outside depths of the 27 nests—top of rim to bottom of compacted portion of nest body and not including leaf streamers if such were present—ranged from 75 to 180 mm and averaged 113 mm. Nest depressions were shallow, rarely an inch deep; and nests became progressively more flattened after the egg hatched. In fact, some nests actually became convex on top as a result of the young boobies moving about on them and a lack of attention by the adults.

The birds tended to gather nest materials from areas where they could fly off into the wind. Twigs and small sticks were broken from the trees, and, on very windy days during the height of the construction period, coarse herbs were pulled up from the ground on the windward shore. The result has been a curious hedgelike shearing of the trees along the southern and eastern borders of the nesting colony, facing the direction of the prevailing winds. As one might guess from previous discussion, many nests were composed of materials that had been taken largely from abandoned nests.

TABLE 1
TREES UTILIZED AS NESTING COVER ON HALF MOON CAY

<i>Species</i>	<i>Total nests</i>	<i>Total trees</i>	<i>Av. no. nests/tree</i>
<i>Cordia sebestena</i>	783	363	2.16
<i>Bursera simaruba</i>	232	77	3.01
<i>Bumelia retusa</i>	210	130	1.62
<i>Pouteria campechiana</i>	86	45	1.91
<i>Ficus</i> sp.	50	25	2.00
<i>Ximena americana</i>	22	7	3.14
<i>Pithecellobium keyense</i>	4	2	2.00
<i>Neca choriophylla</i>	2	2	1.00
Total	1,389	651	2.12

Eight species of trees were utilized for nesting cover (Table 1), and nest density was 312 per hectare (126.7 per acre). The nearest two nests in the colony were separated between their rims by only 17.5 cm.

Most nests were placed near the tops of the trees or on their outer edges where the birds could utilize winds or drop from their perches when taking flight. Nests were situated on top of criss-crossing net-

works of small branches that provided suitable platforms, in the angles of wide, flat crotches, or on top of nearly level limbs. Describing the nest of *Sula sula rubripes* at Moku Manu, Hawaii, Richardson and Fisher (1950) write: "The booby nests when first built consist of a handful of fresh branches, as of *Atriplex*, a foot or two long, bent or placed in a rough circle on top of a low bush. The booby packs these branches down, adds more branches, and bends the living bush down with its weight so that a rather flat, nesting platform results." Murphy (1952) remarks that the Red-footed Booby at El Fondadero, Hermanos group, nests in trees and shrubs on the windward slope in order to have a good windward take-off.

The highest nest in the colony was 12 meters above the ground; the lowest was 1.8 meters, and the average height of 100 randomly selected nests was six meters. I found no record of higher nests in any part of the world. Apparently the nest height depends primarily on the height of available vegetation, and ground nesting is not unknown. On San Benedicto Island, in the Revilla Gigedo group, *Sula sula websteri* nests on grass culms from 0.3 to 0.6 meter high (Anthony, 1898; Beck, 1902; Kaeding, 1905; Hanna, 1926; and McLellan, 1926). At Jarvis Island, Kirby (1925) has photographed *Sula sula rubripes* nesting on piles of sticks 30 cm or more high. And Hutchinson (1950) writes that Hague mentions a booby (presumably *Sula Sula*) with that habit on Howland.

COPULATION

Copulation occurs at the territory, either on the nest or on a perch, but it probably never occurs at sea. Since the birds are rarely together at the territory during midday, copulation must necessarily take place either in the early morning or late evening. My observations indicate that it occurs most frequently in the evening, occasionally in the early morning, and rarely during midday. Copulation by nestless pairs has already been discussed.

Little or no preliminary ceremony preceded copulation, which usually occurred during periods when the male was gathering material for the nest. Occasionally, when returning with a stick, he landed directly on the female's back. The stick was passed to the female, who placed it on the nest. Then copulation followed. More often, the male landed beside the female. A stick-shake display followed, or the female placed the stick directly, and the male mounted. Just as he mounted, the male gave a loud, guttural, drawn-out screech. The female frequently raised one wing slightly, which served to lend support to the male. He put

his bill beside her neck, frequently shifting it from one side of her neck to the other but never taking her nape feathers in his bill. Then he slid backward over either side, sometimes flicking his tail from side to side just prior to cloacal contact and occasionally flapping his wings out to his sides slightly for balance. After the initial screech at mounting, the male began a series of low, guttural notes given at a rate of about 1 to 1.5 per second. Like the note accompanying the four-point, this latter note of copulation is best phoneticized as *walk*. But, unlike the four-point call, the copulatory note has a pronounced inflection in the middle. The series of notes continued until just after cloacal contact was effected and after the male had again assumed a standing position on the female's back. He remained standing there for various periods of time up to two minutes before hopping to a perch or flying off.

No female was ever heard to make a sound during copulation. However, on a very few occasions, I saw the female mount the male and remain a short time without attempting copulation. During those times the female gave part of the typical copulatory call of the male, and once one gave the full sequence of notes! Only nestless females were seen engaging in this activity.

Pair 22 copulated eight days before the female laid. I observed them copulating once each evening on the eighth, seventh, fifth, and fourth days before the egg appeared. The day before Female 22 laid, she remained on the nest all day, and Male 22 stayed in the colony gathering nest materials most of the day. Continuous observation of the nest was maintained from 0530 through 1830. I heard copulatory notes as I climbed to the observation platform at 0530, and when I got within view of the birds, Male 22 was standing on his mate's back. I am certain that they copulated. They copulated again at 0710, 0957, 1106, 1336, 1602, and 1812. When I left at 1830 Female 22 was asleep on the nest with her bill and head tucked back under her scapulars, and Male 22 was standing beside her.

The following morning the pair copulated at 0632 and 0653. The male was away from 0814 until 1652; in the meantime the female had laid. At 1722 and 1731 they copulated again. The next day the male incubated the egg, and the female was away until late in the afternoon. At 1812 they copulated once again, this being 31 hours after the egg had been laid. Illness halted my observations for six days; so I do not know how long Pair 22 continued to copulate after the egg was laid. Pair 72, with an egg on their nest, copulated on the evening of 24 March. The date their egg was laid is unknown, but it hatched on the morning of 5 May. Calculations from determined incubation periods indicate that the egg may have been laid one and a half to five days before the last copulation was observed.

LAYING

By extrapolating from the date (1 April) on which the first flying young were seen, I have fixed the earliest date of laying at Half Moon

Cay that season at about 15 November. Eggs were still being laid up to mid-April, so the laying season for the colony extended over about five months. Courtship and nest building would extend the nesting season backward at least another two weeks, and there were still flying young returning to their nest sites for feeding on 18 September 1958 (Gilbert Saunders, *in litt.*). It therefore appears that the nesting cycle for the colony as a whole runs for about 11 months, and that the cycle for each pair lasts at least six months.

At the time of my arrival, there were wide differences among the pairs in respect to progress in nesting activities. Some pairs were still building while others had young well advanced. This pattern seems to be the rule in colonies of this species throughout its range, a striking example being that cited by Richardson (1957) for French Frigate Shoal in the Hawaiian Archipelago where the only six nests on the island show a range in laying time of "at least three and a half months."

Though I personally never found evidence that the Red-footed Booby lays more than a single egg per clutch, some published accounts state that two are occasionally laid. Some species of boobies lay two eggs (though it is said that only one of the young birds reaches maturity), and perhaps this has led some observers to attribute the same habit to the Red-footed Booby without evidence. No definite record of two *fresh* eggs having been collected from the same nest has been found. Belcher and Smooker (1934) reported that nests on Giles Islet, Tobago, held a single egg each, but that "two appears elsewhere to be the usual clutch." They fail to mention where this is true or how they obtained the information. Kirby (1925), writing of *S. s. rubripes* on Fanning Island, reported: "As has been repeatedly observed regarding these birds, two eggs are laid, but only one young comes to maturity." Kirby also fails to give the source of his information. Bent (1922) and Baker (1929) also report two eggs laid by some individuals, but again no reason is given for arriving at such a conclusion.

In two instances on Half Moon Cay nests were found to contain two eggs, but one of the eggs in each nest was obviously very old while the other appeared fresh. In each case only the fresher egg remained long in the nest. I once observed a booby take a darkly stained egg from its nest into its bill, toss its head back twice, and throw the egg to the ground. The remains of the egg showed no evidence that it had ever begun to develop. It is possible that the birds possessing the nests with one fresh and one apparently infertile egg were able to recognize the bad egg and got rid of it in a similar manner. In addition to the two nests containing two eggs each, 204 nests containing a single egg each and 311 nests containing a single young each were examined.

Eggs of the Red-footed Booby vary in shape from very long ovate to short ovate and are covered with a white limy substance that conceals the light blue or bluish-green shell beneath. Most eggs that were examined had a variety of scratches through the limy coat. Apparently the material is soft when the egg is laid, and the adult booby's

nails scratch through it to the shell. However, it is not easily marred after the material has hardened. A hundred eggs (different ages) were weighed and measured, and the results are summarized in Table 2. One abnormally small egg measured 49.3 x 34.9 mm and weighed 27.0 g. It had very little chalky covering and possibly lacked a yolk. Consequently, it was not included in the table of maximum and minimum measurements, though it was used in determining the averages. The measurements compare favorably with published records (Macgillivray, 1918; Gifford, 1913; Bent, 1922; Belcher and Smooker, 1934; and Fisher, 1903).

TABLE 2
EGG MEASUREMENTS

	<i>Average</i>	<i>Greatest</i>	<i>Least</i>
Length (mm)	59.4	72.2 x 37.6	53.3 x 40.0
Width (mm)	39.8	58.4 x 48.7	61.9 x 36.7
Weight (g)	47.1	58.3	35.0

Sula sula will relay if its first egg is destroyed; however, what percentage of the birds do so I do not know. Pair 1 relaid 27 days, Pair 2, 28 days, and Pair 22, 25 days after the loss of their first eggs. As noted before, Pair 22 deserted their territory enough during the daytime that neighboring boobies removed their nest. However, Pairs 1 and 2 maintained guard on their nests, so that they did not need to rebuild for the second nesting attempt. Richardson and Fisher (1950) reported that storms early in 1948 at Moku Manu, Hawaii, "largely destroyed the eggs and young of this species, and renesting was little attempted even by the end of April." The fertility rate, as determined by tracing the natural fate of 86 eggs and examining all eggs that failed to hatch, was 90.7 per cent.

INCUBATION

Incubation, begun very shortly after laying, required 42.5 to 46 days and averaged 44.5 days for the 12 cases. One pair of boobies incubated an infertile egg for 63 days before finally ridding the nest of it. Since but a single egg is laid per clutch, and since it was found that incubation began within a few hours after laying, determination of the incubation period was simple. I inspected a nest each morning and each evening until an egg appeared and arbitrarily assigned the time of laying as midway in the interval during which the egg was laid. Time of hatching was similarly fixed.

Both sexes incubated, and neither developed a brood patch. At 1112 on 12 March, Female 22 laid an egg. I recorded her movements carefully until she finally began incubation at 1346, just two hours and 34 minutes later. She remained on the egg until after I left at dark, and the male was on the nest at 0500 the following morning. Table 3 summarizes my observations regarding the proportions of total time spent in incubation and attention to the young by males and females.

TABLE 3
TIME IN HOURS AND MINUTES (HOURS/MINUTES) OF ATTENDING THE NEST

	<i>Pre-egg</i>	<i>Incubation</i>	<i>Nestling</i>	<i>Totals</i>
Male 21		39/03	57/27	96/30
Male 22	12/42	47/03	3/03	63/15
Male 23		44/05	31/12	75/17
Male 29		44/47		44/47
Male T39			35/45	35/45
Totals	12/42	174/58	127/54	315/34

Female 21		35/53	33/03	68/56
Female 22	40/51	48/07	3/25	92/23
Female 23		12/32	42/50	55/22
Female 29		58/56		58/56
Female T39			57/12	57/12
Totals	40/51	155/28	136/30	332/49

Apparently the sexes equally share incubation and attendance of young. But the female is at the nest more before the egg is laid than the male. She remains by the nest to perform the construction while the male gathers nest materials; and she spends up to three consecutive days on the nest just prior to, during, and shortly after laying. Although Table 3 indicates that only one pair was studied during the pre-egg stage, periodic observations were made also on two other pairs during their pre-egg stage, and these observations tend to support the conclusions drawn from Pair 22.

Incubating birds frequently held the egg between their feet with the inner web of each foot stretched around the egg. That is to say, they actually *stood* on their egg with the inner web and toe of each foot so that the inner toes nearly met on the upper surface of the egg. At times the inner toe and web of only one foot was stretched up around the side of the egg. The birds also incubated with both feet fully on the nest and the egg nestled among the belly feathers between the legs. At irregular intervals birds stood up for a few minutes, continuing to shade the egg, and then settled once more to incubate.

During the heat of the day the incubating bird sat, panted, or slept—sometimes with its head hanging over the edge of the nest. The egg was turned infrequently with the bill. Time was passed in such seemingly pointless activities as biting at small branches and leaves near the nest or by picking at the nest. I found that males and females alike would catch sticks that I threw toward them, often nearly tumbling off the nest in an effort to get sticks thrown out of their reach. All of the sticks that they caught were added to the nest, and males often performed the stick-wave display with their catch. The stretching of the wings backward and of the head and neck forward and “yawning”—gape opened wide, head frequently shaken—were common activities of birds on the nest. In another activity, the booby opened and closed its mouth two or three times in succession and usually elevated the maxilla independently (the naso-frontal hinge permits enough movement of the maxilla to separate the tips of the bill fully two to three cm) while contracting and relaxing the muscles in the gular area.

Throughout incubation the members of a pair saw little of each other except when one returned from fishing to replace the other on the nest. Frequently, after the female relieved the male at the nest, he spent some time gathering nest materials and bringing them back for her to place. I never saw adults feed each other at the nest. Apparently they go without food while actually incubating. The nonincubating partner usually roosted away from the nest. In cases that I observed, the night roosts were from three to eight meters from the nests of the pairs involved, and each pair had but a single night roost, although one perch might serve as the night roost for more than one pair.

My data indicate that each bird usually incubated for about 24 hours without interruption. Occasionally, a bird was replaced after only about 12 hours of incubation, and apparently, some remained on the nest for 36 and 48 hours without relief. Two exchanges were noted at the same nest during the same day only seven times in 648 nest hours of observation. In five of those cases, the exchanges occurred about 12 hours apart; in one case about seven hours apart, and in the last instance only 17 minutes apart.

Nest exchange, which usually occurred in the late afternoon or early evening, was simple and without ceremony. One bird flew in from its day of fishing, and the sitting bird immediately stood up and shifted to the edge of the nest or to a perch. The returning bird quickly took over at the nest, and its mate flew off. On a very few occasions the returning bird had to crowd the other off the nest. Assuming that 100 exchanges had occurred in a 24-hour period, they would have occurred

at a rate of 6.9 per hour between 0500 and 0700, 1.1 per hour between 0700 and 1500, 2.8 per hour between 1500 and 1700, 16.7 per hour between 1700 and 1900, and 5.5 per hour between 1900 and 0500. Many of the last exchanges certainly took place after dark. The records included pairs still incubating and pairs attending young; the general temporal pattern of exchange seeming to be the same in both cases.

CARE OF YOUNG

For the first few weeks of the life of the nestling, the adults shared the duty of continuous guarding. It was necessary at that time to shield the nestling from the sun; however, the necessity of this became less and less as the young acquired its thick coat of snow-white down. After a young was three or four weeks old, its parents ordinarily left it alone for a part of the day. As the nestling grew older, the adults tended to leave it *earlier* in the day, until, by about the 10th week, it was commonly left unattended for as many as 12 successive hours. Although the adults exhibited a tendency to leave their young earlier and earlier in the day, they seemed to return at about the same time each evening.

Feeding was by regurgitation, a process in which the adult opened its mouth and the young introduced its bill into its parent's throat. Maynard (1889) wrote the following concerning this species on the Cayman Islands: "The newly hatched Gannets are fed at first by true regurgitation, that is the fish eaten by the parents is converted into a peculiar glairy fluid which is given to the young. The old birds introduce the terminal portion of the bill into the mouths of their offspring and the liquid is literally poured down their throats. Later the fish is given to the young in half digested fragments and in the same manner. . . ." Perhaps adults do introduce their bills into the mouths of their newly hatched young to feed them; however, that they continue to do so in the same manner is certainly not the case, at least in the population that I observed. I observed the feeding of nestlings as young as five days, but I never saw any adult introduce its bill into its offspring's mouth. In 206 recorded feedings it was invariably the young that put its bill into the adult's mouth. Usually the adult lowered its head enough to allow the young to reach far back into its throat. Out of the 35 occasions that the sexes were distinguished, females were noted feeding the young during five more periods than males.

Feeding of the young was almost entirely confined to the evening; occasionally, it occurred in the early morning, but apparently only rarely during midday. Usually the adults fed their young almost im-

mediately upon returning from a fishing excursion, and the main mass of the feeding flocks returned in the evening. I recorded 0.26 feedings per hour between 0500 and 0700, none between 0700 and 1500, 0.78 per hour between 1500 and 1700, and 3.04 per hour between 1700 and 1900. From dawn to dark on 26 April, I observed and recorded the activities of 13 pairs with young, and the first feeding noted that day occurred at 1748. Although midday feedings were not observed, they must have occurred. Two young birds were repeatedly weighed in the morning and evening; in 23 such pairs of weighings an increase in weight during the day was noted on three occasions.

There seemed to be only one feeding period per day, usually in the evening as noted above, for each young. There may be more in some cases, but this was never observed. The young were frequently fed several times and sometimes by both parents during one feeding period. Both adults fed their young during the same period only after the nestling was old enough to be left alone for part of the day, so that both could return to the nest from fishing at approximately the same time. In most cases the young was fed five or fewer times per feeding, although in an extreme case a female fed her offspring 16 times in 20 minutes. The young had been weighed just before the feedings so it was weighed again immediately after. The increase was 62.9 g, 31 per cent of the body weight (202.5 g).

"False feedings" were frequent and seemed to be an incomplete response on the part of an adult to the agitation of its hungry young. During false feedings, the adult did not lower its head; therefore the young could get its bill only to the back of its parent's mouth. The adults did not gulp after false feedings as they did after genuine feedings, since no food had been passed and nothing remained in the throat to be swallowed.

Young boobies continued to depend on the parents for food long after they were able fliers. One juvenal that had been flying for a month before I left the colony was still returning to the old nest site each evening to receive food from its parents. In one extreme case, a juvenal from the previous nesting season—certainly nearly a year old—was being fed by one member of a pair that had a nest directly behind the observation platform. The feeding was observed only once, but I suspected it had occurred several times before that. The juvenal flew in to land beside the old bird's nest nearly every evening, and even after their nest was broken up and the adults deserted the territory the juvenal continued to return. It was after the loss of the nest that the feeding was noted; thus the adult involved had to return to the original

territory. It did so just long enough to feed the younger bird. How long young must depend on the adults for food was not determined.

DEVELOPMENT AND ACTIVITIES OF YOUNG

Pipping of the egg occurred up to a full day before hatching. Every hatched egg that I examined had the blunt end removed as a cap. Apparently, the adults simply dropped the pieces of the shell over the side of the nest. Newly hatched birds had pinkish flesh-colored skin with a dark gray or bluish-black area on the dorsum over the synsacrum. The eyelids and face were dark gray to grayish-brown. The bill was blackish-brown, and the feet and legs were flesh-colored. The eyelids were closed, though slit for about three millimeters, and the irides were pearly gray. All feather tracts had ensheathed down. That on the back and on the alar and caudal tracts was not over two millimeters long, and the remainder was not over one millimeter long.

The color of the skin darkened gradually to gray, and by the time the young was eight days old only the neck was still slightly flesh-colored. Also by the eighth day most of the down had "bloomed" from the sheaths, and the young appeared *sparsely* down-covered. However, the birds were about two weeks old before they had enough down to give them any protection, and even then many areas were still virtually naked. My notes on the plumage on one 18-day-old booby read "completely down-covered, though only sparsely on the throat and behind the eyes."

When a young was hungry it went through a regular routine of display before the adult that began with an incessant series of short notes that sounded like *awp*, *awp*, *awp*, *awp*. The young bird doubled its neck up and held it back so its chin rested on its neck. In that position it rocked its head from side to side while *awp*-ing and occasionally flailing its wings out to either side. Finally it began to jab at the pink base of the adult's bill in a similar action to that of young gulls. The adult booby responded either by turning its head away or by opening its mouth and feeding the young. Sometimes a nestling simply *awp*-ed and jabbed at the adult's bill, and sometimes the adult fed the young without any prompting. Young boobies that I fed for several days performed precisely the same feeding display before me as soon as they saw I was walking toward them.

When they were awake, nestlings sat on the nest and panted, fought with small branches and leaves by the nest, or flopped their wings around and bit at their own wrists. They would catch sticks thrown to them or try to take the sticks the male brought in to be added to the

nest. They also jabbed and bit at the wings and tails of their parents. When they slept they either curled up on one side, laid on their stomach with their wings and neck stretched out to hang where they might, or placed their feet slightly apart on the nest and leaned forward to come to rest on top of their head with their bill directed backward toward their belly, thus forming a nice tripod!

Young began exercising their wings long before they could fly. Their first attempts at flight were mainly extended hops on outstretched wings, and they usually strayed far from the home territory during such trials, frequently passing through other territories and being beaten away by attending adults or young. They became fully capable of flight before they lost all their down, and some were seen flying around with down still clinging to the sides of the neck and the top of the head. Down persisted longest on the forehead, and the brown juvenals carried this mark of their age for several days after they were capable fliers.

My notes on the development of young Red-footed Boobies are incomplete, since the period required to attain juvenal plumage is greater than the 12 weeks that I was in the colony. In fact 14 of the 221 nests traced throughout the study had young on the nest when I arrived that still were not through the postnatal molt and could not fly when I left. Through the cooperation of Gilbert Saunders (*in litt.*) I obtained information on eight nests from the time of laying until the young were fledged. Three required 13 weeks, four took close to 15 weeks, and one took 16 weeks from the time of hatching to the time of fledging. The first three hatched the last five days of April, the others during the first 13 days of April, indicating that the young may develop more rapidly if they hatch near the end of the nesting season.

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SUMMARY

The nesting activities of a colony of Red-footed Boobies in British Honduras were studied for three months.

The "four-point," "stick-wave," and "stick-shake" displays appear to have a role in formation and maintenance of the monogamous pair bond, which is probably sustained or life long.

Apparently, the male selects the small territory, which is used for nesting, copulation, and sometimes roosting. The stick-wave may play a part in territorial selection. Territorial defense is by threat display, principally the one-point, or physical contact. Nestless pairs maintain territories for at least two months.

Apparently the female initiates nest construction, after which the male gathers all materials while the female places them in the nest. Nests are added to even after the egg hatches, and the lining is changed during incubation. Nest materials are taken from vacant nests, from trees, and occasionally from the ground. Nests were placed in trees where the birds have access to wind currents; their height appears to depend on the height of available vegetation.

Copulation was noted only on the territory and occurs most often in the evening. It is preceded by little or no ceremony and occurs as much as eight days in advance of laying and as frequently as seven times on the day prior to laying. It is continued for a short period after laying. One nestless pair copulated regularly for at least a month.

Laying begins in mid-November and extends to mid-April; there is a single egg per clutch. Relaying occurred. Fertility rate was 90.7 per cent.

Incubation begins shortly after laying and is shared about equally by the sexes. The mean incubation period was 44.5 days. Exchange usually occurs in the evening; the incubating bird usually sits for 24 hours without relief or food.

Adults shield the young for a time, but after they are three to four weeks old they are left alone for part of the day. They are fed by regurgitation by both adults during a single feeding period per day, usually in the evening.

The young at hatching are helpless, with pinkish flesh-colored skin and ensheathed down on all tracts. Development is slow, and the young continue to depend on adults for food long after they are able to fly. One bird nearly a year old was seen receiving food from a nesting adult. Shortly before they can fly, most young dismantle their nest and spend the remainder of their "nestling" period on a perch.

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