WILLIAM Y. BROWN

Manana or Rabbit Island is a 0.25 km^2 volcanic tuff cone situated about 1.3 km off Oahu, Hawaii (Tomich et al. 1968). The island rises to 110 m on the southeast, and contains a central crater vegetated primarily with grasses, wild tobacco, and scattered palms. A remnant of a second crater forms a bench on the windward side of the island, and a sandy beach fringes the leeward side of the island (fig. 1).

Four species of sea birds regularly breed on Manana at present: Sooty Tern (Sterna fuscata), Brown Noddy (Anous stolidus), Wedge-tailed Shearwater (Puffinus pacificus), and Bulwer's Petrel (Bulweria bulwerii) (Bryan 1935, Richardson and Fisher 1950, Tomich et al. 1968).

I know of no first-hand reports on the Manana sea birds before 1934. Munro (1940) was told by an Hawaiian living on Oahu near Manana that few if any sea birds were on Manana about 1900. On 25 August 1934, Bryan (1935) found "thousands" of Noddies with eggs and young on Manana, but no Sooty Terns. Hatch (1940) reported eggs and young of Noddies on Manana, 17 August 1940. The island was bombed and strafed during World War II (Green 1942) but the effect on the sea birds is not known. Since 1945 the islet has been a territorial and state bird sanctuary. Richardson and Fisher (1950) visited Manana 14 times between October 1946 and August 1948. They reported that in 1947 "several hundred adult Sooty Terns were present, apparently only five to ten eggs were laid and perhaps less than five young raised. In 1948, probably between 150 and 200 eggs were laid." Richardson and Fisher reported that the Sooty Terns laid eggs in April and May. They estimated a maximum of 7,000 Noddies on Manana during the study and reported that the Noddies laid eggs in March, April, and May. Thirty-five percent of the Noddies had laid eggs by the end of March in 1947. Dingus (1949) reported Noddy and Sooty Tern eggs and young on Manana, 4 July 1949, and observed that the Noddies still out-numbered the Sooty Terns. Hatch (1950) reported three to four times as many Sooty Terns as Noddies on Manana, 4 July 1950. Richardson and Hatch (1954) estimated by

counts in known areas 7,620 Noddy eggs and 16,010 Sooty Tern eggs on Manana, 30 May 1954. Only a few chicks (unidentified species) had hatched. Hatch (1956) reported 10,085 Noddies on Manana, 30 May 1956 that "apparently had not yet laid." Hatch estimated 16,878 Sooty Tern eggs on Manana the same day. N. P. Ashmole (pers. comm.) visited Manana on 30 March 1963 and found many Sooty Tern eggs but no chicks. When he returned to the island on 7 April, he found Sooty Tern chicks, and a member of his party (M. Ord) reported Noddy eggs. On a third visit to the island on 19 May, Ashmole found several hundred Noddy eggs and a few chicks. Whitten (1963) reported eggs and young of the Noddy on Manana, 8 September 1963. Donaghho (1965) reported that on 27 July 1965, Sooty Terns were "all over the place" and had both eggs and young. Donaghho cited Kridler, who was with him, as finding a ratio of 300 Noddies with eggs to nine with chicks, and as estimating that 200,000 Sooty Terns and 40,000 Noddies were on Manana. Ord (1966) reported that on 28 August 1966, all the Sooty Terns had left Manana, whereas there were eggs and young of the Noddy. Shallenberger (1970) reported most Sooty Terns laid in April and most Noddies laid in June of 1969, although he found one Noddy incubating an egg on 25 April.

METHODS AND MATERIALS

I lived on Manana from June through August 1971 and from March through August 1972. In addition, I visited the island twice weekly from March through June 1971 and at least once monthly over the winter of 1971–1972. This allowed me to follow the activities of the Sooty Terns and Noddies on Manana as no previous author had been able; for that reason I am presenting a calendar of these activities.

In 1971, I delimited 17 areas on Manana, then counted and marked the Noddy eggs in each section. The count was made when the Noddy chicks first began to hatch, after about 75% of the Noddies on the island had laid. In 1972, I marked on aerial photographs the laying distributions of the Sooty Terns and Noddies on Manana. I estimated the total number and varying densities of Sooty Tern eggs by sampling the densities of eggs within the different sub-colonies on the island, then multiplying area by density and summing the results for each sub-colony. I estimated the densities of Noddy egg distribution in 1971 by combining the counts of eggs in different areas in 1972 with the distribution of eggs mapped



FIGURE 1. Aerial photograph of Manana or Rabbit Island.

in 1972. This was reasonable because the distribution of Noddy laying was similar in both years.

In addition, I periodically counted and marked all new eggs laid in certain squares 37.2 m^2 in area. I sampled two of these squares within the laying areas of the Sooty Tern; one square on the northeastern rim of the crater and one on the sandy western slope of the island. The seasonal distributions of laying were similar in both quadrats, and because I did not sample the quadrats on the same days and cannot plot the results together simply, I am presenting only the information from the sandy quadrat. Within the Noddy laying areas, I sampled four quadrats distributed around the inside and outside rocky slopes of the crater. I sampled all four quadrats on the same days, and present the data from all four.

RESULTS

THE LAYING SEASON

The results of periodic sampling of Sooty Tern and Brown Noddy egg-laying on Manana in 1971 and 1972 are presented in figure 2. In both years the Sooty Terns began to lay before the Noddies although the difference was less in 1972.

THE NUMBER OF EGGS

Between 18 and 22 June 1971 I counted and marked 12,111 Noddy eggs on Manana. I counted an additional 1,200 incubating adults in inaccessible areas, for a total of at least 13,300 Noddy eggs on 22 June. Approximately three-fourths of the Noddies had laid by then; therefore about 17,500 eggs were laid during the season. Allowing that some of these may have been replacement eggs, a conservative estimate for 1971 is 15,000 breeding pairs or 30,000 breeding adult Noddies.

I estimated 50,000 Sooty Tern eggs on Manana the last week in May 1972. Most of the Sooty Terns had laid, and 50,000 pairs or 100,000 adults may be taken as a conservative estimate of the number of Sooty Terns breeding on Manana in 1972.

LAYING AREAS AND DENSITIES

Laying areas and densities within those areas are represented in figures 3 and 4 for the Sooty Tern and Brown Noddy, respectively, on Manana. High grasses excluded nesting of either species from the central crater and parts of the western slope of the island in 1972. Sooty Terns nested extensively in these areas in 1973 when, following a dry winter, the grass was much shorter than in 1972.

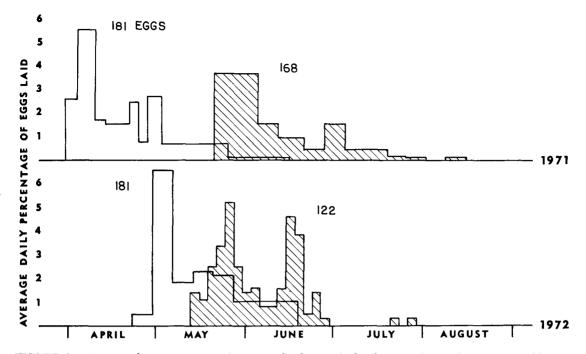


FIGURE 2. Tern egg-laying season on Manana Island. Hatched columns refer to the Brown Noddy and unhatched refer to the Sooty Tern. Based on counts of eggs laid in defined areas. The eggs were marked so as not to be recounted; the same areas were used in 1971 and in 1972. The widths of columns of the histograms indicate the time between counts; the heights of the columns indicate the percentage of eggs laid during the interval divided by the number of days of the interval (average daily percentage).

The Noddies laid only on rocky substrate, excepting a very few nests on tussocks of grass. Nesting areas included all but the steepest portions of the crater slopes and some parts of the crater rim densely colonized by Sooty Terns. The Sooty Terns nested on the crater rim and on the gentler slopes of the crater; their nest substrates included rock, dirt and sand. The greatest density of Sooty Terns occurred on partially consolidated sandy substrate just above the loose beach sand on the western side of the island. In this area the nesting density of Sooty Terns was twice as great as that of Noddies anywhere on the island.

A CALENDAR OF EVENTS

 20 Feb. No terns were on the island in the day, and the crater slopes were not stained with guano. 27 Feb. The inner north slope of the crater was stained with guano, indicating that many terns had begun roosting on Manana since 20 Feb. No terns were on the island during the day, but Noddies began landing in the guano-stained area after dark, and at least 2,000 were present at midnight. Many Sooty Terns were flocking in the air west of Manana during the 20 Feb. No terns were flocking in the air west of Manana during the 20 Feb. No terns were flocking in the air west of Manana during the 20 Feb. No terns were flocking in the air west of Manana during the 20 Feb. No terns were flocking in the air west of Manana during the 20 March 30 March 30	1971		27 March	I counted 98 Sooty Tern eggs in the
 27 Feb. The inner north slope of the crater was stained with guano, indicating that many terns had begun roosting on Manana since 20 Feb. No terns were on the island during the day, but Noddies began landing in the guano-stained area after dark, and at least 2,000 were present at midnight. Many Sooty Terns were flocking in the air west of Manana during the 27 Feb. The inner north slope of the crater scope on Oahu and found no terns on the ground on the outer western slope of the island, including the beach area. Sooty Terns and Noddies were on Manana when I arrived in the after-noon. The Sooty Terns had laid hundreds of eggs both in the beach colory and completely around the crater rim. Noddies were scattered around 	20 Feb.			beach colony, but neither species of tern was on Manana during the day.
was stained with guano, indicating that many terns had begun roosting on Manana since 20 Feb. No terns were on the island during the day, but Noddies began landing in the guano-stained area after dark, and at least 2,000 were present at midnight. Many Sooty Terns were flocking in the air west of Manana during the		stained with guano.	30 March	I looked at Manana through a tele-
atternoon and evening, but none the crater rin among the sooty Terns.	27 Feb.	was stained with guano, indicating that many terns had begun roosting on Manana since 20 Feb. No terns were on the island during the day, but Noddies began landing in the guano-stained area after dark, and at least 2,000 were present at midnight. Many Sooty Terns were flocking in	31 March	scope on Oahu and found no terns on the ground on the outer western slope of the island, including the beach area. Sooty Terns and Noddies were on Manana when I arrived in the after- noon. The Sooty Terns had laid hun- dreds of eggs both in the beach col- ony and completely around the crater rim. Noddies were scattered around the crater rim among the Sooty Terns.

landed on the island. No terns were on Manana or visible offshore at 08:00 28 Feb.

- 5 March Noddies roosted on the island as previously. At least 500 Sooty Terns landed just above the beach on the west side of the island at 21:30. They left the island before sunrise.
- 16–17 March Noddies and Sooty Terns continued to land on Manana after dark and to leave before sunrise. The Sooty Terns flew closer to the island in the afternoon than on 5 March, and many were flying in pairs.
- 20 March I found about 30 Sooty Tern eggs in the beach colony when I arrived on Manana in the afternoon, but no Sooty Terns were on the island. Many thousands of Sooty Terns were visible offshore, and both Sooty Terns and Noddies landed at night as previously.

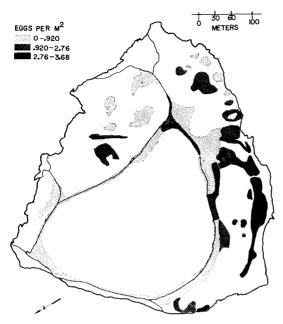


FIGURE 3. The distribution and the densities of Sooty Tern eggs on Manana Island, Hawaii in 1972.

29	April	The first Sooty Tern chicks hatched (none had hatched on 28 April). I found one chick in the beach colony	numbers
18	May	and one on the west rim of the crater. The first Noddy eggs were laid be- tween 15 May and 18 May. I counted	11 Dec.
		57 Noddy eggs on the inner north and	28–29 I
т	June	east slopes of the crater on 19 May. I began to live on Manana full-time.	
	June	I first found a fledged Sooty Tern	
τ,	June	chick.	
20	June	The first Noddy chicks hatched.	1972
	July	The last day I found a freshly hatched	23 Jan.
_	55	Sooty Tern chick.	20 Juni
1	August	Nearly all the Sooty Tern chicks were fledged.	
3	August	I first found a fledged Noddy chick.	
17	August	I ceased living on Manana full-time.	12 Feb.
30	August	Fifty adult and 50 juvenile Sooty	
		Terns remained on Manana, most of	20 Feb.
_	~	them in the beach colony.	
2	Sept.	All the adult Sooty Terns were gone,	21 Feb.
		and just a few starving juveniles were	
10	Comt	left on the beach.	00 12 1
10	Sept.	The last day I found a freshly hatched Noddy chick.	23 Feb.
18	Sept.	All the Noddy chicks were fledged.	
	-3 Oct.	The number of Noddies on Manana in	
~	0 000.	the day was much less than on 18	27 Feb.
		Sept.	21 100.
23	Oct.	About 1,350 Noddies were on the is-	
		land in the day, and nearly all were	
		juveniles.	5–6 M
6	Nov.	About 575 Noddy juveniles were on	
		Manana in the day.	
14	Nov.	About 205 juvenile Noddies were on	
		Manana in the day. At least 4,000	
		Noddies landed on the island after	
07	NT	dark, and nearly all were adult.	
27	Nov.	Twenty juvenile Noddies and one	
		adult were on Manana at 16:00. Sev- eral thousand adults landed after	10 Mar
		dark.	10 Marc
		uain,	

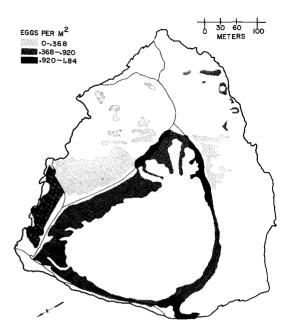


FIGURE 4. The distribution and the densities of Brown Noddy eggs on Manana Island, Hawaii. Based upon an egg count in 1971, and mapping of the Noddy laying areas in 1972. The distribution and numbers of birds in the two years appeared similar.

- 11 Dec. No Noddies were on Manana in the day, but thousands of adults and a few juveniles landed after dark. 28-29 Dec. About 4,000 adult Noddies landed
 - after dark, but I found no juveniles. I heard a few Sooty Terns calling from the sky over the island.
- 1972
- About 600 adult Noddies landed on the inner slopes of the crater after dark, and thousands of Sooty Terns were in the air to the south and west of the island.
- 12 Feb. About 10 adult Noddies roosted on Manana.
- 20 Feb. Only three roosting Noddies could be found.
 - More than 1,000 Sooty Terns landed in the beach colony at night; none had landed on 20 February.
 - I found six adult Noddies roosting on Manana, and several thousand Sooty Terns had landed in the beach colony at 23:00.
 - Sooty Terns were visible to the west of Manana at 17:00, although none landed that night. I found five Noddies roosting on the island. Thousands of Sooty Terns were vis-
- 5-6 March ible west of Manana at 18:30. One pair performed a "high flight" (Dinsmore 1971). Several hundred Sooty Terns landed on the western rim of the crater after dark, and at least 5,000 Sooty Terns landed in the beach colony. About 1,200 Noddies roosted on the inner slopes of the crater. 10 March I began to live again on Manana full
 - time.

- Only a few hundred Sooty Terns 19 March landed on Manana at night. The number had decreased steadily since 14 March.
- 28 March The number of Sooty Terns landing at night had increased gradually since 19 March. Five hundred to 1,000 Sooty Terns in the beach colony stayed until 06:20 (well after first light), when the entire flock suddenly flew out to sea.
- Thousands of Sooty Terns were flying 2 April about Manana-probably the most yet in 1972-and thousands landed at night. Over 1,000 Noddies roosted on the island as previously.
- 3 April No Sooty Terns landed at night, and I saw few offshore during the day.
- Sooty Terns landed at night for the 6 April first time since 2 April.
- No Sooty Terns landed on Manana. Thousands of Sooty Terns landed in 12 April the beach colony after dark.
- Thousands of Sooty Terns had been 14 April on Manana in the beach colony during the night, but all were gone by Hundreds suddenly began 07:30. landing on the west rim of the crater between 09:00 and 09:15. Noddies were scattered among them. The Sooty Terns gradually spread around about one-eighth of the crater rim.
- Hundreds of Sooty Terns had laid, and hundreds of Noddies spent the 15 April day on the crater slopes.
- 16 April Several Noddies flew in pairs, and one pair performed a "butterfly flight" (Moynihan 1962).
- Many Sooty Terns on the west rim of the crater had deserted their eggs. 17 April The Sooty Terns had laid around most of the crater rim and in the grass above the beach colony, but most of the sandy area where the Sooty Terns had laid most densely in 1971 was still unoccupied.
- 27 April Less than one-fourth of the number of Sooty Terns on the island this date last year were present.
- 30 April More Sooty Terns were arriving each day, and the number and distribution of Sooty Terns was approaching that of 1971.
- Thousands of Noddies were present on 2 May the crater slopes during the day.
- The first Noddy eggs were laid on the 8 May inner slopes of the crater.
- The first Sooty Tern chick hatched. 14 May
- The first Noddy chick hatched. 14 June
- I first found a fledged Sooty Tern 7 July chick.
- 9 July The last day I found a freshly hatched Sooty Tern chick.
- I ceased living on Manana full-time. 20 August The last day I found a freshly hatched 22 August Noddy chick. None could have hatched more than a few days later. Nearly all the Sooty Terns had left 31 August
- Manana. 16 Sept. Two adult and 43 juvenile Sooty Terns were on Manana, and nearly all the Noddy chicks were fledged.

6 Oct. 13 Oct.

- 20 Oct.
- the day, mostly juveniles. No Sooty Terns were left on Manana. About 850 Noddies were on the island in the day, mostly juveniles. Thousands of adults and many juveniles landed on Manana at night.

Terns were on Manana.

Two adult and 14 juvenile Sooty

One juvenile, but no adult Sooty

Terns were on Manana, and about

1,500 Noddies were inside the rim in

DISCUSSION

The changes in the number of the Manana terns are striking, but analysis of these changes is difficult. The Sooty Tern population has increased from few or no birds before World War II to about 100,000 breeding adults in 1972. The old Hawaiians ate both sea birds and their eggs, and Richardson and Fisher (1950) suggested that the Hawaiians may have exterminated the sea birds on Manana prior to 1900. Sooty Tern eggs are considered a delicacy on many tropical islands. (Ridley and Percy 1958). It apparently is not coincidental that the Sooty Terns colonized Manana shortly after the island was made a sanctuary in 1945. The meteoric increase in the number of Sooty Terns on Manana since the war can be explained only by a high rate of immigration from other colonies. The only Sooty Tern colony in the main Hawaiian islands besides Manana is on the small islet of Moku Manu, about 17 km from Manana. Some of the Sooty Terns on Manana may have come from Moku Manu, but because Richardson and Fisher (1950) estimated a maximum of only 15,000 Sooty Terns on Moku Manu in 1947, it appears unlikely that most of the Sooty Terns colonizing Manana could have come from Moku Manu. However, the Sooty Terns on Moku Manu may have been disturbed by shelling during World War II, and the Sooty Tern population Richardson and Fisher found there may have been atypical. This conjecture is supported because Richardson and Fisher found Sooty Terns beginning to lay on Moku Manu in November of 1947 and 1948, although later observers have found only a spring laying season (Richardson 1957, Ord 1964). Whatever the relative importance of Moku Manu as a source of Sooty Terns for Manana, it is likely that some of the Sooty Terns came from more distant colonies, and the number of Sooty Terns in the waters around Oahu may have increased considerably since World War II.

The Brown Noddies on Manana have increased from about 7,000 in 1947 and 1948

- 7-11 April

to about 30,000 in 1971. It is likely that this increase has occurred at least partially because the island was made a sanctuary in 1945, but the relative contributions of colonization and reproduction are unknown.

SUMMARY

About 100,000 Sooty Terns and 30,000 Brown Noddies bred on Manana Island, Hawaii in 1971 and 1972. The Sooty Terns have colonized Manana since World War II, and the Noddies have increased several-fold in number since that time. Maps showing the densities and distributions of the eggs of each species in 1972 are presented, and a calendar of the major breeding events of the terns in 1971 and 1972 is provided.

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LITERATURE CITED

- BRYAN, E. H., JR. 1935. Insects from Rabbit Island. Proc. Hawaii Entomol. Soc. 9:39-43.
- DINGUS, R. 1949. Nesting notes from Manana Island. Elepaio 10:16-17.

- DINSMORE, J. J. 1972. Sooty Tern behavior. Bull. Florida State Mus., Biol. Sci. 16:129–179. Donachho, W. 1965. Rabbit Island. Elepaio 26:
- 23.
- GREEN, T. H. 1942. Destruction of bird life on Rabbit Island. Elepaio 3:16–17. Натсн, G. 1940. The Audubon Society has a
- night out. Elepaio 1:30-32.
- HATCH, G. 1950. Manana Island. Elepaio 11:17-18.
- HATCH, G. 1956. Census of the terns on Manana or Rabbit Island. Elepaio 17:25-26.
- MOYNIHAN, M. 1962. Hostile and sexual behavior patterns of South American and Pacific Laridae. Behav. Suppl. 8:1-365.
- MUNRO, G. C. 1940. The Wedge-tailed Shear-water. Elepaio 1:40-43.
- ORD, W. M. 1964. Nesting status of sea birds on Moku Manu. Elepaio 24:49-50.
- ORD, W. M. 1966. Field trip to Rabbit Island. Elepaio 27:34.
- RICHARDSON, F. 1957. The breeding cycles of Hawaiian sea birds. Bull. Bishop Mus., Honolulu 218:1-41.
- RICHARDSON, F., AND H. I. FISHER. 1950. Birds of Moku Manu and Manana Islands off Oahu, Hawaii. Auk 67:285-306.
- RICHARDSON, F., AND G. HATCH. 1954. Census of the terns on Manana or Rabbit Island, May 30,
- 1954. Elepaio 15:7–8. RIDLEY, M. W., AND R. PERCY. 1958. The exploitation of sea birds in Seychelles. Colon. Res. Stud. 25:1-78.
- SHALLENBERGER, R. 1970. Manana field notes: April-August 1969. Elepaio 30:61-64.
- TOMICH, P. Q., N. WILSON, AND C. H. LAMOUREUX. 1968. Ecological factors on Manana Island, Hawaii. Pac. Sci. 22:352-368.
- WHITTEN, H. 1963. Field trip to Manana Island. Elepaio 24:24.

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