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BIRDS OF MOKU MANU AND MANANA ISLANDS OFF OAHU, HAWAII

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THERE are some 17 small islands, all but one within a mile of shore, along the windward or east coast of Oahu, T. H. (Lat. 19–22° N.). Although most of these islands serve as breeding grounds for at least

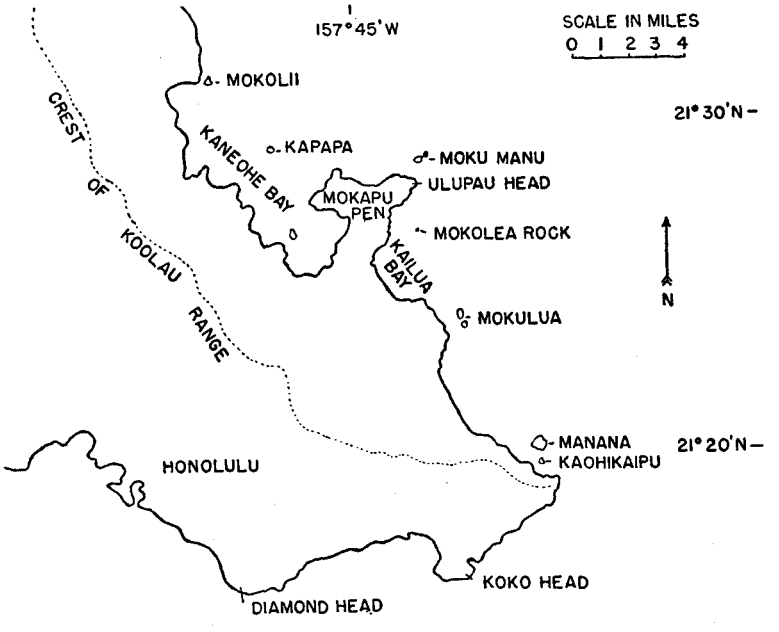
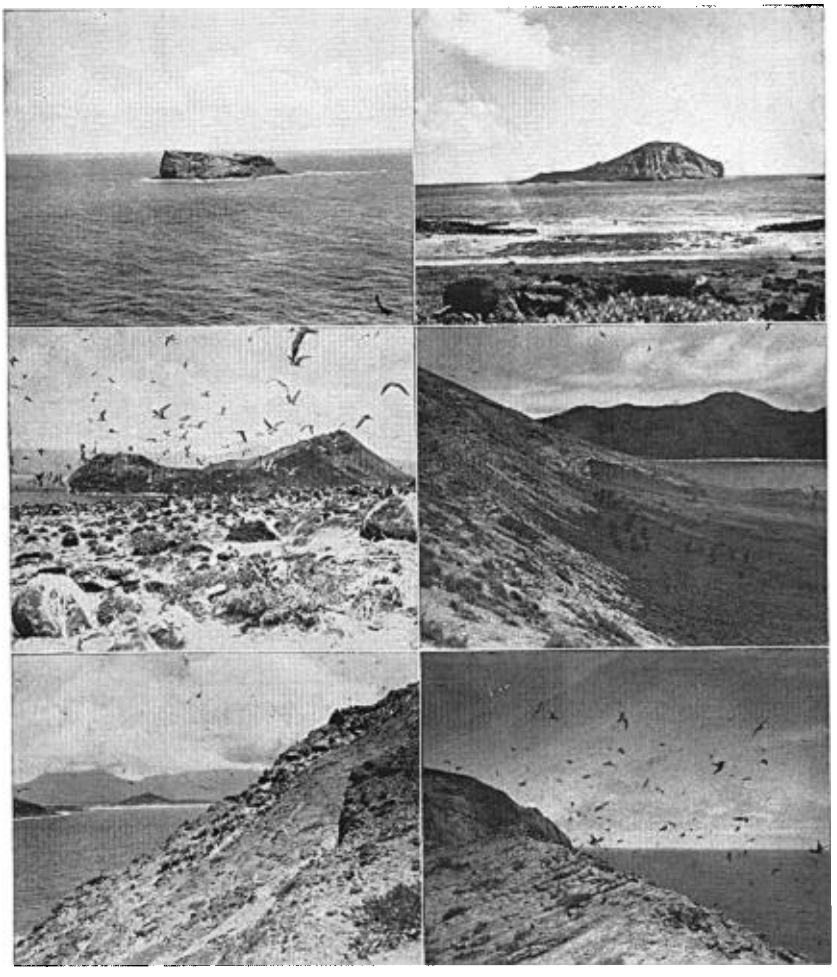


FIGURE 1.—Southeast part of Oahu, Hawaiian Islands, showing the location of the principal offshore islands.

11 species of sea birds, Moku Manu and Manana islands (Fig. 1) are the principal islands as far as variety and number of breeding birds are concerned. Manana, or Rabbit Island as it is frequently called,



(*Top, left*) MOKU MANU. PICTURE TAKEN FROM ULUPAU HEAD, OAHU. (*Top, right*) WEST SIDE OF MANANA ISLAND, OFF OAHU. (*Middle, left*) BREEDING AREA OF SOOTY TERNS ON MOKU MANU; ULUPAU HEAD IN NEAR BACKGROUND AND KOOLAU RANGE IN DISTANCE. (*Middle, right*) INSIDE OF WEST CRATER OF MANANA ISLAND; KOOLAU RANGE IN BACKGROUND. (*Bottom, left*) SOUTH SLOPE OF MOKU MANU, SHOWING EROSION POCKETS. (*Bottom, right*) CREST SEPARATING EAST AND WEST CRATERS OF MANANA ISLAND.

is the largest, being some 65 acres in area, while Moku Manu is less than a third as large. Both of these islands are among those set aside (since 1945) by the Territorial Division of Fish and Game as bird sanctuaries with no landing permitted. During the war, Manana was used as a bombing and strafing target at various times; Moku Manu was "buzzed" by naval aviators from nearby Kaneohe Air Station. The effect of these activities on the birds is unrecorded but apparently has not been lasting.

Surprisingly, the avifauna of these two islands was barely known until 1937, and has been little studied since then. Moreover, it was felt that a comparison of the birds of Moku Manu and Manana islands would be of particular interest because different islands attract different species of birds, although they have much in common as regards topography and climate. Furthermore, it was early recognized by Fisher that certain colonies of the same species of breeding birds had markedly different breeding seasons on the two islands. It was to analyze these conditions and suggested problems, and to study aspects of the natural history of all avian species present, that the authors undertook a series of trips to the islands from October, 1946, to August, 1948. During that time 14 trips were made to each island, a total of 28 trips; also, numerous trips to other islets were made for comparative data. Mr. Paul Breese made many additional trips to Manana, and data from his notes have been of much value. Mr. George Munro has given valuable information from trips as early as 1937—apparently the earliest accurate data on the ornithology of these two offshore islets. The University of Hawaii has aided this study, especially in affording the use of its boat and pilot and in making research funds available. The cooperation of the Territorial Division of Fish and Game is also acknowledged.

Physical Features.—Moku Manu is separated from precipitous Ulupau Head of Mokapu Peninsula by a deep channel three-fourths of a mile wide. The island is actually of two parts; the main western one is about 18 acres in extent and the smaller outer part is about three acres. Access from the larger to the smaller island is possible over rocks during unusually quiet weather, but even then only to the base of overhanging cliffs. The great cliffs of Moku Manu drop directly into the sea around more than half of the island. A shelving shore of loose boulders extends along some 200 yards on the south (Plate 8, *top*). A low wave-cut bench, up to 200 feet in width, extends around the western end.

Moku Manu is a remnant of a much eroded volcanic cone and is made up of tuff, basalt, and cinders. It has a relatively flat top,

(Plate 8, *middle*) averaging about 165 feet in height but running up to 202 feet. Over half of this upper surface is of shallow sandy soil interspersed with loose rocks. The best and most extensive region of soil and vegetation covers several acres on the fairly gradual south slopes of the island.

Manana is 10.5 miles south and somewhat east of Moku Manu and near the southeast tip of Oahu. It also is three-fourths of a mile offshore but is much larger. It is roughly circular in outline and has a variety of types of shorelines (Plate 8). High cliffs drop into the sea along the north shore. A wave-cut bench extends below the cliffs on the south, east, and northeast sides. Part of the south shore is sandy beach with rocky points and shelves at the sides.

Manana Island is made up of the remnants of two adjoining tuff cones. Less than half of the seaward crater remains, and the surf washes over its old floor. The western cone and its crater (Plate 8, *middle*) make up most of the island. This crater has a complete rim which is highest (almost 200 feet) on the east (Plate 8, *bottom*) where it runs south toward the island's major peak of 361 feet. The floor of the crater is rather flat and extensive and is about 80 feet above sea level. It has soil up to the points where the rim becomes steep and rocky. A large, gently sloping area also covered with soil lies below and outside the crater rim on the southwest.

Climate.—Meteorological data for the islands are not available. Neither island has any surface water. The islands are dry most of the year but are subject to occasional heavy rains, especially during the winter. In one January storm, 25 inches of rain fell in 24 hours at nearby Kaneohe Bay. Such rains may assume flood proportions, for large deposits of alluvium have been found on the shores of both islands. Manana has erosion gullies up to 10 feet in depth, although they are not numerous (Plate 8, *top*). The top of Moku Manu is washed during heavy rains by actual sheets of water which have been known to wash away thousands of eggs (Richardson, 1948: 53). Moku Manu appears to receive decidedly less rain than Manana. This is to be expected, as Moku Manu is farther from the main Koolau Range on the east side of Oahu (Fig. 1), which forces air masses upward and brings about precipitation.

Both islands are completely exposed to any northerly or easterly winds. The walls of the crater on Manana afford considerable protection, however, and the outer, south, and west slopes do not receive the worst of the wind. In contrast, the major breeding area on Moku Manu is on the top which is exposed to the full force of winds. Most booby nests, rather large platforms of twigs, completely disappeared

after a heavy wind and rain storm (Richardson, *loc. cit.*), and almost no species were able to stay on their nests. Noddy Terns have been observed to stay on their eggs on Manana even when the eggs became half buried in silt. On Moku Manu, wind and rain sometimes combine to make this impossible.

History.—Moku Manu is perhaps the least accessible to humans of any of Oahu's offshore islands. This fact seems to explain to an important degree the breeding of several species there that do not nest on any other of Oahu's offshore islands. Landing on Moku Manu almost always necessitates swimming onto the wave-cut bench, and not infrequently even this is impossible. As a result, the island is rarely visited by unauthorized persons and not often by others. It seems true that during the last century or more, when the bird populations of more accessible offshore islands were depleted by man, and domestic plants and mammals sometimes introduced, Moku Manu remained relatively free from such influences. The much longer canoe trip (there are no beaches near the head of Mokapu Peninsula opposite Moku Manu), the rough channel, and the uncertainty of being able to get on the island must have combined to keep even the old Hawaiians away much of the time.

TABLE 1

PLANT SPECIES ON MOKU MANU AND MANANA ISLANDS

Moku Manu	*Manana*
Sporobolus virginicus—a grass	*Portulaca oleracea*—Portulaca
Sesuvium portulacastrum	*Atriplex semibaccata*—Australian saltbush
**Lycium sandvicense*	*Trichachne insularis*—sour grass
**Chenopodium oahuense*	*Chloris inflata*—chloris grass
Portulaca oleracea	*Cenchrus echinatus*—burgrass
Sida cordifolia	*Cocos nucifera*—coconut tree
Atriplex semibaccata—Australian saltbush	*Nicotiana* sp.—tobacco
Tribulus terrestris—puncture vine	

* Native species.

Manana, in contrast, can usually be approached and landed on without much difficulty. When a small boat cannot land on the beaches, a person can usually jump onto the rocks from a skillfully handled boat or can swim ashore. Protected beaches are opposite the island on Oahu and the rather shallow channel between is rarely very rough. Consequently, Manana has been frequently visited by man for centuries. Even now, although landing is prohibited, unauthorized people occasionally disembark. Munro (1940: 43) cites probably good authority that few or no sea birds were on Manana at about the turn of the century. The Hawaiians may well have killed off the birds for food before this time. The more recent reappearance

and increase in numbers and species of the birds may reflect the disappearance of many of the old Hawaiians and their customs, and the protection of the birds.

Plants.—The species of plants identified from the islands are indicated in Table 1. The list may not be complete for either island but includes at least the predominant types. It will be noted that the islands have at least two species in common (of *Atriplex* and *Portulaca*) but are otherwise quite different in their vegetation. Perhaps a significant difference with regard to nesting sea birds is the lack of substantial woody shrubs on Manana. The *Lycium* on Moku Manu often serves as a base for booby nests, and the large twigs of this plant and other fairly large species serve in building up the nest platform. The *Atriplex* on Manana is woody but is quite low and scattered and would probably not serve to support such a nest as that of the Red-footed Booby. Some of the grass on this island grows in clumps two or three feet high and serves as protection to some birds, as young Noddy Terns, although not as nesting sites for any species. The group of coconut trees on Manana may attract certain birds but observations are lacking. The total amount of vegetation is, of course, much greater on Manana and is more dense in general. On both islands the grasses and portulaca begin to dry up late in May or early in June, depending upon the year, and by July all vegetation is brown and sear. Insects, especially Hemiptera, become extremely numerous on Manana at times but this was not observed on Moku Manu. The several species of native plants present on Moku Manu and their absence on Manana corroborate the idea of the relative isolation of Moku Manu and its freedom from many introductions.

Land Vertebrates Other Than Birds.—Skinks, *Lygosoma hawaiiensis*, were observed on the outer part of Moku Manu and these constitute the only record of vertebrates other than birds on this island. Manana, however, has a variable population of rabbits of domestic extraction (first introduced sometime before 1900) and house mice, *Mus musculus*. Manana, in addition, has geckos, *Lepidodactylus lugubris*, which make their homes in the coconut trees.

The relationships between rabbits, mice, and birds on Manana did not seem to be particularly significant in the present study. Potentially, the rabbits might defoliate the island to the extent that so much soil would be lost as to preclude burrowing by shearwaters. This possibility has not been indicated during at least two decades and does not seem likely. The number of rabbits seen during our visits (usually of three or four hours' duration) varied from two to about 30, the maximum being observed in June, 1948. Common use of burrows

by shearwaters and rabbits must occasionally occur (as when rabbits are seeking protection) but seems unlikely to be at all frequent. The absence of all rats from the islands is more noteworthy, perhaps, than the presence of other mammals; rats are present on other offshore islands, for example—Popoia and Mokolii. Many species of birds may suffer from predation by rats, and the success of Moku Manu and Manana as breeding islands would probably not be possible if rats were present.

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Table 2 lists the species of birds which have been observed on or from Manana and Moku Manu. It will be observed that although the number of species recorded for each island is about the same, the

TABLE 2

SPECIES OCCURRING ON MANANA AND MOKU MANU ISLANDS

Manana	*Moku Manu*
BREEDING SPECIES	
1. *Puffinus pacificus chlororhynchus*—Wedge-tailed Shearwater	1. **Diomedea immutabilis*—Laysan Island Albatross
2. *Bulweria bulweri*—Bulwer's Petrel	2. *Puffinus pacificus chlororhynchus*
3. *Sterna fuscata oahuensis*—Sooty Tern	3. **Puffinus nativitatus*—Christmas Island Shearwater
4. *Anous stolidus pileatus*—Noddy Tern	4. *Bulweria bulweri*
5. *Anous minutus melanogenys*—Hawaiian Tern	5. *Sula sula rubripes*—Red-footed Booby
6. *Acridotheres tristis*—Mynah	6. *Sula leucogaster plotus*—Brown Booby
	7. **Sterna anathaetus lunata*—Gray-backed Tern
	8. *Sterna fuscata oahuensis*
	9. *Anous stolidus pileatus*
	10. *Anous minutus melanogenys*
MIGRANTS	
7. *Pluvialis dominica fulva*—Pacific Golden Plover	11. *Pluvialis dominica fulva*
8. *Heteroscelus incanus*—Wandering Tattler	12. *Heteroscelus incanus*
9. *Arenaria interpres*—Ruddy Turnstone	13. *Arenaria interpres*
10. **Crocethia alba*—Sanderling	
VISITANTS	
11. †**Phaethon rubricauda rothschildi*—Red-tailed Tropic Bird	14. *Fregata minor palmerstoni*
12. †**Phaethon lepturus dorotheae*—White-tailed Tropic Bird	15. **Liothrix lutea*—Pekin Nightingale
13. †*Sula sula rubripes*	16. *Acridotheres tristis*
14. †*Sula leucogaster plotus*	17. †**Diomedea nigripes*—Black-footed Albatross
15. †*Fregata minor palmerstoni*—Frigate Bird	
16. **Nycticorax nycticorax hoactli*—Black-crowned Night Heron	
17. †**Gygis alba rothschildi*—White Tern	
18. **Asio flammeus sandwichensis*—Hawaiian Owl	

* Not seen on other island.

† Not seen to land on island.

number of breeding species is decidedly greater on Moku Manu. All of the species, except the Mynah, that are known to breed on Manana, also breed on Moku Manu. The nesting of four additional species on Moku Manu is probably indicative of lack of molestation and of more suitable breeding conditions. Breeding species will be discussed individually in the following text. The same migrants are attracted to each island, with the exception of Sanderlings seen on Manana. The lack of any appreciable sandy beach on Moku Manu would make unlikely the occurrence there of such a species.

Most of the irregular visitants to Manana were seen flying near or over the island. The records of Tropic Birds over Manana and not over Moku Manu seem to be related to the greater proximity of Manana to main island cliffs and canyons frequented by these birds. The presence of rabbits and mice on Manana may explain the several records there of Hawaiian Owls. The Pekin Nightingale recorded from Moku Manu was found dead on top of the island. It is to be considered a purely accidental occurrence and most likely due to a storm. Oceanic species like the Black-footed Albatross are more likely to be seen from Moku Manu for it is off prominent Mokapu Peninsula and is, in effect, farther out to sea.

Wedge-tailed Shearwater.—This shearwater nests in rather large numbers on both islands. Estimates of nesting pairs can best be judged by determining the occupied burrows, whether with eggs, young, or adults, in a given area. On Manana there is a large nesting area, with soil suitable for burrows, along the west slopes and on the floor of the main crater. The estimate of breeding pairs was from 2,000 to 3,000 in 1948. The most suitable burrowing area on Moku Manu was much smaller (almost restricted to one part of the south slope) and the number of breeding pairs there is not likely to have exceeded 500.

On Eastern Island of Midway this shearwater commonly nested among or beneath rocks, but it was only occasionally seen to do this on Moku Manu and never on Manana. On Moku Manu, where the soil is shallow, burrows were sometimes merely a groove beneath the low-growing portulaca. On this island about a dozen instances were noted in which shearwaters had dug a little dirt from under the pillar-like nests of the Red-footed Booby and settled down to breed there. The length of burrows varied with soil conditions, burrows typically being about three feet long on Manana but shorter on Moku Manu and on Mokulua Island (one-half mile from shore and about half way between Manana and Moku Manu) where soil was shallow and hard. The greatest measured concentration of occupied burrows on Manana

was about 40 in 10,000 square feet in October, 1946. Smaller areas with relatively greater numbers of nests were undoubtedly present. In October, 1947, on Manana, 16 occupied burrows (about two-thirds of those present) were found in approximately 2,500 square feet, a concentration equivalent to 64 burrows in 10,000 square feet.

No significant differences were observed in the breeding of this species on the two islands. The earliest record of arrival for these shearwaters on Moku Manu was February 28, 1948 (when two pairs were seen under rocks) and on Manana on March 20, 1947 (when many pairs were in burrows). Most burrows on both islands seemed occupied by March 28, 1947. No trips were taken to Manana between February 23 (when no shearwaters were found) and March 20, 1947, but it is probable that the birds returned early in this period. A single shearwater, apparently one of a very few new arrivals, was seen on Mokulua Island on March 7, 1948.

Well grown, young Wedge-tailed Shearwaters were observed on Moku Manu as late as November 9, 1947, when perhaps one-third of the young had left, but no other visits were made here in November and December of that year. Young were studied as late as November 29, 1946, on Manana, when it was estimated that 50 per cent of the young had left. It appeared that almost all adults of this species had left and that the remaining young, although not being fed, were nearly mature and could be expected to leave within a week or two. The ability of young shearwaters to fast for as long as three weeks has been noted by Richardson (1949: 97) and fasting before departure from a breeding ground is a normal occurrence.

The usual complete absence of this species from the islands from approximately December through February (none found on visits of December 14, 1946, and February 23, 1947) indicates a well established annual breeding cycle. It is not known whether migration takes place or the birds just spread over large adjacent sea areas. If they stay about as far north as the Hawaiian Islands (19–22° N. latitude), photoperiodicity, with the effect of increasing periods of daylight on gonad recrudescence, might explain the annual cycle of their breeding. Banding returns show that Wedge-tailed Shearwaters return with considerable regularity to the same islands (Munro, 1944: 22).

Bulwer's Petrel.—This species breeds in small numbers on both islands; seven individuals, each with an egg, seemed to represent the population on Manana on June 10, 1948; fewer were seen on Moku Manu. They apparently arrive and leave rather regularly, although our data are sketchy. The first arrival noted was on April 24, 1948,

on Moku Manu, while the latest record was September 13, 1947, on Manana. No birds could be found on the latter island on October 4, 1947.

This petrel nests in deep recesses in rocks and cliffs on Moku Manu and Manana, but on the north islet of Mokulua it nests largely under the low-spreading, large-leaved *Scaevola* which is absent from Moku Manu and Manana. Bulwer's Petrels are much more abundant on this islet; 150 pairs were estimated as present on June 14, 1947. This apparently indicates a preference for this type of breeding habitat which is similar to that occupied on Midway. Yet, they are abundant on Popoia Islet where they breed in the holes and crevices formed by water erosion of rock (Fisher, 1945). The nesting sites on Manana were found without exception in eroded pockets of stratified lava, far back in narrow horizontal crevices. These sites were typically about ten feet above high tide level, and it seemed evident that at times spray would bathe the nesting cliffs. Nests of these petrels were observed to be frequently bathed by spray on Mokulua. On Moku Manu, though, the few Bulwer's Petrel nests found were in deep cracks high above the shore line.

Sooty Tern.—The breeding habits of this species were of great interest in our study for, although the Sooty Tern has in the past apparently bred in large numbers on Moku Manu, it just started to breed on Manana, at least in recent years, in 1947. Moreover, this species shows a striking divergence in its breeding cycle on the two islands, its laying and incubating period being about November to March on Moku Manu but April to July on Manana.

Before inquiring into explanations of the above conditions we may best describe the breeding of this tern on the two islands. On Moku Manu, adults are present throughout the year with minimum estimated numbers (under 1,000) in August and September (600 estimated on September 21, 1947), and maximum estimates (10,000 to 15,000) from January through March (15,000 estimated on February 23, 1947). This general picture must be upset at times, as it was in February, 1948, when after severe storms the adult population became very small (400 estimated). Probably the normal breeding cycle on the island is—pairing starts in October, laying starts in November, and raising of young continues through May. Second nestings were apparently made by many birds in December and early January of 1948, after storms destroyed large numbers of eggs. However, very severe storms late that January again destroyed thousands of eggs and young, and it appeared that nesting, for what perhaps would have been the third time for most birds, was rarely attempted.

The progressive extension of the breeding areas of Sooty Terns on Moku Manu with the gradual arrival of large numbers of adults was of particular interest. The high eastern end of the inner island was the first part densely settled by breeding birds, although when renesting (probably not of early arriving adults) finally started in April, 1948, after the disastrous storms mentioned above, the new colony was on the southwestern part of the top of the island. Next, by degrees, the large high center (Plate 8, *middle*) of the island was taken over. One small colony present on November 9, 1947, in the north center of the island's top, became enveloped by the main colony of nesting terns by January 11, 1948. The steeper, less desirable sides of the island, with more rocks, vegetation, and other species of nesting birds, were utilized last. On top of the island, the areas with some soil or sand were preferred over the flat, bare, rocky areas. Although perhaps 85 per cent of the nesting of Sooty Terns took place in the dense colonies on top of Moku Manu, late breeding birds especially became scattered over the slopes, but not the cliffs, of the island. The density of the colonies, in contrast, was estimated to be one bird or pair with egg to about every four square feet. Indications were, then, that a large population on Moku Manu caused some birds to nest alongside the usual colony, thus forming a more sparsely occupied fringe.

It might be that Manana received its new breeding colony of Sooty Terns as an overflow from Moku Manu. The Sooty Tern is much less numerous on Manana, the maximum number of adults (in July, 1948) being estimated at 2,000. Birds were first seen on the ground on Manana on March 28, 1947, when 50 to 75 were seen near the region which later became their nesting site.

The differences in the breeding cycle between this small colony and that on Moku Manu, and the possible relations between the two, are of much interest. In the two years of observation, adults were absent from Manana (or only a few seen flying overhead) from October through almost all of March. Eggs were first laid at the beginning of April, nearly six months later than on Moku Manu; on Midway Island laying begins in early May. In 1947, although several hundred adults were sometimes 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. The location of the colony was on the upper south slope of the northeast peak and rim of Manana, spreading (in 1948) along the ridge toward the main peak. Sooty Terns were largely surrounded by breeding Noddies but stayed together in an almost continuous, however tenuous, elongated colony.

Some 200 birds were seen on the tip of the main peak on June 8, 1947, but nesting was not known to take place there.

Manana does not afford a large, rather flat and bare area that Sooty Terns appear to prefer for their colonies, as evinced by the large population on Moku Manu. Nevertheless, the breeding of this tern on Manana seems likely to continue to increase, if the island remains protected, since adults and young now here will probably tend to return. The Sooty Tern seems more aggressive than the Noddy and may take over the rather flattened ridge between the peaks on Manana. However, there would appear to be sufficient additional nesting area for both species.

Chapin's work (1946: 313) with Sooty Terns of another subspecies on Ascension Island in the tropical Atlantic is of special interest in comparison to the present study. Chapin established the earlier belief that the Sooty Tern has a very nearly regular nine-months cycle on Ascension (six months on the island and three away), thus breeding very close to four times in three years. Ascension is nearer the equator (8° S. Lat.) than Oahu, a fact which may explain part of this marked difference in breeding cycles. If the recent colonization of Manana was by Sooties from Midway (about 28° N. Lat.) or other Leeward Islands, this might help explain the similarity in cycle between Midway and Manana; the colony on Moku Manu, because of isolation, may have evolved the other annual cycle.

In an undated manuscript compiled by G. H. Castle, Lt. Commander (MC) USNR, on the birds of Palmyra in the South Pacific Ocean is evidence of two breeding seasons for Sooties there. He stated that the main colony arrives about May 15 and that all of these disappear from the island "except for a few stragglers that remain until a few return for the late fall nesting period." The fact that these fall breeders use nesting grounds separate from that used by the spring nesters on Palmyra perhaps indicates different birds breeding in the two periods.

On the other hand, Kelvin Nicholson (personal letter to James P. Chapin, Sept. 28, 1949) is positive that the Sooty Terns on Christmas Island breed twice a year, June and November, and that they use the same breeding grounds each time. He is informed by natives on Kuria Island, which is practically on the equator in the Gilbert Islands, that the terns arrive and lay eggs only in August.

Noddy Tern.—This tern nests in considerable numbers on both islands, its populations apparently being fairly stable in recent years. Although less variation was observed in its breeding cycle than in that of the Sooty Tern, comparison of the islands is significant. On Moku

Manu, a few eggs and young were found from early January through May (four eggs observed on January 11, 1948, being the earliest record), but the majority of the eggs were laid, and young raised, from July through September. In July, 1947, apparently a new group of Noddies had started nesting, although a few other pairs had been nesting since January. Maximum numbers of adults (up to 200–300) were seen on Moku Manu in July and August, with a minimum between October and February.

The Noddy Tern is decidedly more numerous on Manana; in fact the breeding population on this island may well be the largest in existence. As many as 7,000 breeding birds were estimated in May and June of 1948, 5,000 to 7,000 in October of 1946, and 5,000 in April and June of 1947. In 1947, it was estimated that about 35 per cent of the adults present had laid eggs by the end of March. The breeding cycle appears to be much more regular on Manana than on Moku Manu. The terns are almost completely absent from Manana from December through February, even though they nest during this time on Moku Manu and on Mokolea Rock to the south. They return in large numbers to Manana in March and soon start egg-laying. It would appear that the large breeding population of Noddy Terns on Manana is on a northern hemisphere cycle but that small populations of this bird, as that on Moku Manu, are not.

Darling's work on seabirds suggests that small size in a colony may result in a slower beginning and less success of the breeding cycle, a factor which might help explain some of the chronological differences in the colonies off Oahu. However, the small colony on Manana started breeding earlier than the large colony on Moku Manu, and the large colony on Manana was six months behind the cycle of the small colony. We may have here a condition similar to that found in Sooty Terns by Chapin, or it may be that both colonies are on a yearly cycle. Obviously, more work needs to be done before any statement of cycle is made. It is notable that the relatively few Sooty Terns nesting in recent years on Manana seem to have a regular northern hemisphere cycle as do the Noddies there; the larger population of Sooties on Moku Manu appears not to have—in contrast to the Noddies on Moku Manu.

Some details of nesting on the two islands may be given. On Manana, Noddies nested chiefly on the barren, rocky, upper slopes and rims of the main crater (Plate 8, *bottom*). They also nested on the patches of soil or pebbles on the south face of the main peak and, in 1947, on the top of the peak itself. Nesting was not attempted on bare rock slopes but a ledge as narrow as four inches enabled nesting

on quite steep slopes. Sites were somewhat different on Moku Manu because of the nature of the island and because of competition with Sooty Terns for space. A group of Noddies nested in 1947 in the rocky outcrop on top of Moku Manu between the two large open areas where the majority of the Sooty Terns nested. Most of the Noddies on this island, though, nest separately and in small groups on the scattered rocky and earthen ledges of the southwest slope.

Nests consisted typically of a slight depression in the ground with a few pebbles around the edge or sometimes pieces of green vegetation, as portulaca and grass, loosely placed on the floor of the nest. Limpet and typical snail shells were found around some of the nests on Manana Some of these were high on the island, indication of the shells having been carried several hundred yards.

TABLE 3

BREEDING NODDY TERNS ON MANANA TEST AREA

Data	*Eggs*	*Young*	*Date*	*Eggs*	*Young*
March 28, 1947	36 (About 100 nests)	0	April 3, 1948	12	0
June 8, 1947	14 (Laid since March)	45 (At about ¾ of nests)	May 16, 1948	70	70
Sept. 13, 1947	0	103 (Unable to fly)	June 10, 1948	40	90
Oct. 4, 1947	0	70–100 (About six unable to fly)			

The breeding population of Noddy Terns on a rather clearly separable part of the south rim of the main crater of Manana was given particular study, and censuses, chiefly of young and eggs, were taken on a number of visits. The area was about 50 yards long with breeding birds scattered along a rounded ridge and down as much as 15 yards on each side. Results of these censuses are tabulated in Table 3. The increase in number of young between June and September, 1947, is probably explained by the fact that eggs may have been laid and hatched between our visits. Some new young may have moved into the area. The test area seemed representative of much of Manana; thus, times of egg-laying, flying of young, etc. can be judged for the whole island.

It was impossible to gather data on the success of nesting because of the length of the breeding season and the constant intermingling of so many stages of the reproductive cycle. From February through July, birds were moving into the test area and starting to nest.

A rather high mortality of nearly-grown Noddies was noted in 1947. By October 4, most of the estimated 950 Noddies on Manana ap-

peared to be flying young; many of the earlier young had already left the island. Well over a hundred dead young were found in a cursory search. Almost all of the dead birds were well grown, fully-feathered, and apparently old enough to fly. However, all the fairly fresh dead birds were very thin with typically only about one-eighth inch of muscle on the sternum. Several non-flying older young were caught and they also were extremely thin. One was so weak it could move only slowly and could not manage its wings. The possibility of disease was not adequately investigated, but the explanation that seemed best to fit our observations was that most adult Noddies had left Manana and the last young to mature were starving. This might well result when two different or unsynchronized cycles are present in a single species breeding on such a restricted area. The parents of the last young may be stimulated to leave too early by the normal departure of early-breeding adults.

The difference in number of breeding Noddy Terns on the two islands is so striking as to demand explanation. Limitation of space on Moku Manu appears to be the chief factor, for when the large numbers of Noddies return in March, the colonies of Sooty Terns are already utilizing a great part of the territory that would probably be most acceptable to the Noddy Terns. Apparently as a result, no large colonies of this tern are found on Moku Manu, and those birds that do nest are scattered on suitable but separate ledges on the south side of the island. Nevertheless, Noddy Terns might nest in much larger numbers on Moku Manu (conditions are more crowded on some breeding islands) if nearby Manana with its large suitable breeding areas were not available.

If space is the limiting factor, we may expect the early-breeding Sooties on Manana to crowd out the Noddies breeding in the summer. It might even be possible that such crowding in the past was responsible for the inception of the off-cycle breeding of some Noddies.

Hawaiian Tern.—This species nests in small numbers on Moku Manu and has been reported to nest on Manana. As many as 130 birds were estimated as present on Moku Manu on February 28, 1948, although not more than 25 were recorded on separate visits from April through July, 1947. Many were nesting by the end of April, 1948. Typically, nests were on rocky ledges of cliffs with a low platform of twigs and grass. Some 15 occupied nests, apparently with eggs, were found in April in the large sea-cave on the north side of the island. Some nests were more than 75 yards back in this cave and were almost in darkness. Nests were always at least eight feet above the deep, surging water of the cave. Other nesting areas were on the vertical

cliffs of the northwest end of Moku Manu and on the outer small island. Munro (1944) recorded newly-hatched young on August 18, 1943, but in the period 1946 to 1948 Hawaiian Terns were almost entirely absent from the island from September through February. Curiously, a colony was starting to nest (five new nests with eggs) on Mokolea Rock on January 11, 1948. Hawaiian Terns were observed throughout the year, but not nesting, at such points in the vicinity of Moku Manu as Kailua Bay, Kaneohe Bay, and Mokapu Peninsula.

This species was not found by us to nest on Manana, but Mr. David Woodside has found a few nesting on the northeast cliffs of the island in past years. Conditions may not be too attractive to this species, for Manana's sea cliffs lack desirable ledges. The species does nest on the rougher, less frequented, small island of Kaohikaipu about one-half mile to the south.

It is interesting to note that this species which is congeneric with the Noddy, exhibits much the same pattern of nesting throughout the year—with major variations in time being associated with different colonies, rather than with seasons. On Midway Island (Fisher and Baldwin, 1946; Fisher, 1949) the main breeding period of the Noddy is in the winter months, but the Hawaiian Tern there breeds in more or less constant numbers throughout the year.

Laysan Albatross.—This is one of five species of birds that has been found to breed on Moku Manu but not Manana. The first known record of the breeding of this albatross on Moku Manu, or anywhere in the main Hawaiian group, has been described by Fisher (1948: 66). One pair then raised a single young which was observed from late February, 1947, when newly hatched, to mid-July, when it was ready to fly. On January 11, 1948, a deserted albatross egg was found in the same spot the above young had occupied, but no further nesting was attempted nor were adults seen near the island. One adult, perhaps a parent of the above egg, was observed repeatedly on the south side of Mokapu Peninsula, about three miles south of Moku Manu, on December 14, 1947. Probably the unusually severe storms in January led to the desertion of the above albatross egg and discouraged further breeding.

Christmas Island Shearwater.—This species was present on Moku Manu by late February in both years of our study. Fourteen individuals, each with an egg, were counted on April 19, 1947. Young were raised and all birds gone by October. Breeding was restricted to a small area (about 100 by 30 feet) of outcropping rock and rock piles partly covered by low brush, toward the eastern end of the top of Moku Manu's main island. Nests were usually well under or back

between rocks, but some were almost out in the open under only a partly concealing ledge of rock. Apparently this is the only area on Moku Manu acceptable to this shearwater. On Manana there is no closely similar habitat and this species was not recorded there. On Eastern Island of Midway, Fisher and Baldwin (1946: 6) and others have found this species breeding in small numbers under *Scaevola* plants; eggs were present in early May when the species was first observed. The lack of vegetation under which it could nest on Manana is still another factor in its absence.

Red-footed Booby.—Although this species is not known to nest on Manana, it nests on Moku Manu and, in recent years, has started a large breeding colony on Mokapu Peninsula. The nesting cycle was decidedly irregular on Moku Manu, for eggs were found in January, February, April, June, October, and November. Young in different stages were also found throughout the year. Nevertheless, there were peaks in the extent of nesting with a maximum of 200 nests estimated on February 23, 1947, on Moku Manu. The greatest number of adults and/or flying young estimated to be on the island was 300 in September, 1947. Surprisingly, by October 18, 1947, some 50 new nests had been made, perhaps indicating a second nesting for some individuals. Storms early in 1948 largely destroyed the eggs and young of this species, and renesting was little attempted even by the end of April.

Nests of Red-footed Boobies on Moku Manu were found chiefly on the high east end and on the upper parts of the south slopes. The greatest concentration of nests was found in the fall of 1947 when about 40 nests were located on a high southeast slope in an area about 60 by 150 feet. Brown Booby nests were sometimes near those of the red-footed species on the lower southern slopes. On the top of the islands nests of Red-footed Boobies were sometimes surrounded by nesting Sooty Terns, the terns even being under the edges of the bushes supporting the booby nests. 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.

Breeding of Red-footed Boobies on Mokapu Peninsula seemed roughly to parallel that on nearby Moku Manu and did not suggest overflow from one colony to the other. Still, crowded conditions and limited nesting bushes on Moku Manu may partly explain the "need" for the peninsular colony. It is possible, too, that severe persecution

of boobies by the many Frigate Birds on Moku Manu has been an added reason for establishing a new colony. For some reason the Frigates rarely harry the peninsular birds and do not spend much time on the steep cliffs of the peninsula. The peninsular colony was larger, with estimates of some 500 birds present in April and May, 1947, and again on December 14 of that year. Eggs were again found over much of the year. The fact that no boobies of this species nested on Manana may be explained by the lack of bushes of sufficient size on which to build nest platforms. The colony on Mokapu Peninsula takes advantage of suitable nesting bushes and kiawe trees even though molestation of nesting, as by people and predatory mammals, must be much more frequent than it would be on Manana.

Brown Booby.—Adults or flying young of this species were seen on all visits to Moku Manu. However, the number seen varied considerably and the breeding season was somewhat better defined than that of the Red-footed Booby. In both years of observation, nesting first reached its peak in January or February with as many as 75 nests counted on February 23, 1947. Partly grown young present at this date indicated that some laying must have started in December, 1946. Some young were flying by the end of July, 1947, although a few eggs were still being incubated at the end of that month. Very few young were unable to fly by the end of September, 1947. A minimal number of adults or flying young were seen on the island in October and November (24 estimated in October, 1947). This apparently fairly regular cycle was upset in 1948 when the destruction of many nests by January storms made renesting necessary for most boobies. Some 60 adult Brown Boobies, mostly nesting, were estimated as present on January 11, 1948. On February 28, though, only 20 birds and five nests were counted. On April 24, 22 nests with eggs were found.

The nest sites of this booby were rather generally scattered over the lower south-facing slopes of the island, but one gully on the north, top slope had a group of about 20 nests in 1947. This group was next to the perching site of some 30 Frigate Birds. The main area of concentration of nests during both years of study was on a fairly level, sparsely rocky area just above high tide level on the southeast corner of Moku Manu. Nests were either right on the ground or on very low vegetation. The nest seems to be less important to these boobies than to the red-footed species, for most often almost no real nest is present and, even when some sticks are used, a fairly solid platform elevated on a bush is not made. Two eggs were the rule for this species but three were once recorded. We have no certain record of two young being raised to maturity. In 1947, two small young were

sometimes seen in the same nest but two young as much as half-grown were never seen in a single nest.

The greater regularity of the breeding cycle of this species, compared to the Red-footed Booby, is noteworthy. Both species tend to have about the same peak of laying activity early in the year, but much more variation after that was exhibited by the latter species. It is not clear why the Brown Booby does not nest on Manana or the peninsula. It does not normally utilize bushes in building its nest, and there would seem to be more suitable nesting space on Manana than on Moku Manu. Molestation by man may be the important factor, even though boobies are subject to much predation by Frigate Birds on Moku Manu. However, the population on Moku Manu is small and there is no crowding in the colony, as judged by human interpretation.

Gray-backed Tern.—This tern bred in small numbers each of the two years of observation on Moku Manu but was recorded only as a visitor on Manana. On May 10, 1947, about 30 adults and three young were seen on the lower middle south slope of Moku Manu. Only six adults of this species were found from January through April in 1948. They were in the same local region of the island as before. At least three young were successfully hatched in spite of adverse weather conditions early in that year. One nest found on February 28, 1948, was well back under large rocks. This may explain the successful raising of young even though all the Sooty Tern nests which had surrounded the nesting area of the Gray-backed Terns were destroyed by storms. These records, although for few individuals, indicate a regular breeding cycle with the species not present in the fall. This species was noticeably more wary than the other terns, and it seems understandable that it has not attempted to nest on less isolated Manana.

Mynah.—The Mynah has been observed in most months of the year and in numbers up to 30, on Manana, but only once on Moku Manu. This may be explained by the fact that Moku Manu is farther from suitable Mynah habitat on Oahu than is Manana Island. None was seen on Manana in July, August, September, and December, but no trips were made in July and only one in each of these other months. A nest was found on Manana but no eggs or young were observed. Northwood (1940: 35) recorded a Mynah nest with three young on Manana in June, 1939. Tern eggs that had probably been eaten by Mynahs were found on both islands, but no direct observation of predation was recorded. On April 19, 1947, on Moku Manu, a freshly opened Sooty Tern egg was found in an area from which several Mynahs had just been frightened. Many pecked eggs, each with a hole a few millimeters wide, had been found in this region some two

months before. On April 18, 1947, Breese observed on Manana some 30 broken Noddy Tern eggs, each with a hole in the side about 20 millimeters wide. Groups of Mynahs were seen on the island that day but, again, none were actually seen to peck tern eggs.

Migrants and Occasional Visitants.—Such species are listed in Table 2 as to their occurrence on both islands and will not be treated in detail here. The Frigate Bird was perhaps the species of greatest interest to us in this group. Actually, it was constantly present on Moku Manu and had the behavior characteristics of a resident species except that it was not known to nest on the island. Its numbers were at a minimum in January and February (as few as an estimated 120 were seen on February 28, 1948) but built up to a maximum of some 1,000 from May through the fall. Immature birds were seen throughout the year. Inflated gular pouches of the males, presumably a courtship display, were seen as early as January but especially from April through July. Nevertheless, no nests were ever found, even though repeatedly searched for. While it is probably true that Frigates prefer denser and higher vegetation for nesting than that found on Moku Manu, some of the bushes appear adequate, and isolated slopes and ledges are present. However, this is the only factor to which we can attribute the absence of nests. Apparently this species nests on distant islands but is present on Moku Manu only to prey on other birds, principally boobies, nesting there and feeding in the vicinity. Frigates were not seen to alight on Manana, but only to fly over or near it.

The group of Frigates on Moku Manu is probably entirely non-breeding and immature individuals. Development of the gular pouches and other courtship appurtenances occurred here at the same time as on Laysan and Midway where the birds nest in August. There was no apparent decrease in numbers present in the summer months—actually, an increase occurred; hence, it seems unlikely that the Frigates here were migrants or that they would breed during the year.

DISCUSSION

The ornithology of Moku Manu and Manana islands off Oahu discloses that some eleven species of birds breed on these islands, ten breeding on Moku Manu and six on Manana. Moku Manu is and has been definitely less disturbed than Manana and the birds on it seem to have reached a relatively stable population as to breeding species, breeding areas, and numbers of birds, although quite variable during the year. The vegetation on Moku Manu contains fewer introduced and more native species. Manana appears to have less

stable conditions as indicated in particular by the recent addition of the Sooty Tern to its list of breeding species. The greater number of introduced plants, the presence of introduced rabbits and mice, and the more frequent visitation by people seem to be associated with fewer breeding species and less stable conditions on Manana.

TABLE 4

OCCURRENCE OF BREEDING BIRDS ON MOKU MANU AND MANANA ISLANDS

January February March April May June July August September October November December	
SPECIES BREEDING ON BOTH ISLANDS	
.....--*-o o o- - - - - - - - - - - - ..	Wedge-tailed Shearwater
..--*-o o - - - - - - - ..	Bulwer's Petrel
..-*-o-o-o - - - - - - - - ..	Manana } Sooty Tern
o - o - o - o - - - - - - - - - - - - - - - - - - *-o-o	Moku Manu } Sooty Tern
....*-o-o-o - - - - - - - - - - - - - -...	Manana } Noddy Tern
* - o - o - o - o - o - o - o - - - - - - - -	Moku Manu } Noddy Tern
-o† - - - o - o - - - - o-o - - - - - - - - - -	Hawaiian Tern
SPECIES BREEDING ON MOKU MANU ONLY	
..--*-o-o - - - - - - - - - ..	Christmas Island Shearwater
...* - - - - - - - - - - - - - - - ...	Laysan Albatross
o-o-o-o - - - - - - - - - - - - - - - - - - *	Brown Booby
o - o - - - o - - - o - - - - - - - - - - o-o-o-	Red-footed Booby
...*-o - - - - - - ..	Gray-backed Tern

Dashed lines indicate approximate duration of stay on islands. Asterisks indicate beginning of major breeding cycle. O's indicate times of egg-laying.

† is a record for Mokolea Rock.

Table 4 lists the breeding sea birds of the islands and summarizes the usual duration of stay and the time of egg-laying of each species. Inspection of the table shows that seven of the ten species have a northern hemisphere breeding cycle with egg-laying starting in the winter or spring. Two of these same species (the Sooty and Noddy Terns), when on Moku Manu, do not show this type of cycle. These two species and three others, the two boobies and the Hawaiian Tern, either start laying in the fall or early winter or have their times of egg-laying spread over much of the year.

The above variations in breeding cycles cannot be clarified by this study although some explanations are suggested. It will be noted, for one thing, that all the species which are present throughout the year have protracted breeding seasons. This was particularly true with the two boobies and the Hawaiian Tern, species whose populations seem resident and more or less constant throughout the year. It was less true with the Sooty and Noddy Terns on Moku Manu for, although these terns were present here over the whole year, their

populations varied greatly, and the times of egg-laying, even though prolonged, showed definite starting peaks.

It would appear that the resident breeding sea birds have lost or tended to lose a northern hemisphere cycle, but that the species which are migratory (hence, away from the islands part of the year) have retained such cycles. Photoperiodicity does not appear to be the primary cause because most of the migratory species studied here go to regions which are nearer the equator and have even less fluctuation in length of daylight than does Hawaii. The contrasting cycles of Sooty and Noddy Terns on Manana and Moku Manu may indicate that migratory and resident populations are involved. Presumably, these two terns on Manana are migratory, although almost nothing is known of the movement of these rather cosmopolitan tropical species (Murphy, 1936: 1152). These terns on Moku Manu may well migrate, but in a less regular fashion, with some of the birds breeding at different times. The lack of sufficient suitable nesting space might, in the case of the Sooty Terns, lead to populations with irregular breeding cycles. This would not seem to be likely, though, with the less numerous Noddy. Breeding cycles are known to become less regular, on a yearly seasonal basis in particular, as one nears equatorial regions. Murphy (1936: 1125 and 1154) pointed out that Noddy and Sooty Terns breeding near South and North America are definitely migratory on a seasonal basis in the northern and southern parts of their range, but are irregular in the tropics. Sooty Terns in the Dry Tortugas (24° N. Lat.) begin laying in May while laying becomes earlier and less regular toward the equator.

The two islets of this study appear to be comparable to islands of similar latitude in both the North and South Atlantic. Such islands seem to be near a borderline where seasonal periodicity has been preserved in some species but is being or has been lost in others. In equatorial regions, wet and dry periods, with breeding starting after the wet season, may over-ride seasonal cycles. Murphy (1936: 123) found this to be true with most sea birds of the Caribbean coast of South America, at about 12° N. latitude. In the Hawaiian region the most severe storms and somewhat greater rainfall seem to be in the late fall and early winter. This may be a factor with the several species that start breeding after this time. It definitely is not a factor with such species as the Sooty Tern on Moku Manu, which may start breeding during the most inclement weather.

One cannot disregard the possibility that the breeding populations of Sooty and Noddy Terns now present on each of these two islands are made up of stocks from two or more different colonies which may

have been on different cycles. The small breeding population of Noddies on Moku Manu and of Sooties on Manana Island may represent new "pioneers" from islands of far different latitude, and their cycles may be indicative of their former home, not their present breeding grounds.

It is to be hoped that further study of Hawaiian sea birds can help answer the questions raised by this investigation. An extensive banding program could yield very interesting information on several points. Perhaps more important would be a study for which the observer could stay on the islands, especially Moku Manu, for a period of several months, particularly during the fall and winter when the picture of bird populations and breeding activities can change so rapidly.

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