THE BREEDING CYCLES OF HAWAIIAN SEA BIRDS

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INTRODUCTION

The problems related to cyclical, usually annual and seasonal, behavior in birds have received much attention in recent years. The renewed interest in such subjects as cyclical breeding and migration, phenomena which have impressed man for centuries and about which he has observed and written much, has been due, perhaps, both to newly opened fields of evidence and keener observation and inquiry. Probably the greatest new field has been the detailed, including microscopic, study of the bird gonads and the complex of the hormonal control of their annual recrudescence regulated by seasonal changes in diurnal periods of daylight and other factors. Rowan (1929) was eminent in starting this field of investigation and such workers as Wolfson (1952) and Blanchard (1941) have expanded and refined the field.

Combined with the greater understanding of the rhythm of gonadal development has been the analysis of environmental factors, especially food and its seasonal changes such as with temperature and rainfall, that are the more immediate explanation of cyclical bird behavior. Outstanding in these studies are such men as Thomson (1950), Moreau (1950), Lack (1950), and Skutch (1950). Their general consensus has been that the food supply during the raising of the young is the primary factor that has determined establishment of the typical spring breeding cycle of most birds of the world, but this may be modified for each species by such factors as the particular feeding habits, period of incubation, distribution as to latitude, and the effect of major rainy or dry seasons.

The breeding cycle of birds which are residents of tropical regions are at once of special interest, since in these regions changes in day length are relatively slight and photoperiodicity cannot be expected to assume the significance it does in higher latitudes. Moreover, the correlation of food abundance with summer's maximum light and temperature is much modified in the tropics and the time of rainy seasons often determines breeding. Exceptions to spring or summer breeding are frequently found; and cycles, which may even lose their annual nature, show many variations even within some species.

The Hawaiian Islands extend from about 19° to 28° N. latitude, thus lying in both the Tropic and Temperate Zones. They show conditions intermediate between these zones as well as characteristic of them. The islands thus afford an unusual opportunity to evaluate the factors related to breeding cycles of birds and to study their significance in both higher and lower latitudes. Most of the ornithological work in Hawaii has been done on the unique endemic passerine family Drepaniidae, Hawaiian honey creepers, and it is in this group that the first detailed ecologic study, including reproductive cycles, has been made (Baldwin, 1953).

Reproductive cycles of sea birds in general, especially insular populations, are often subject to somewhat different determining factors than are the cycles of continental birds. Since sea birds obtain their food from the sea, their occurrence tends to be correlated with the temperature and biotic zones of the oceans. These zones, although tending to be latitudinal, are greatly affected by currents and other factors, and the distribution of oceanic birds may be correspondingly influenced. Murphy (1936) emphasizes such relationships in his outstanding work on South American sea birds. Moreau (1950) analyzes more particularly the breeding cycles of African sea birds. Fisher and Lockley (1954) have written the most complete recent analysis of sea birds of the North Atlantic. Sea birds, then, are much a part of their water environment and their time on land is often restricted solely to the breeding season. They may have great mobility over expanses of sea, but relatively infrequently have north-south migratory habits comparable to mainland migrants.

The nesting Hawaiian sea birds—namely 22 species of tube-nosed swimmers, pelecaniform birds, and terns—are, except for certain endemic varieties, mostly widespread or pan-tropical forms. However, the group of species and the complex of conditions under which they breed, many species over a range of more than 1,000 miles and with a latitudinal change of some nine degrees (623 miles), is not closely paralleled in any other archipelago. Though Hawaiian sea birds have been studied, especially on the main islands, and at Laysan and Midway Islands by Munro (1944) and others, except for a study of sea birds near Oahu (Richardson and Fisher, 1950), breeding cycles and the factors bearing on them have been little analyzed. The present study was undertaken with this in mind and with the hope of filling in gaps in the still

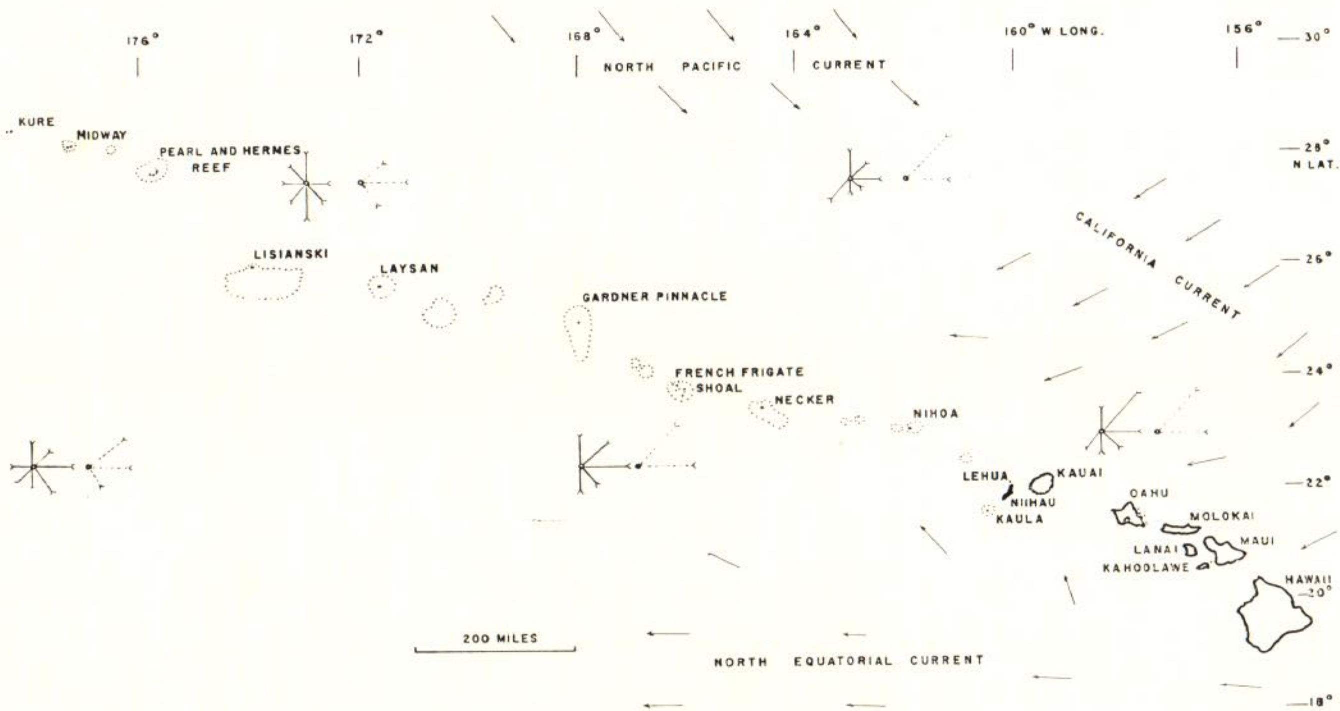

FIGURE 1.—The Hawaiian Archipelago. Shoal areas of the leeward islands are dotted at the 100 fathom line. Wind roses show prevailing wind directions in the 5 degree area where centered. Solid lines are for January, dotted lines for July. Ocean currents are somewhat variable with the North Pacific Current, for instance, getting near the Hawaiian Islands as shown, in the winter only.

incomplete picture of the occurrence and breeding cycles of sea birds along the whole Hawaiian chain.

Primarily, I wish to acknowledge the Yale-Bishop Museum Fellowship which made this study possible. Important, too, were the kindness and help of the Museum's fine director, Dr. Alexander Spoehr, and staff. The parts played by Yale University and the University of Hawaii in enabling and encouraging my project, and by the University of Washington in the completion of the manuscript, are also gratefully acknowledged. The United States Coast Guard was of great help in affording transportation to distant and otherwise inaccessible islands of the Hawaiian chain. I also thank members of the Territory of Hawaii Division of Fish and Game for their help and for permission to study and collect on various islands. The Pacific Ocean Fisheries Investigation staff of the United States Fish and Wildlife Service was of real assistance, as were the Hawaii Audubon Society and the Honolulu Zoo, under the directorship of Paul Breese. I should like to give full credit to all of the individual observers whose work, whether published or not, forms an important basis of my study. Many of these workers are cited in the text and bibliography, but it has seemed unwise to attempt to cite them all.

THE HAWAIIAN ARCHIPELAGO

Major environmental conditions on the Hawaiian Islands and in the seas around them are best summarized first. Then, following a description of the breeding cycles of the sea birds, the importance of environmental factors in regulating these cycles will be evaluated.

The Islands

The main islands of Hawaii are primarily formed by Hawaii, Maui, Oahu, Kauai, Molokai, Lanai, and Niihau; but the some 30, often widely spaced, small islands extending to Kure (Ocean Island), more than 1,200 miles west-northwest of Oahu, are no less a part of the archipelago and are of great interest in a study of sea birds (fig. 1). The main islands of the southeast end of the great oblique chain are large and mountainous. Hawaii is 4,030 square miles in area and up to 13,784 feet in altitude, having coastal and inland cliffs available to sea birds. Small unmolested islands especially suitable for sea birds are numerous along the windward or northeast shore of Oahu, where there are some 13 islets; but there are only about 10 altogether around the other main islands. Moku Manu and Manana are the two islets off windward Oahu on which most studies of sea birds have been made.

West and north of the main islands, Nihoa (fig. 2) and Necker are the first islands. They are fairly sizable, each almost a mile long; are rocky and precipitous; and essentially lack beaches or level open areas. Beyond them, La Perouse and Gardner Pinnacles are the only rocky islands, each of which is barren and less than 210 yards long. From French Frigate Shoal to the northwest end of the Hawaiian chain at Kure, all the islands except the two pinnacles

FIGURE 2.—Nihoa Island from the southwest. This great rocky island about 900 feet high and a mile long offers not only extensive cliff nesting sites but also soil, bushes and, to a small extent, trees and barren areas.

mentioned are low, none more than 45 feet high, and composed of coral reef or sand (fig. 3). Six of these islands are between one and two miles long and all 27 have open sandy areas and varying amounts of usually low vegetation. Bryan (1942) gives much useful information, both physical and biological, on the Hawaiian chain.

All of the Hawaiian Islands are of oceanic origin and are widely separated from continents and other islands, facts that have largely determined their flora and fauna. Sea birds, even though generally wide-ranging, reflect the isolation of the Hawaiian Islands in the occurrence of several endemic races. The nearest islands to the Hawaiian chain are Johnston and the Line Islands, including Palmyra and Christmas; but they are approximately 500 and 1,000

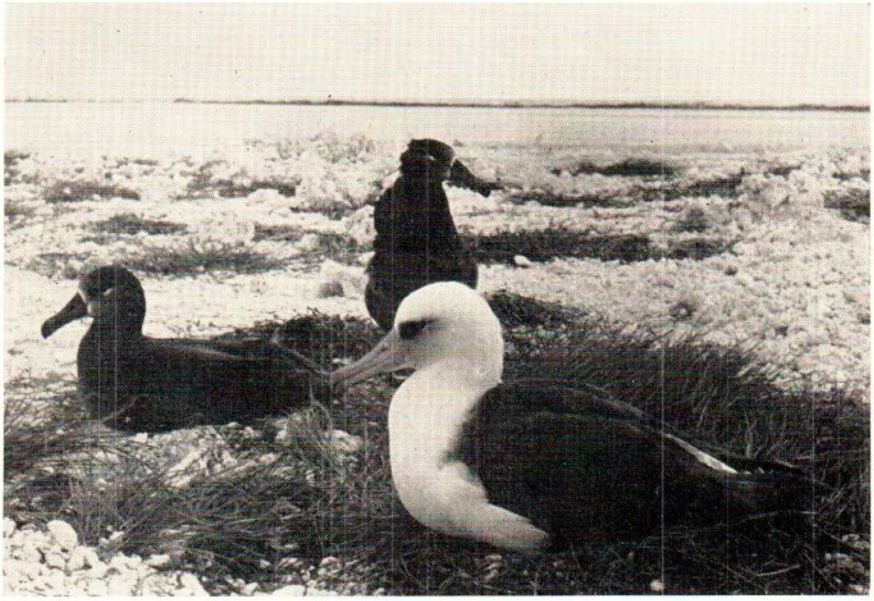

FIGURE 3.—Laysan (in foreground) and black-footed albatrosses on eggs on French Frigate Shoal, December 18, 1953. This island is an example of a flat coral type. The two species of albatrosses, here nesting close together, are ordinarily more widely separated. Note higher nest here built up by the Laysan albatross.

miles to the east and south respectively. Data from these islands and others, both in the Pacific and other oceans, will not be stressed in this study but will afford some valuable comparisons.

CLIMATE

Some salient and contrasting climatic features, especially of the two ends of the Hawaiian chain, may well be brought out here so that the possible roles of these environmental factors in determining breeding cycles can be evaluated later. Admittedly, conditions in surrounding seas are most important for sea birds, but certain climatic conditions on their breeding islands are also significant. Unfortunately, little detail is known of the climates on various isolated Hawaiian Islands, so they must be judged—and they can be usually fairly well—on the basis of known stations. Temperature and precipitation data are from the United States Weather Bureau "Annual Summaries for Hawaii."

Temperatures, as shown in the following table, do not vary greatly either diurnally or seasonally, compared to inland continental stations at Hawaiian latitudes. The moderating effect of the ocean is apparent throughout the Hawaiian Islands, but temperature differences are still marked, especially in comparing high and low altitudes or the ends of the chain.

Table 1.—Selected monthly temperature means and annual extremes in degrees Fahrenheit

STATION	YEAR	FEB.	AUG.	MAY	NOV.	TEMP. EXTREMES
Midway	1917-38	64.6	78.3	71.7	70.6	91-45(1927?)
	1952		78.9	73.6	73.2	
	1953	66.6	79.5	72.5	74.8	88-55
	1954	64.9	78.7	70.2	72.1	86-55
French Frigate	1952	71.8	78.1	74.7		
Shoal	1953	72.4	79.9		76.6	-63
	1954		78.7	73.3	76.6	88-
Makapuu Point,	1952	70.9	75.3	71.5	72.7	86-63
Oahu	1953	70.7	75.2	71.4	72.1	84-60
	1954	70.5	75.8	71.8	75.2	89-59
Haleakala, Maui	1952	49.5	56.2	50.8	52.6	75-32
Ranger Station	1953	50.7	58.5	54.5	55.5	80-34
Alt. 7,030 ft.	1954	52.8	58.4	53.2	56.7	75-30

Rainfall, even at a given locality in the Hawaiian Islands, is quite variable —much more so than temperature. The general picture is that of considerable rainfall on the windward, northeast, sides of the main islands, but much less on the lee sides of the islands or their mountains. The low islands in the northwestern part of the archipelago are relatively dry; and this is true also of the small windward islands, such as Moku Manu and Manana, in the main group. Meteorological data from Makapuu Point, near Manana, on Oahu, probably most closely represent these latter islands, since this point is not very high and extends well out from the main mountain range.

Probably the most significant rainfall, as regards its effect on sea birds, is in the form of cloudbursts. Sheets of run-off water may, at such times, sweep eggs and young before them (Richardson, 1948). Unfortunately, such storms do not show in rainfall totals, especially since the storms may be of such local occurrence as to miss weather stations. This applies particularly to bird islands in the main group. It is less applicable to the data from flat coral islands like French Frigate Shoal and Midway, where, too, appreciable run-off is not to be expected.

Table 2.—Monthly rainfall

STATION	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
Midway												
1917-38	5.05	3.47	3.33	3.65	2.39	2.20	3.29	4.60	4.43	3.88	3.34	3.72
1952					0.65	13.42	3.06	4.18	4.11	2.88	1.96	1.10
1953	9.28	2.44	2.74	3.80	4.92	2.66	3.00	2.01	7.38	3.39	2.79	2.30
1954	2.76	0.89	1.76	5.78	0.27	1.56	3.09	1.19	5.73	0.70	1.66	1.80
French Frigate Shoal												
1952			2.20	1.58	0.57	0.74	1.29	0.15	1.28	1.22	0.63	
1953	2.19	2.83	1.22	0.34	0.72	0.94	1.63	0.61	2.00	1.79	1.00	2.76
1954	6.05	2.03		4.51	0.53	0.58	1.73	2.25	2.77	2.12	3.33	2.51
Makapuu Pt.												
1952	2.66	1.85	1.64	1.80	1.93	0.37	0.52	0.35	0.13	3.54	2.30	0.71
1953	2.60	1.50	5.45	0.51	0.28	0.37	0.68	0.31	0.13	0.85	0.67	2.72
1954	1.90	5.17	3.35	1.13	0.45	0.65	2.50	0.79	0.36	3.32	3.88	2.56
Haleakala Ranger Sta.												
1952	2.87	1.84	7.78	0.64	0.99	0.48	2.40	0.37	0.75	2.24	6.92	
1953	0.47	2.53	7.12	0.16	1.80	0.18	0.13	2.29	0.19	1.24	0.80	2.70
1954	3.32	3.86	5.00	2.21	1.88	0.65	6.95	1.31	1.35	1.47	2.84	37.63

There is a fairly regular season of greatest rainfall from late fall to early spring in the main islands and west to Nihoa. This rainy season is sufficiently marked to be reflected in considerable vegetational change on some islands. Manana, for instance, becomes quite green during the winter and spring, and this is true to a less noticeable degree on Moku Manu and Nihoa. French Frigate Shoal, perhaps the driest of all of the islands, showed some increase in plant growth in the late winter of 1953-1954, but this was not a very marked change. Summer months tend to be the driest on the main islands, including the high Haleakala area on Maui, but the amount of summer rainfall tends to increase toward the northwest end of the archipelago and Midway often receives its heaviest rains during these months.

Table 3.—Total annual rainfall and departure from normal

	1952		1953		1954	
STATION	ANNUAL	DEPART.	ANNUAL	DEPART.	ANNUAL	DEPART.
Midway	22.94 (1950)	—19.66	46.44	+3.84	27.19	
French Frigate Shoal			18.03		28.41 (for 11 months)	
Makapuu Pt.	17.80	—4.28	16.07	—7.07	26.06	+2.92
Haleakala Ranger Sta.	34.65	—18.01	19.61		68.47	

Length of daylight may be considered a climatological phenomenon and the significance of facts presented here will be considered later in this study. The extremes of latitude in the Hawaiian Islands are 18° 55′ N., at the southern tip of Hawaii; and 28°25′ N., at Kure Island. The principal sea bird breeding localities from Oahu to Midway would span only about a degree less than this almost 10 degree change in latitude. Day length and related figures from the "American Ephemeris and Nautical Almanac," are for even 10 degree parallels; so rather than make uncertain interpolations, data for 20°N. and 30° N. are given below. Corresponding night lengths are included, since they may be significant in nocturnal species. Periods of twilight extend approximately one hour 17 minutes before sunrise and after sunset and, accordingly, extend incomplete light or darkness.

Table 4.—Annual maximum and minimum periods of daylight and darkness at approximate north and south extremes of Hawaiian Islands

LAT.	LENGTH OF DAYLIGHT (sunrise to sunset) DEC. 26	JUNE 19	DIFFERENCE BETWEEN LONGEST AND SHORTEST DAYS AND NIGHTS	LENGTH OF NIGHT (sunset to sunrise) DEC. 26	JUNE 19
20° N.	10 hr. 56 min.	13 hr. 20 min.	2 hr. 24 min.	13 hr. 4 min.	10 hr. 40 min.
30° N.	10 hr. 13 min.	14 hr. 4 min.	3 hr. 51 min.	13 hr. 47 min.	9 hr. 56 min.
Diff.	43 min.	44 min.	1 hr. 27 min.	43 min.	44 min.

Winds, although essentially part of the extensive wind systems of the Northern Hemisphere, may be briefly considered here for they impinge on the Hawaiian Islands (fig. 1). Their effects on sea birds may be such as to determine breeding or possibly feeding success, and ability to take off, especially with young albatrosses. The following discussion of winds is based on the "Atlas of Climatic Charts of the Oceans" (United States Weather Bureau, 1938) compiled from some million observations covering over 50 years in the north Pacific.

The usual surface winds throughout the year in the Hawaiian Islands are the northeast to east trade winds. They may blow even more than 80 percent of the time, especially during the summer and spring; but their force is not great, usually averaging from 10 to 16 miles per hour. There is considerable variability in the trade wind regime, however, especially in late fall and winter and toward the northwest of the archipelago, where west and southwest winds may predominate. Islands from Laysan to Midway are often on the variable borderline between trade winds and calmer, more variable, west to north winds. Moderate gales, 32 to 38 m.p.h., and occasionally stronger winds occur five to 10 percent of the time from Laysan to Midway between December and March, but are less frequent in the main islands. Calm, a condition probably unsuitable for gliding sea birds, especially procellariiforms, is almost unknown in the Hawaiian region.

Great and rather constant wind systems occur over the Pacific Ocean north and south of the Hawaiian Islands and may well be important in helping sea birds return to their breeding islands. A broad belt of regular trade winds extends across much of the ocean from the islands south toward the equator. The Pacific region from Japan to Canada is characterized by strong and constant northwest winds except in late spring and in summer when south or southwest winds are more common. The most variable belt of winds extends across the Pacific usually north of the Hawaiian chain but sometimes including its more northern parts.

Cloud cover averages about 0.4 to 0.5 of the sky during the year in the Hawaiian region; a relatively clear condition as compared to many oceanic areas. Fog, which would be inimical to some sea bird activity, is of insignificant occurrence in the islands. The northern north Pacific is, however, the foggiest region of the world's oceans.

Vegetation

Major differences in the type or presence of plant cover may be summarized here, but this study will not include detailed mention of plant species except in the unusual cases of a close interrelationship with sea birds. Except for urban and agricultural areas, the main islands are generally covered with dense vegetation. However, plant growth becomes low or sparse high on the mountains of Hawaii and Maui and on the lee sides of islands. Neighboring islets, such as Manana and Moku Manu, are rocky but have some soil-covered slopes bearing a variety of annual and perennial plants, including a number of grasses and bushes up to about three feet in height. A few coconut palms are present on Manana but no other trees.

As one goes out the chain to the northwest, Nihoa and Necker Islands are rather similar to Manana and Moku Manu; although Nihoa is much higher and Necker, rockier. The southerly slopes of Nihoa are largely covered with native plants, including bushy *Chenopodium oahuense*, and an endemic palm tree grows in some canyons. All of these islands present a desert like, scrubby appearance except in the winter and spring when new growth may make them relatively green.

Beyond Necker, La Perouse and Gardner rocks and some of the small coral islands of shifting sands occasionally washed over by stormy seas are practically devoid of vegetation. Most of the larger coral islands have a cover of vegetation—very low and sparse on French Frigate Shoal where *Portulaca*, *Boerhaavia*, and the puncture vine, *Tribulus*, are examples. Perhaps most typical are the large perennial grass *Eragrostis variabilis* and beach *naupaka* (*Scaevola*), which forms thickets up to some 8 feet high. The most notable exception to this usual picture is the extensive growth of introduced ironwood (*Casuarina*) trees on Midway.

The most important general relationship of plants to sea birds in the Hawaiian Islands is their function of holding the sand or soil. This was illustrated on Laysan, where earlier in this century introduced rabbits completely devastated the island's once varied and dense vegetation of more than 26 species and left a barren sand-blown waste. Although there has been fair revegetation by a few plants, the once millions of sea birds have never regained their earlier numbers and three of the four native and endemic land birds have been exterminated.

Surrounding Waters

Except for part of the breeding season, albatrosses, petrels, and shearwaters spend the whole year at sea. Most other sea birds, although spending the night on islands, spend much of each day at sea. The sea is of primary significance in understanding sea birds, as it is the source of their food and can thus determine the very presence of the birds and their successful raising of young. The foods and feeding habits—how far from islands, what times of day, and so forth—of each species become important, as well as seasonal variation in the abundance of food.

Temperatures of the sea's surface reflect the abundance of life in the waters, and Murphy (1936) has forcefully correlated the occurrence and abundance of sea birds with isotherms of the southern oceans. The cooler waters, especially when they originate by the up-welling from deep levels rich in nutrients, support the greatest amount of plankton and hence the most fish and squid, the two chief types of food of Hawaiian sea birds. Temperatures of Hawaiian waters are given in the following table, which forms a basis for consideration of their significance:

Table 5.—Average monthly temperatures of surface waters in Hawaiian and other regions in degrees Fahrenheit*

REGION	JAN.	MAR.	MAY	JULY	SEPT.	NOV.	DIFF. (warmest and coldest month)
Main Hawaiian Is. 155°-160° W., 20°-25° N.	73.5	72.3	74.6	76.7	77.9	76.4	5.6
NW. end Hawaiian Is. 175°-180° W., 25°-30° N.	68.4	66.4	69.5	76.4	78.1	73.2	11.7
Line Is. 155°-160° W., 0°-5° N.	79.7	80.3	80.9	81.1	81.1	81.1	2.2
North Pacific 175°-180° W., 40°-45° N.	48.8	46.4	47.5	56.3	61.4	52.9	16.6

* From Atlas of Climatic Charts of the Oceans, U.S.D.A., Weather Bur., 1938.

Detailed temperature studies of main Hawaiian Island waters at different depths (Leipper and Anderson, 1950) show that at 400 feet temperature ranges between about 70° to 72°, whereas at the surface the range is from about 73° to 79°. There is little indication, except in local areas, of up-welling of deeper cool waters that might greatly enrich surface waters. Major ocean currents washing the islands apparently are not such as to bring deep waters to the surface. However, Hawaiian waters are always relatively cool and are not the warm tropical waters of 80° and over that tend to be markedly poorer in life. Moreover, as Murphy (1936) points out, the shallows around islands in a broad expanse of ocean concentrate the surface-water life. These conditions indicate abundant aquatic life in Hawaiian seas throughout the year, probably especially in the winter and spring in the northwest islands where ocean temperatures are lower and great shallow areas exist.

Ocean currents may greatly affect sea birds, as the cool rich Humboldt Current off western South America so strikingly shows by supporting multitudes of birds. There is some parallel in the Hawaiian Islands; for the cool California Current sweeps south and west to bathe the islands, especially the more northern ones, more or less throughout the year (fig. 1). The warmer North Equatorial Current flows north from tropical America and then west to Hawaii, but these waters are cooled by mixing with the California Current, and by the remoteness and relatively high latitudes of the Hawaiian Archipelago.

The seasonal abundance of plankton and aquatic vertebrate life in Hawaiian waters must have direct bearing on bird populations, but not too much is known about this abundance. King and Demond (1953) show that zooplankton is decidedly more abundant within 10 degrees of the equator south of the Hawaiian Islands, in a zone where currents converge and deep waters come to the surface, than near the islands. However, a measure of 0.1 cc.of plankton in a cubic meter of water taken in the fall near the main islands was a maximum for all stations. It is likely that the most pelagic of Hawaiian sea birds, the procellariiforms, take advantage of the rich more equatorial ocean regions even during their breeding season. Fish and Wildlife Service records indicate that tunafish, feeding largely on smaller fish and squids, as do sea birds, are more abundant in these waters.

The correlation between abundance of sea birds and abundance of fish is strongly suggested by data of Murphy and Ikehara (1955) and Royce and Otsu (1955). They observed by far the most flocks of birds feeding at sea and associated schools of fish from April through August in Hawaiian waters. The commercial catch of tuna in this region is much the greatest from June to August, less fishing being done in April and May because the tuna are smaller. It was found that some 85 percent of all fish schools observed were associated with birds; a measure, too, of the dependence of fishermen on birds for locating fish. Since far fewer sea birds are present before April, it is suggested that fewer schools of fish are then present.

Murphy and Ikehara have also compiled interesting information on the general abundance of sea birds at different distances from the Hawaiian, Line, and Phoenix Islands. Their conclusion is that the number of birds is little diminished up to about 180 miles from islands, but beyond this, birds and, apparently, fish schools are much fewer. Birds are more frequent, perhaps because of migration, in these more pelagic waters from September through November—the same months they are most frequently seen near the Line Islands.

DISTRIBUTION AND BREEDING

The 22 species of sea birds regularly occurring and breeding in the Hawaiian Islands may best be listed first, by way of introduction, and their relationships briefly discussed, before the separate species are considered. Nomenclature follows Peters (1931 and 1934) with some changes by Murphy (1951 and 1952). The first vernacular names given, sometimes with synonyms, are specific and follow Murphy (1936), Fisher and Lockley (1954), or Alexander (1954). A second vernacular name is given for certain well-established endemic Hawaiian races and follows Munro (1944) and other Hawaiian workers.

Procellariiformes	*Diomedea nigripes:* Black-footed Albatross
	Diomedea immutabilis: Laysan Albatross
	Puffinus pacificus chlororhynchus: Wedge-tailed Shearwater
	Puffinus nativitatis: Christmas Island Shearwater
	Puffinus puffinus newelli: Manx Shearwater; Newell's Shearwater
	Pterodroma phaeopygia sandwichensis: Dark-rumped Petrel; Hawaiian Petrel
	Pterodroma leucoptera hypoleuca: Collared Petrel; Bonin Island Petrel
	Bulweria bulwerii: Bulwer's Petrel
	Oceanodroma castro cryptoleucura: Madeiran Storm Petrel; Hawaiian Storm Petrel
	Oceanodroma markhami tristrami: Markham's or Sooty Storm Petrel
Pelecaniformes	*Phaëthon rubricauda rothschildi:* Red-tailed Tropic bird
	Phaëthon lepturus dorotheae: White-tailed Tropic bird
	Sula dactylatra personata: Blue-faced or Masked Booby
	Sula sula rubripes: Red-footed Booby
	Sula leucogaster plotus: Brown Booby
	Fregata minor palmerstoni: Great Frigate or Man-o'-War bird
Charadriiformes	*Sterna lunata:* Grey-backed or Spectacled Tern
	Sterna fuscata oahuensis: Sooty Tern
	Procelsterna cerulea saxatilis: Grey Ternlet or Blue-grey Noddy; Necker Island Tern
	Anoüs stolidus pileatus: Brown or Common Noddy
	Anoüs minutus melanogenys: White-capped or Black Noddy; Hawaiian Tern
	Gygis alba rothschildi: Fairy or White Tern

Despite the isolation of the Hawaiian Islands and the great amount of endemism shown by their fauna, their sea birds apparently include no endemic genera or species. The closest approach to such species would be the two species of albatrosses whose breeding range is very largely just on the Hawaiian Islands.

The number of endemic races of sea birds may be considered a significant measure of the long existence and isolation of the islands. Such races would include the following (although, as Peters remarks, Pacific races of at least *Sterna fuscata* and *Gygis alba* are badly in need of revision):

Puffinus puffinus newelli	*Procelsterna cerulea saxatilis*
Pterodroma phaeopygia sandwichensis	*Anoüs minutus melanogenys*
Oceanodroma castro cryptoleucura	*Gygis alba rothschildi*

It is interesting that the albatrosses and endemic races of procellariiforms, the most pelagic sea birds, are more numerous than the endemic forms of the less oceanic terns and pelecaniforms. Perhaps petrels and their relatives were the first sea birds to become established in the Hawaiian Islands and have had a longer time to differentiate. The lack of any endemic pelecaniform races may correspondingly indicate that this least pelagic group of sea birds arrived most recently in the islands.

The affinities of Hawaiian sea bird species are indicated by the fact that 12 of the 22 species have pan-tropical distributions, occurring in Pacific, Atlantic, and usually, Indian Oceans. As an example, Murphy (1936) lists ten species of sea birds nesting on Fernando Noronha Island at 4°S. in the Atlantic, and eight of these species occur in Hawaii. Of the other 10 of the 22 Hawaiian species, eight are found just in the Pacific (two species of *Diomedea, Puffinus nativitatis,* two species of *Pterodroma, Oceanodroma markhami, Sterna lunata,* and *Procelsterna*), while two (*Puffinus pacificus* and *Phaëthon rubricauda*) also breed in the Indian Ocean. Most of the species are tropical or subtropical throughout the year, but the albatrosses and some petrels and shearwaters regularly range into higher latitudes. The Hawaiian Islands mark the northernmost breeding localities of nearly all the species and the highest breeding latitude of all Hawaiian races. However, *Bulweria bulwerii* breeds near Madeira, 32°N.; *Oceanodroma castro* in the Azores, 38°N.; *Puffinus puffinus* even north of 60°N. in the Atlantic; *Phaëthon lepturus* in the Bermudas, 32°N.; and *Sula leucogaster* off Baja California to approximately 30°N. At least three races of Hawaiian species breed at higher latitudes in the Southern Hemisphere: e.g., *Anoüs minutus* on Tristan de Cunha, 37°S.; *Puffinus pacificus* on southern South Wales, 36°S.; and *Phaëthon rubricauda* on Lord Howe, 31°S.

Following the theories expressed by Serventy (1953) and Ekman (1953), we may consider the Hawaiian sea birds as chiefly part of a pan-tropical avifauna tracing its ancestry back to the Tertiary Tethys Sea south of Eurasia. Fisher and Lockley (1954) suggest an East Indian origin for Pelecaniformes. Added to this pan-tropical element primarily of the pelecaniforms and terns would be the procellariiform species which have apparently had their chief origin in southern cold oceans. Some tube-nosed swimmers, namely *Oceanodroma* and *Puffinus puffinus,* have probably evolved in northern oceans and later spread into the central Pacific. The presence on Hawaiian Islands of species of essentially southern genera, such as species of *Diomedea* and *Pterodroma,* may reflect a past climate such as that of a glacial period when cooler ocean waters enabled a trans-equatorial extension of southern forms which no longer, at least in the case of Hawaiian albatrosses, habitually range south into tropical waters.

FIGURE 4.—Laysan and black-footed albatrosses with young on Lisianski Island, March 26, 1954. Note approximate uniformity in age of young, here about six to eight weeks old. Albatrosses nest relatively little in the rather dense growth of the grass *Eragrostis variabilis* in the background.

In the following species accounts, information is reasonably complete for a few years on Moku Manu, Manana, Laysan, and Midway, but is often fragmentary and too frequently just from spring or summer on other islands. The breeding cycle for a species is thought to be essentially uniform on all of its breeding islands except where variations are described. Records from Kaula are by Caum (1936) and may not indicate present conditions, for the island has been used for intensive bombing practice in recent years. Examples only are given of the sources, other than my observations, of Hawaiian distributions and cycles. The published notes of Fisher (1903), Donaghho (1953), and others have here been especially helpful. Fisher (1947) has prepared a bibliography of Hawaiian ornithology from 1890 to 1945. Locations of islands are given only to the nearest degree of latitude.

Diomedea nigripes—Black-footed Albatross (figs. 3, 4).

Breeding distribution: Breeds on Necker in small numbers on fairly level and open ridge-top areas. Is abundant on French Frigate, Laysan, Lisianski, Pearl and Hermes, and Midway where flat, relatively barren areas are preferred.

Breeding cycle: Adults arrive regularly during the last half of October. Eggs are laid starting about the middle of November. Young hatch starting in late January. Young and adults are generally all gone by end of July.

Breeding elsewhere: Breeds also in Marshalls (about 10°N.) probably starting one to two months earlier.

Diomedea immutabilis—Laysan Albatross (figs. 3, 4, 5, 9).

Breeding distribution: Breeds rarely on rocky Moku Manu, in small numbers on Nihoa, and in fair numbers on Necker. Uses high open areas but also steep slopes and rocky recesses on Necker and Nihoa. Breeds abundantly on open areas of French Frigate, Laysan, Lisianski, Pearl and Hermes, and Midway.

Breeding cycle: Similar to *D. nigripes,* but about two weeks later with adults arriving in early November and a few young remaining into middle or late August.

Does not breed elsewhere.

Puffinus pacificus chlororhynchus—Wedge-tailed Shearwater (fig. 5).

Breeding distribution: Breeds on Manana, Moku Manu, and at least eight other islets off windward Oahu; on Molokini (between Maui and Kahoolawe); on Kilauea Point, Kauai; on Lehua and all leeward islands, including La Perouse Pinnacle, from Kaula to Kure. Typically burrows in sand or soil but also nests under vegetation and rocks and in rocky recesses and caves.

Breeding cycle: Adults arrive as early as March 1, mostly somewhat later, and, although they leave irregularly, even for weeks, some are always present up to time of general egg-laying about the middle of June. Young leave islands by end of November, adults two or more weeks earlier.

Breeding elsewhere: Breeds on many Pacific islands, east to Revilla Gigedo (19°N.), as reported by Blake (1953). Season is close to six months earlier in southern Pacific (20° to 30°S.) but populations near equator agree more closely with southern regime (Murphy, 1951).

FIGURE 5.—Laysan albatross feeding young on French Frigate Shoal, March 20, 1954. Note three wedge-tailed shearwaters to the right.

Puffinus nativitatis—Christmas Island Shearwater.

Breeding distribution: Nests on Moku Manu, Nihoa, French Frigate, Laysan, Lisianski, and Midway; and probably on Lehua and Necker. Usually found under rocks or vegetation but birds were paired on open sand at French Frigate (Trig Is.). Never abundant.

Breeding cycle: Adults start arriving in early March. Eggs are laid from early April to late July. Young are fledged by September or October, occasionally later. Breeding appears to start later at Midway (28°N.) than at Moku Manu (21°N.), but there is one record of a downy young on October 3 from Moku Manu.

Breeding elsewhere: On Christmas Island (2°N.), apparently the nearest non-Hawaiian breeding locality, eggs and young are known from both early June and November. On Canton (3°S.), birds were mating in early June, 1937 (Buddle, 1938).

Puffinus puffinus newelli—Manx Shearwater; Newell's Shearwater.

Breeding distribution: Bred at least on Maui, Hawaii, Kauai, and Molokai in 1894 and before 1907. Adults have since been seen at sea a few times and one was collected in 1954 on Oahu (Richardson, 1955). Nesting burrows were typically at the foot of cliffs 500 to 1,000 feet in altitude along windward coasts (Munro, 1944).

Breeding cycle: From meager evidence it appears that the adults arrived in April, laid eggs in May and June, and young were fledged by late October.

Breeding elsewhere: This variety of Manx shearwater does not breed elsewhere but *P. p. puffinus* starts nesting in the spring in the North Atlantic. Blake (1953) reports *P. p. opisthomelas* breeding in the summer on islands off Baja California (27° to 30°N.).

Pterodroma phaeopygia sandwichensis—Dark-rumped Petrel; Hawaiian Petrel.

Breeding distribution: Discovered breeding in 1954 at 7,000 to 9,000 feet altitude on volcanoes of Maui and Hawaii (Richardson and Woodside, 1954). Nested as late as 1917 on Molokai and probably, originally, on other main islands. Recent nesting burrows are deep under rocks on high mountain slopes but earlier sites were in lower, more forested areas.

Breeding cycle: Said originally to lay in April and May, but recent records indicate laying in May and June. Young apparently are fledged by late October or November.

Breeding elsewhere: The other race of this species breeds in the Galapagos Islands (near equator) apparently laying in June and July.

Pterodroma leucoptera hypoleuca—Collared Petrel; Bonin Island Petrel.

Breeding distribution: Breeds in western Hawaiian Islands at least on Laysan, Lisianski, and Midway; possibly on Lehua by main islands. Typically makes deep burrows in sandy soil.

Breeding cycle: Adults arrive regularly in large numbers in August but there are no records of eggs until January. Young have usually all flown by late June.

Breeding elsewhere: Breeds in Bonin Islands (27°N.). Another race breeds in Juan Fernandez (33°S.), probably about May to November.

Bulweria bulwerii—Bulwer's Petrel.

Breeding distribution: Breeds on small islets (Keaoi, Molokini, Manana, Mokulua, Popoia, Moku Manu, and Kaoikaipu) off Hawaii, Maui, and Oahu; and at least on Kaula, Nihoa, Necker, Laysan, and Midway. Usually nests under rocks or in cliffs, also under thick vegetation such as *Scaevola*.

Breeding cycle: Adults arrive starting in early April. Eggs are laid in late May or early June. Young and adults are generally gone by late September. Vanderbilt and de Schauensee (1941) found many downy young of this species on Nihoa on August 7-16, 1940.

Breeding elsewhere: Breeds on several western Pacific islands including Bonins and Volcanoes (25°N.). On Desertas (32°N.) and Salvage Islands (29°N.) of the Atlantic, this petrel lays in about May and is gone by September (Lockley, 1952).

Oceanodroma castro cryptoleucura—Madeiran Storm Petrel; Hawaiian Storm Petrel.

Breeding distribution: Probably nests in cliffs of large volcanic islands including Kauai.

Breeding cycle: No nest or egg records are known. Several barely flying young were found in October in the late nineteenth century, indicating a breeding season starting approximately in May.

Breeding elsewhere: One race lays in Salvage Islands (29°N.) in July, another race in the Galapagos lays in May or into July, and a fourth race on Ascension (8°S.) apparently lays in about September. The species nests as early as March in the Cape Verde Islands (16°N.) according to Moreau (1950).

Oceanodroma markhami tristrami—Markham's or Sooty Storm Petrel.

Breeding distribution: Breeds on Laysan, Pearl and Hermes, Midway, and perhaps Necker. Now uncommon.

Breeding cycle: Eggs are recorded as laid on Laysan from January 1-15 (Willett, 1919), but there seems to be no record of when adults arrive. Young apparently fly by end of May.

Breeding elsewhere: A race occurs off western South America, but its breeding is unknown.

Phaëthon rubricauda rothschildi—Red-tailed Tropic Bird.

Breeding distribution: Breeds on Lehua, Kaula, Nihoa, Necker, Gardner Pinnacle, Laysan, Lisianski, and Midway. Bred on Kauai in last century and possibly on Niihau. Nests may be found in steep, rocky areas but are typically on sand under thickets, as of *Scaevola*, or under other protection.

Breeding cycle: Adults arrive in late February or in March. Some eggs are laid in April but may be present even into August. Young are first recorded in mid-May. Adults and young are usually gone by mid-November, but young not fully fledged may occur even in December (Necker, December 20, 1953).

Breeding elsewhere: This race breeds also in the Bonin Islands. Other races occur in the tropical Indian and Pacific Oceans, apparently breeding throughout the year. In the most southern part of their range (30°S. near New Zealand), however, eggs are usually laid in December but even on into May (Oliver, 1955).

Phaëthon lepturus dorotheae—White-tailed Tropic Bird.

Breeding distribution: Possibly nests on all main Hawaiian Islands; definitely nests on Hawaii, Maui, and just off Oahu on Mokolii. Nests are in holes or recesses of cliffs and are often inaccessible.

Breeding cycle: Adults are present throughout the year. Eggs are known at least from April, May, and August, indicating a prolonged breeding season similar to that of the previous species. Both small and nearly fledged young are known from August.

Breeding elsewhere: This pan-tropical species—the Hawaiian race extending through the tropical Pacific—breeds on hundreds of islands. Alexander (1954) gives egg dates as December to September.

FIGURE 6.—Blue-faced booby with young on Lisianski Island, March 26, 1954. The young is about three or four weeks old indicating laying by this pair in mid-January. Almost all blue-faced boobies on Lisianski were still incubating eggs at the time of the above picture. *Scaevola frutescens* is the plant in the background.

Sula dactylatra—Blue-faced or Masked Booby (fig. 6).

Breeding distribution: Breeds on all islands from Kaula and Nihoa to Midway including Gardner but not La Perouse Pinnacle. Nests on sand or, less typically, open ridge areas as on Necker. One or a pair of these boobies were present on Moku Manu at least from September 1953 to June 1954, but did not lay eggs even though a nest was started.

Breeding cycle: Adults are present throughout the year. Eggs are usually laid from February through April but sometimes earlier or later. Young are generally fledged by late August or even by April.

Breeding elsewhere: This pan-tropical species apparently breeds throughout the year in the tropics. For example, King (1955) reports both fresh eggs and large young from Christmas Island (2°N.) on October 23, 1953.

Near the southern limit of its range, as in the Kermadec Islands (30°S.), eggs are generally present from late August into November (Oliver, 1955). A few degrees (2° to 10°) south of the equator in the west Indian Ocean the species seems to be a spring breeder (Moreau, 1950).

Sula sula rubripes—Red-footed Booby (fig. 7).

Breeding distribution: Breeds from Oahu to Midway on all islands affording brushy or higher vegetation for nesting. This excludes La Perouse and Gardner Pinnacles and such barren sandy islands as those comprising French Frigate Shoal, where a few of these boobies nest on the only two bushes of the many islands. Breeds on Moku Manu off Oahu, off Kilauea Point of Kauai, and on Ulupau Head of Mokapu Peninsula of Oahu, apparently the only locality on a main island. This latter colony appears to have started in 1946.

Breeding cycle: Adults are present the year around and eggs and young are known from all months. There is something of a peak of reproduction from March through October. This tends to be less noticeable in the Oahu region, where there is great irregularity and a moderate peak of breeding activity extends through the fall and winter of some years.

FIGURE 7.—Red-footed boobies on tree heliotrope (*Messerschmidia argentea*) on French Frigate Shoal, December 19, 1953. This small tree and one other were the only shrubby plants on the 13 islands of French Frigate Shoal and were the only nesting spots of this booby. Note the great range in egg-laying time (at least three and a half months) indicated by stages from eggs through fledged young in this picture.

Breeding elsewhere: This race breeds irregularly throughout the year in the tropical Pacific. In September of 1953 on Palmyra (6° N.) there were many fledged and also large downy young. On Christmas Island south of Palmyra indications are that this booby nests much of the year but especially in October to April. Murphy (1936) records all three species of Hawaiian boobies nesting chiefly from November to June, the drier season of the year, on islets (11° N.) off Venezuela.

Sula leucogaster plotus—Brown Booby.

Breeding distribution: Breeds apparently just on Moku Manu of the main group, but also on Nihoa and apparently less commonly and somewhat irregularly on Kaula, Necker, La Perouse, Laysan, Lisianski, and Midway.

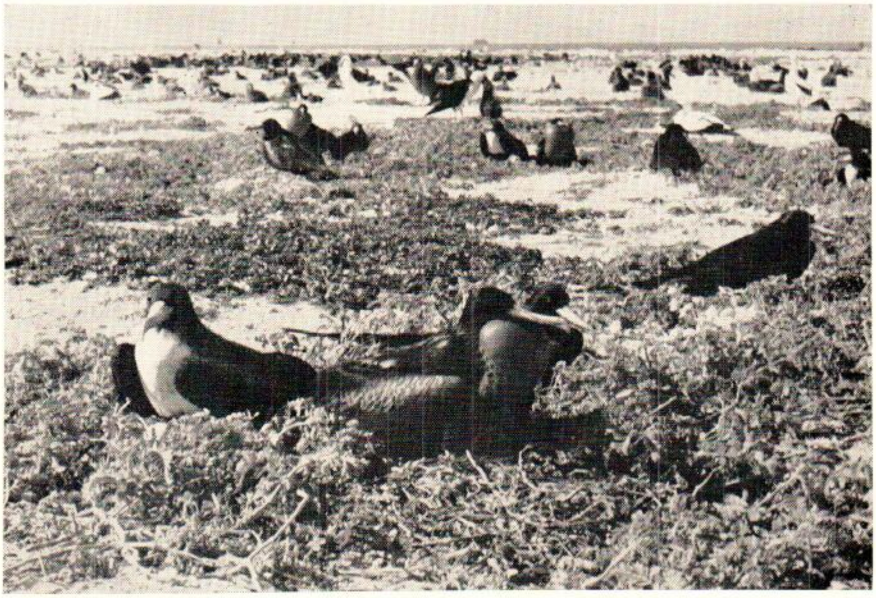

FIGURE 8.—Frigate birds nesting on French Frigate Shoal, March 20, 1954. Egg-laying was starting at about this time. The large red gular pouches of the males are fully inflated only during the breeding season. Frigate birds are usually tree or bush nesting but here build up nesting platforms chiefly of branches of *Tribulus cistoides*, the plant in the foreground.

Breeding cycle: Adults are present throughout the year but nesting almost always starts in early winter. Eggs are occasionally laid as early as late October or early January, but usually somewhat later, and may be present even into June. Most young are fledged by late September but occasional large young are known as late as December.

Breeding elsewhere: This species apparently breeds throughout the year in tropical oceans. On Palmyra (6° N.) general egg laying of *S. l. plotus* had started during August and September 1953. On Marcus (26° N.) in August of 1902, Bryan (1903) found eggs to half-grown young of this race. On Clipperton (9° N.) breeding may start regularly at the close of the spring and summer rainy season. In the Indian Ocean, the species may breed in October at 16° N., but in June and July at 27° N. (Moreau, 1950). Blake (1953) reports the three above-mentioned species of boobies breeding on islands about 20° to 30° N. off Baja California.

Fregata minor palmerstoni—Great Frigate or Man-o'-war Bird (figs. 8, 9).

Breeding distribution: Breeds just on western Hawaiian Islands including at least Nihoa, Necker, French Frigate, Laysan, Lisianski, and Midway. Brush or higher vegetation is generally required for nesting sites but on French Frigate the birds pile up stems of the prostrate *Tribulus* to make nests. No nesting is yet known on Moku Manu in spite of year-round presence of many frigate birds.

Breeding cycle: Adults are present throughout the year. Egg laying starts

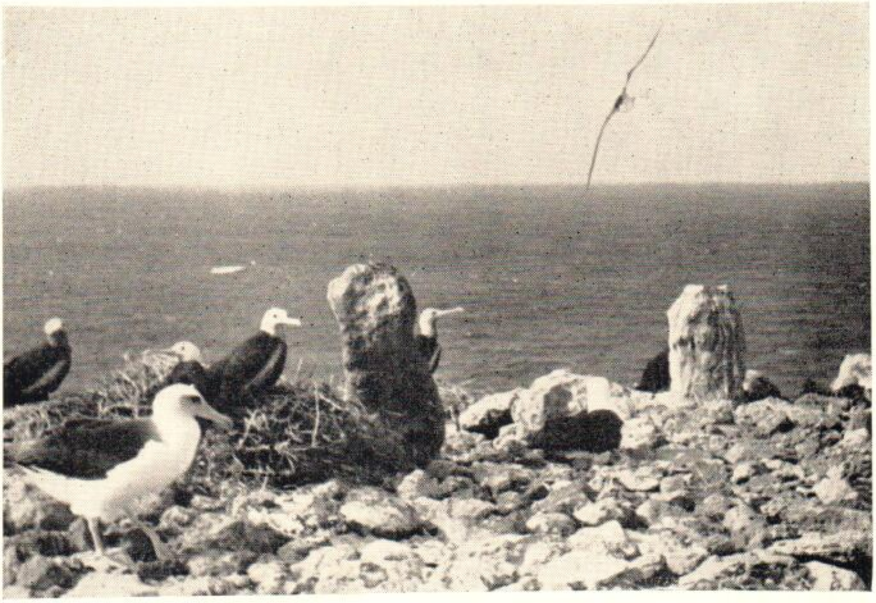

FIGURE 9.—Immature frigate birds on built-up twig nests on Necker Island, December 20, 1953. All young frigates on Necker, except two half-grown ones, could fly at this time. Some Laysan albatrosses (one in foreground and one in flight) were nesting atypically on this rocky ridge. The upright stones are part of an ancient marae, or temple, site.

regularly in March and April although nest building may start even in December. Young are first recorded from mid-May and are mostly fledged by October. As an exception, two unfledged young, one not more than half-grown, were found on Necker, December 20, 1953.

Breeding elsewhere: This frigate bird may breed in any month in such tropical Pacific islands as the Galapagos and Canton, but on Christmas Island and a number of other breeding stations, its cycle seems much like that in Hawaii.

Sterna lunata—Grey-backed or Spectacled Tern.

Breeding distribution: Breeds on Moku Manu in small numbers, on Nihoa, Kaula, French Frigate, Laysan, Lisianski, and Midway. Prefers flat areas with low vegetation but may nest on slopes and on flat, barren areas.

Breeding cycle: Adults apparently arrive at breeding islands in late February or early March. Eggs are laid in March or April. A few young are fledged by late May and all generally are by September.

Breeding elsewhere: The few nesting records of this species from the tropical Pacific suggest a spring and summer breeding season comparable to that of the Hawaiian Islands.

Sterna fuscata oahuensis—Sooty Tern (fig. 10).

Breeding range: Breeds on Moku Manu and Manana and all islands west of the main group with the exception of La Perouse and Gardner. Open flat or gently sloping areas on sandy or rocky islands are typical for nesting but rather steep rocky ridges may also be used, as they are on Manana.

Breeding cycle: Adults are generally away from the islands from late October to late February; arrive after this time; and lay in March, April, or May. The young are all fledged by late October. However, on Moku Manu in some known years (1900, 1937, 1938, 1940, 1946, and 1947), adults arrive, if ever entirely gone, in about October, and commence a late fall and winter breeding cycle that overlaps or replaces the spring and summer cycle (Richardson and Fisher, 1950). Sooty terns on nearby Manana seem regularly to follow a late spring cycle similar to that of Midway and other western Hawaiian Islands. However, when this tern had just a spring breeding cycle on Moku Manu in 1954, it started in early March.

Breeding elsewhere: This pan-tropical species is noted for its breeding at slightly more than nine-month intervals on Ascension (8°S.), as stated by Chapin (1954). Such a cycle is not known elsewhere but much variation is known including year-round breeding in various tropical localities. There is evidence of both a regular summer and winter breeding cycle on Palmyra and Christmas Islands south of Hawaii. Breeding toward the southern limit of the species, as at Lord Howe Island (32°S.), starts in September to November,

FIGURE 10.—Sooty terns flocking preparatory to nesting on French Frigate Shoal, March 20, 1954. This species typically wheels and flocks for many days after its return to its breeding islands before settling to nest.

corresponding to early spring of the Northern Hemisphere. The species breeds from June to August off the east African coast from 21°N. to 28°S. (Moreau, 1950).

Procelsterna cerulea saxatilis—Blue-Grey Noddy; Necker Island Tern.

Breeding distribution: Known only to breed, in the Hawaiian Islands, on the rocky ledges and cliffs of Nihoa, Necker, and La Perouse. Has been reported to breed on Kaula.

Breeding cycle: The few nesting records indicate a very extended breeding cycle, with egg-laying starting in December and continuing at least through April. Nesting and laying were apparently just starting on both Necker and Nihoa in late December 1953.

Breeding elsewhere: This species nests on Christmas Island, at least in October and November; on Canton in July.

Anoüs stolidus pileatus—Brown or Common Noddy.

Breeding distribution: Breeds on Moku Manu and nearby Mokolea Rock, Manana (its greatest breeding population), Kaula, Nihoa, Necker, French Frigate, Laysan, and at least on Midway to the west, although in small numbers. Flat areas and steep slopes are utilized as well as rocky ridges. Not found nesting in bushes or trees.

Breeding cycle: A few adults may be present, as on Moku Manu, during the whole year, but perhaps more typically the species is away during late fall and early winter. Egg-laying may start in February and March but is later especially in big populations. All young are usually fledged by early October. Variations of this already extended cycle are not infrequent. On Necker, Nihoa, and French Frigate fair numbers of this tern had started a definite breeding season in November and December of 1953. The start of breeding in November is also recorded from Midway, although spring and summer seem to be the usual season.

Breeding elsewhere: Alexander (1954) speaks of this pan-tropical species as breeding throughout the year. The Hawaiian variety apparently has a spring and summer cycle at Marcus (26°N.) but breeds in both winter and summer at Christmas Island. The species breeds during much of the year in the Galapagos (Lack, 1950): usually in the rainy season, January to April, in the southern islands but starting in July in the northern islands. Marshall (1951) reports the species breeding in large numbers on Eniwetok (12°N.) in October 1944, but not breeding on Arno (7°N.) in June to September 1949, although numerous. It breeds chiefly in April to August in the Seychelles (4° to 10°S.) off east Africa (Moreau, 1950).

Anoüs minutus melanogenys—White-capped or Black Noddy; Hawaiian Tern.

Breeding distribution: Breeds on Moku Manu, Mokolea Rock, Lehua, and coasts of Hawaii and Maui and probably other main islands. Also breeds on Nihoa, Necker, La Perouse, Laysan, Lisianski, and Midway. Nests only on cliffs or in sea caves except on Lisianski and Midway where ironwood (*Casuarina*) trees are used.

Breeding cycle: Adults are present all year. Eggs are recorded from all months except August and September, with perhaps the greatest numbers laid from March into June. There may be a lesser cycle starting in October or November, as indicated by young and eggs on Necker and La Perouse in late 1953. A small group that laid eggs in early January 1948, on Mokolea Rock, and newly hatched young recorded on August 18, 1943, from Moku Manu, show even greater variation in the breeding of this species.

Breeding elsewhere: The classification of the white-capped noddies is confused but records of other races of the species indicate breeding during much of the year on Christmas Island, while egg-laying is usually in October in the Kermadecs (30°S.) near the southern limit of the species. A single nesting record from Marcus indicates young mostly fledged by early August. Marshall (1951) reports the species breeding in large numbers on Eniwetok in October 1944.

Gygis alba rothschildi—Fairy or White Tern (fig. 11).

Breeding distribution: This endemic race breeds only to the west of the main islands on Kaula, Nihoa, Necker, La Perouse, Laysan, Lisianski, and Midway. Eggs are laid in cliffs or high ledges of the first four islands, but on bare branches of introduced trees, chiefly *Casuarina*, on the last two. Nests are recorded on low blocks of coral on Laysan.

Breeding cycle: Adults may be present the whole year or, as in some years on Midway, may leave for about December through February. Eggs are known from all months except January and September, with perhaps the greatest numbers laid from March into July. A secondary cycle may start in

FIGURE 11.—White terns on eggs on *Casuarina* sp. branches, Lisianski Island, March 26, 1954. Several small, largely dead clumps of this introduced ironwood tree afford the only likely nesting sites of the white tern on Lisianski.

November and December, judging from eggs and young found on La Perouse and Necker in late 1953. A few nearly fledged young on Necker in December 1953, indicated a very extended earlier breeding season.

Breeding elsewhere: Alexander speaks of this pan-tropical species as having eggs from May to January. King (1955) found it with both eggs and large young in November and early June on Christmas Island. Bryan records eggs and flying young on Marcus in August 1902. Oliver states the adults usually arrive to breed in September in the Kermadecs. Records from Canton indicate at least spring and summer breeding. On Palmyra on September 19, 1953, white terns were just starting to lay eggs.

DISTRIBUTION WHEN NOT BREEDING

Little is known about the distribution of many Hawaiian sea birds during months other than their breeding seasons. In general it may be said that the procellariiforms are on the open ocean, often quite distant, during these months; the pelecaniforms, with the chief exception of the tropic birds, usually return each night to their breeding islands throughout the year; and the terns, with the exception of the Hawaiian tern and probably the Necker Island and white terns, stay on the open ocean or go to distant islands when not breeding. Following the arrangement of sea birds as used by Fisher and Lockley (1954) and others, Hawaiian procellariiforms are pelagic, or oceanic, species; pelecaniforms (although the tropic birds may be considered pelagic) and terns are offshore or marine species; and inshore or coastal sea birds, such as various gulls and terns of other regions, are lacking. Insufficient evidence is at hand to indicate a definite migration of any Hawaiian sea bird, although it is likely that at least certain petrels and shearwaters have such. What little information is available, taken from personal observations and other records, is summarized for each of the groups of sea birds in the following paragraphs. Banding records are so few that migrating or wandering individuals are indistinguishable. The significance of many oceanic records is uncertain, especially if made very far from the Hawaiian Islands, since individuals of breeding populations from other islands may be involved. Moreover sight identification of birds at sea, especially of different shearwaters and petrels, is often uncertain.

Under the Procellariiformes something is known of the off-season distribution of the following:

Black-footed albatross. Some breeding birds, as from the Marshalls, are south of Hawaii to about 10°N., from winter to summer. Many birds are north to about 23°N., both in summer and winter. Yokum (1947) records many individuals from February to September 400-800 miles west of San Francisco at about 37°N. Kuroda (1955) has many June and July records for 1954 chiefly off Honshu at about 40°N., but some as far north as 52°. Observations (Miller, 1940) show the species is regularly present off southern California. Blake (1953) reports the species as a visitor near Revilla Gigedo Is. at 19°N. off Mexico.

Laysan albatross. This species seems to stay consistently farther north than the black-footed albatross, perhaps preferring the Aleutian region although scattering widely in the north Pacific at all seasons. Bailey (1952) gives many Pacific records of this and the black-footed albatross.

Bulwer's petrel. In the Atlantic this species appears to migrate south to winter in tropical waters of northeast Brazil (Van Oordt and Knight, 1953).

Hawaiian storm petrel. Sea records from near the Hawaiian Islands are from April, June, July, August, and October. Kuroda (1955) gives many July 1954 records off Honshu at about 40°N., suggesting a northern spreading or migration of the species when not nesting.

Of the Pelecaniformes, the red-tailed tropic bird is the only species that regularly leaves when not breeding. It is occasionally seen near Oahu in winter and spring, two were seen November 5, 1953, between Nihoa and Kauai, numbers were recorded between Palmyra and Oahu by King, July 29 to August 3, 1950, and January 1953. A large non-breeding population of frigate birds is present the year round, although with some fluctuation in size, on Moku Manu. The nearest certain breeding island of this species is Nihoa, some 300 miles northwest. Most of the Moku Manu birds are in adult plumage.

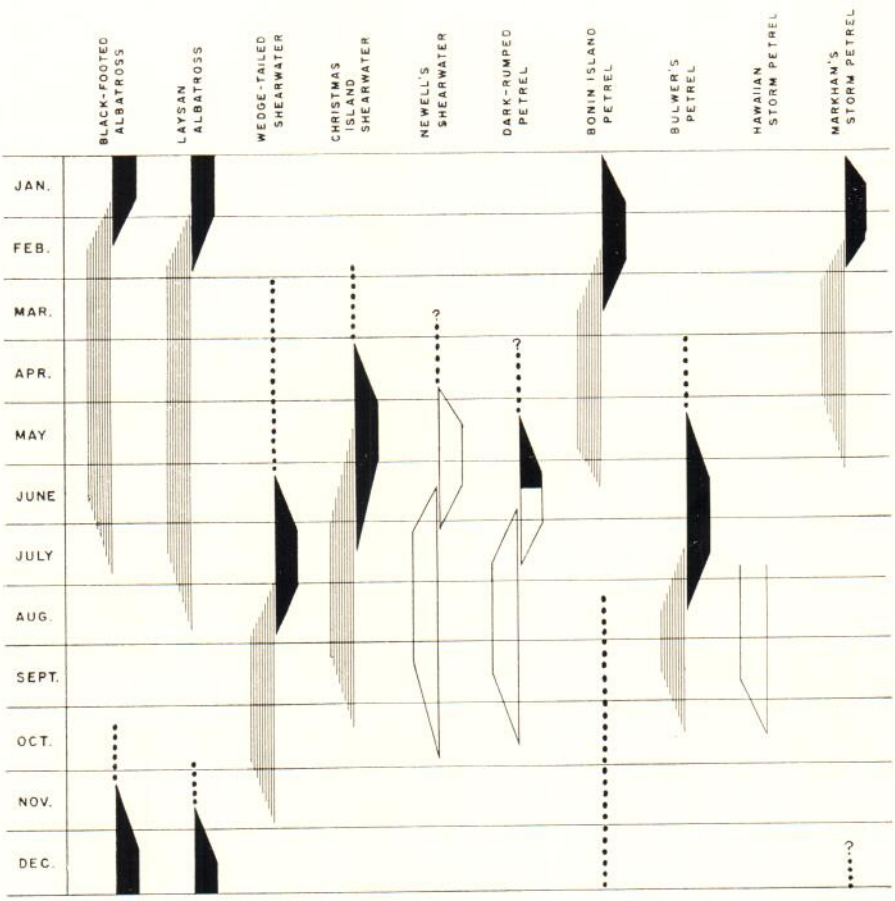

FIGURE 12.—Breeding seasons of Hawaiian Procellariiformes. Black columns indicate eggs; lined columns, young; the thickness of the columns showing approximate abundance. Length of incubation coincides approximately, when information is sufficiently complete, with time from start of black column to start of decrease in column. Heavy dotted lines indicate arrival and occurrence of adults before breeding. Hollow columns indicate scanty evidence.

The non-breeding distribution of terns in Hawaiian waters is suggested by these notes which seem to indicate a lack of migration:

Sooty tern. Numerous flocks of sooty terns and a few of common noddies were seen (Fish and Wildlife records) in late January and early February 1953, in waters 30 to 100 miles off Hawaii. Flocks of this species and *Sterna lunata* were observed flying toward Wake by Dixon and Starrett (1952) when about 80 miles west-southwest of Wake on March 6, 1946.

White tern. A number of small groups, two to 20 birds, of this tern were recorded usually with sooty terns in February 1953, off Hawaii (see above). Fisher and Lockley (1954) state that this tern does not often fly far from its breeding islands.

Common noddy. Lack (1950) states the Galapagos race of this tern migrates south to Peru.

ANALYSIS OF FACTORS RELATING TO BREEDING CYCLES

Inspection of figures 12 and 13, or study of the preceding breeding summaries, show that Hawaiian sea birds may be grouped as: (1) spring and summer breeders; (2) fall and winter breeders; and (3) irregular or year-round breeders. These groups vary and overlap in some degree, especially in certain species which may nest in any month but show a tendency toward spring breeding, but will be a satisfactory basis for discussion. Of the 22 species of Hawaiian sea birds, 12 generally start breeding in the spring; five, in the fall or winter; and five, in any month. An attempt to understand the factors which determine or have led to the establishment of the times of breeding, or the lack of regular times, can best approach the problem on the basis of these rather definite groups. (See table 6.)

Table 6.—Breeding seasons*

SPRING AND SUMMER BREEDERS	FALL AND WINTER BREEDERS	YEAR-ROUND OR IRREGULAR BREEDERS
Wedge-tailed Shearwater	Black-footed Albatross	
Christmas Island Shearwater	Laysan Albatross	
Newell's Shearwater	Bonin Island Petrel	
Dark-rumped Petrel	Markham's Storm Petrel	
Bulwer's Petrel		
Hawaiian Storm Petrel		
Red-tailed Tropic Bird		
White-tailed Tropic Bird		
Blue-faced Booby	Brown Booby	Red-footed Booby
Frigate Bird		
Grey-backed Tern		Necker Island Tern
Sooty Tern		Common Noddy
		Hawaiian Tern
		White Tern

* The three orders—Procellariiformes, Pelecaniformes, and Charadriiformes—are separated for comparison. Variations are shown in figures 12 and 13 and described in the text.

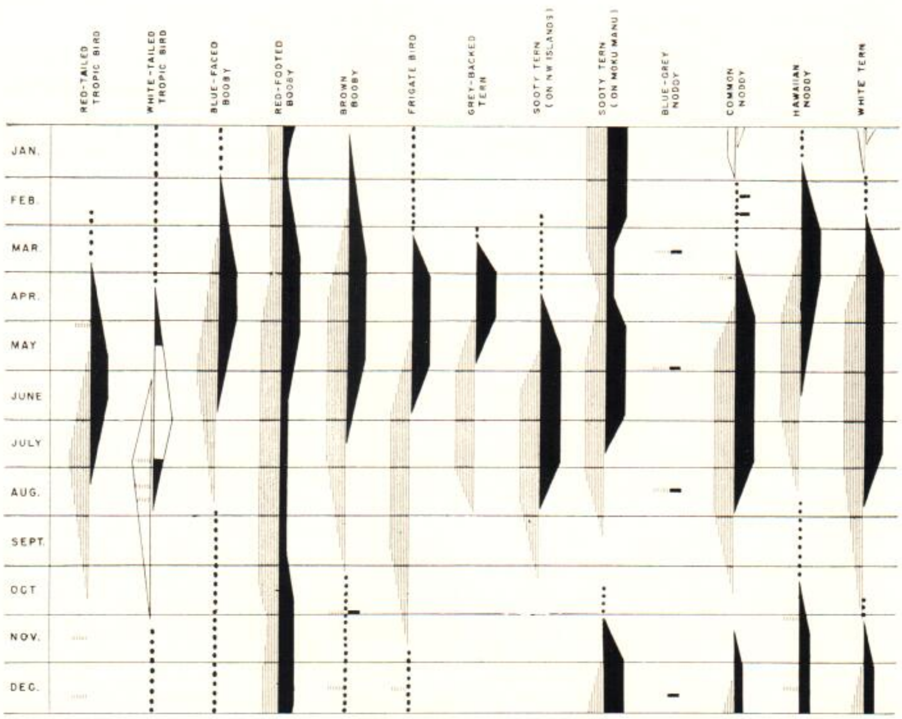

FIGURE 13.—Breeding seasons of Hawaiian Pelecaniformes and terns. Explanation is as for figure 12. Isolated records of eggs or young are shown by black or lined bars. Note that adults are present throughout the year especially in pelecaniforms. Extensive periods of egg-laying in some species make it impossible to show here the length of incubation or fledging.

Spring and Summer Breeders

Of the 12 species, about 54 percent of the total, of spring and summer breeders, six are procellariiforms; four, pelecaniforms; and two, terns—although of these, the sooty tern breeds in the fall and winter in some years in the southern Hawaiian Islands. Of these 12 species, seven start laying between late February (the blue-faced booby) and early April, while the others start laying even as late as early June (the wedge-tailed shearwater). In spite of this range in start of laying and considerable variation in the length of time before laying that the adults arrive and commence nesting, we can consider the following underlying causes for the establishment of this general type of breeding cycle:

1. Increasing periods of daylight in winter and spring. As shown in table 4, there is considerable change in the period of daylight even in the southern Hawaiian Islands. This change is decidedly greater in the most northern islands

and certain species, namely the sooty tern and red-footed booby, placed in the group of irregular breeders, are spring breeders here but may nest in the fall or throughout the year respectively in the southern islands. These species illustrate the principle of progressively later laying at increasing latitudes by a given species, as does also the Christmas Island shearwater, which breeds earlier in the spring in the main Hawaiian Islands than at their northwest end. It is noteworthy, though, that the majority of the spring breeders do not confirm this principle.

2. Greater amounts of suitable food in spring and summer. Insufficient evidence is available on this subject but tuna catches in the region of Oahu indicate a greater abundance of small fish in the summer (see p. 12).

3. Infrequent destructive storms in spring and summer. Meteorological data (see pp. 8 and 9) indicate that downpours and violent winds are not likely at this time of year. This factor has been considered of importance by Baldwin (1953) in determining the usual spring breeding of Hawaiian honeycreepers.

4. Seasonal temperature changes. At least in the case of the dark-rumped petrel, which nests even well above 7,000 feet and where snow falls at times, warmer average or higher minimum temperatures in spring or summer may be significant. The more marked seasonal temperature changes, as at Midway compared to Manana (table 1), may help explain the more regular spring breeding of some species, such as the sooty tern, at Midway. Seasonal temperature changes, although not great in the southern Hawaiian region, make one of the most regular environmental cycles and so may possibly be of importance in determining spring or summer breeding.

Although it is possible that some species of spring breeders have evolved in regions north of the Hawaiian Islands and retained an inherent breeding cycle, this is not known to be the case and seems unlikely. Rather, the above factors seem to have been responsible for the establishment of a spring cycle in species with more tropical distribution and affinities. In at least five of the 12 spring breeders, tropical populations of the species seem to have a more extended or a year-round breeding cycle. This suggests that Hawaiian conditions have established spring cycles in these species.

The fairly definite fall and winter rainy season on the major breeding islets off windward Oahu (see rainfall for Makapuu Point in table 2) suggests that spring breeding species may here respond to rainy seasons. However, this seems negated by the fact that many of the same species are spring breeders on Midway and other northwest Hawaiian Islands where rainfall is not noticeably seasonal.

Since a preponderance of Hawaiian sea birds breed in the spring and summer compared to other seasons, we may assume this to be the more usual result of Hawaiian conditions. Species breeding at other times may, as we shall later discuss, gain certain advantages, such as less crowded nesting conditions or less competition for food.

The possibility may be suggested that some of the species in this group are in more northern waters in the fall and winter months and hence are affected by the greater spring changes of higher latitudes. With the possible exception of the Hawaiian storm petrel, the meager off-season records do not support this explanation.

Fall and Winter Breeders

Of the five species, about 24 percent of the total, in this category, four are procellariiforms; and one, a pelecaniform. The range in the start of laying is again extensive with the two species of albatrosses starting in about mid-November, the Bonin Island petrel and Markham's storm petrel in early January, and the brown booby, variably from December through May. The four species of albatrosses or petrels are quite regular in starting egg-laying. With the exception of the Bonin Island petrel, which arrives some five months before laying, winter-breeding procellariiforms lay soon after returning to their islands. The brown booby, the only pelecaniform and only permanent resident of the fall and winter breeders, is the least regular in its laying. Its nesting activity seems to start fairly regularly about in December but with just a part of a population involved and without much success until perhaps two months later. The blue-faced booby, even though apparently laying chiefly in late winter, has been placed with the spring and summer breeders since most of its cycle would fall in these seasons. Nevertheless, this species would indicate an almost intermediate condition. Factors which may explain a fall and winter breeding cycle include the following:

1. Retention of a Southern Hemisphere spring and summer cycle. This factor seems likely to be especially significant in the Procellariiformes, which order is considered to be of southern origin where the majority of the species occur. The albatrosses, particularly, are a southern family with the Hawaiian species being two or three subtropical or northern Pacific breeding species. *Diomedea albatrus*, the only other northern species and one which is now extremely rare, also was known to lay in the fall (Alexander, 1954). It may be reasonable to suppose that since albatrosses rarely get to the tropics from their typical range in south temperate waters—there is one tropical species only, *D. irrorata* of the Galapagos region—species have only rarely become established in the Northern Hemisphere. The two Hawaiian species may thus be fairly recent members of the Hawaiian avifauna and be the more likely to have retained the spring and summer breeding habits of all nine of the Southern Hemisphere species. The above explanations may apply to some degree to the

winter breeding Bonin Island petrel and Markham's storm petrel, but cannot apply to their brown booby.

2. Longer nights during the breeding season. Significantly, the Hawaiian albatrosses have a non-breeding distribution, including winter and spring for immature birds, generally well north of their breeding islands; but, in spite of this, retain a breeding cycle starting in the late fall. Since the Procellariiformes probably feed a great deal at night (Alexander, 1954), when their chief food, squid, is most available, there may be this particular advantage to winter breeding. It must be pointed out, however, that the young are still being fed when nights have become shortest.

3. Decreasing periods of daylight. This factor seems to regulate the breeding cycle in some mammals (Bullough, 1951), so it may be considered as a possibility in birds. Such a factor might reinforce an inherent fall breeding cycle as found in the Hawaiian species of albatrosses, especially since their non-breeding distribution is in a northern region with greater decrease in day length. The same may be true of the Markham's storm petrel.

4. Less competition for nesting sites or food. Early authors have emphasized the advantage of seasonal succession of breeding times of species with similar nesting habits. This hardly seems valid in the spring when all winter breeders overlap the start of spring breeders, but it is certainly true that the group of fall and winter-breeding procellariiforms start their nesting, and complete incubation, with the minimum of competition. Their periods of raising young, when food demands are heaviest, overlap very little with the young of spring and summer breeders.

5. Long period of incubation and growth of young. Especially in the case of the two albatrosses, where incubation is over two months and the growth of the young about five months, spring laying with resulting fledging of young in fall or winter might be disadvantageous. It is true that the large sea birds in general have a long incubation and growth period and the young of some species, such as boobies, are fledged in the fall. However, these species do not leave for distant ocean regions as do the albatrosses. Summer conditions may be more suitable for initial flying of the young of albatrosses, the most highly specialized of gliders.

It may be pointed out that factors that were suggested as significant or advantageous in spring and summer breeders might be considered insignificant or disadvantageous in fall and winter breeders. Thus the poorer weather conditions in the winter may be a disadvantage. Presumably, though, such detrimental factors are not great enough to offset the beneficial factors of winter breeding to certain species or to cause the loss of an inherent winter breeding cycle. Any factor involved in breeding cycles may affect each species differently, and stormy weather, as an example, may be less significant to winter breeding species, since these are all large or burrowing forms.

Irregular or Year-Round Breeders

Of the five species (about 24 percent of the total) in this category, one is a pelecaniform, the red-footed booby, and four are terns: Necker Island, common noddy, Hawaiian, and white. Although the red-footed booby may have eggs at any time of the year, especially in its southern breeding colonies, as on Ulupau Head and Moku Manu, it shows a definite tendency toward starting breeding in late winter. This is particularly true of its northern breeding colonies, such as those of Midway.

The noddy, Hawaiian, and white terns have their egg-laying times chiefly spread out from March through August. At the same time, the red-footed booby and these three terns, and possibly the Necker Island tern, show a definite tendency toward a secondary breeding cycle starting with egg-laying in the late fall. Factors which may explain the irregular breeding of the above group of sea birds may include the following:

1. Lack of marked environmental changes. There is little to indicate that any of these species have or have had a regular yearly breeding season anywhere in their pan-tropical and sub-tropical ranges. Partial exceptions would be some regularity in breeding of the red-footed booby around northern South America correlated with marked rainy seasons (Murphy, 1936), and the white tern at one of the highest latitudes at which any of the species breed, 30° S. near New Zealand (Oliver, 1955). In the Hawaiian Islands, apparently, annual environmental changes even at 28° N. are not marked enough to have established annual breeding seasons in those species which are least responsive to changes.

2. Possible advantages of prolonged breeding seasons. The breeding potential may be increased if the individuals of these species breed more than once a year. If food supply or nesting space is limited at any time of the year, a spreading out of breeding could be advantageous.

3. Shortness of breeding cycle. Terns as a group show more variation in breeding cycles than either procellariiforms or pelecaniforms. This may well be correlated with terns having a much shorter period of incubation and growth—about two months compared to four to seven months—and seems associated with a greater renesting ability. Terns are physiologically able, for instance, to repeatedly lay more eggs if their eggs are taken or destroyed, whereas albatrosses are not.

4. Spring and fall breeding. A tendency toward two seasons can be noted in all of these species, but that the same individuals are involved seems impossible in the booby, with its long incubation and growth periods, and unlikely in the terns, where relatively few individuals start nesting in the fall. The best, although not conclusive, evidence of regular breeding twice a year seems to be for the sooty tern on Christmas Island (King, 1955).

5. Size of populations. The markedly regular spring breeding of the great colony of common noddies on Manana, by far the largest colony of any of the irregular breeders, is striking. Breeding of this species in small numbers is generally earlier and less regular (Richardson and Fisher, 1950), even on the nearby islands of Mokolea and Moku Manu. Thus there seems to exist, at least in this species, a correlation between large numbers and a definite cycle, with a spring-summer cycle proving most advantageous. In the large red-footed booby colony on Ulupau Head, however, where numbers may be at their maximum at different times of the year, no regular breeding cycle has become established.

6. Irregular severe storms. Some species which breed in the winter and early spring are particularly subject to extensive destruction of their eggs, nests, or young, because the worst wind and rain storms usually occur at that time of year. Thus sooty terns and red-footed boobies have been forced several observed times to begin their nesting over again on Moku Manu and Ulupau Head.

All of the Hawaiian sea birds which lack a regular breeding season show some tendency toward a spring cycle, this being especially marked in the common noddies on Manana. Perhaps in these species, all of which probably have had a tropical origin and year-round breeding in that region, a consistent spring and summer cycle, as for the majority of other Hawaiian sea birds, is still becoming established. There is the possibility, too, although confirmation is lacking, that irregular species were the latest to arrive in the Islands so there has been less time for the establishment of regular cycles.

DISCUSSION AND SUMMARY

The great variety and frequently large populations of Hawaiian sea birds attest generally favorable conditions for breeding, although these factors are not so favorable as they were before the influence of man. The most favorable conditions are found on many of the unfrequented islands which offer a variety of nesting habitats, such as extensive open areas, sand or soil suitable for burrowing, cliff areas, and bushes and trees. Also favorable is the general lack of predators on all but the main islands, where cats and mongooses may be common and where human predations have been common in the past. The establishment in 1909 of the Hawaiian Island Bird Reservation, encompassing approximately all but the main islands, has been beneficial. However, it cannot compensate entirely for the early devastation caused by feather hunters and introduced rabbits and the more recent devastation caused directly or indirectly by war (Fisher and Baldwin, 1946) on some leeward islands.

The feeding and climatic conditions are also markedly favorable for sea birds in the Hawaiian Islands. Extensive shoal areas and rich moderately cool waters are essential in producing the fish and squid utilized by sea birds.

Convergence of cool waters from the north and warm waters from the south, and up-welling of enriched waters near the islands are probably important in maintaining this rich food supply. The year-round mild climate, with few severe storms, moderate or little rainfall in the breeding areas, and no fog, appear also to be particularly suitable.

The above favorable conditions for sea bird abundance combined with various other factors have led to the establishment of a variety of breeding cycles in Hawaiian sea birds. The latitude (20° N.) of even the most southern islands is sufficient so that seasonal changes, as in period of daylight and temperature, seem to be sufficient to have established or maintained a spring-summer breeding cycle in just over half of the species; and in the latitude (28° N.) of the most northern islands these changes are even more marked. Overriding the factors determining spring-summer cycles, and associated with fall and winter breeding, are such factors as inherent tropical or Southern Hemisphere breeding patterns and less competition for food or nesting sites. Apparently associated with irregular breeding habits are such factors as the lack of sufficient seasonal change for some species, small or scattered populations, and destructive storms.

Where breeding cycles occur, as they do in most Hawaiian sea birds and to some degree in even the most irregular breeders, they are annual cycles, whether starting in spring or fall or other times. It seems likely that when irregular breeding occurs, the individual birds are still following an annual cycle. There is the possibility, though, of breeding more than once a year in some terns. In any case, it has seemed impossible to find in Hawaiian sea birds any definite non-annual breeding cycle comparable to the nine and a fraction month cycle of sooty terns on Ascension Island (Chapin, 1954). Presumably, environmental conditions are sufficiently cyclical on an annual basis in the Hawaiian region to preclude other types of cycles.

The general question of how colonial nesting habits may affect the time or success of breeding in Hawaiian sea birds is of interest. Colonial nesting is not characteristic of the majority of the species—with suitable nesting conditions in parts of certain islands sometimes bringing populations loosely together to give what might be called a false colony—but is fairly marked in the boobies and noddy terns and quite so in the sooty tern. The principle illustrated by the studies of Fisher and Lockley (1954) in Atlantic sea birds of large colonies starting to nest earlier because of competition is not shown by Hawaiian colonies. Here, smaller colonies, as of noddy and sooty terns on Moku Manu, generally start to breed much earlier than greater colonies on the same island or on Manana. However, many of the scattered fall and winter nestings of irregularly breeding species, as noddy terns on French Frigate or red-footed boobies on Ulupau Head, are unsuccessful and appear to exemplify the need for a minimum number of a colonial species to initiate successful breeding. It does seem true that the irregular Hawaiian species, and also some of the more regular ones, such as the sooty tern and brown booby, often suffer a marked decrease in nesting success due to abortive nesting attempts and the lack of a well-defined breeding cycle.

The present study has tried primarily to accumulate adequate field data and to analyze possible external or environmental controls of breeding cycles. It has not investigated internal inherent reproductive rhythms by such methods as experiment or histologic study. It may be pointed out, though, that breeding activity at any time reflects the internal state of a bird. As has been well summarized by Bullough (1951), this internal reproductive state, especially as shown in birds by the histology and size of the gonads, is under a hormonal control which may be attuned to different seasonal environmental changes in different species. The most definite breeding cycles are usually associated with the most definite seasonal environmental changes, so in Hawaii, where seasonal changes are relatively small, it is not surprising that many sea birds show variations in their breeding cycles and show a tendency toward extended breeding. Much of the cyclical breeding of the species is sufficiently regular, however, to indicate definite environmental control of the internal reproductive rhythm. Irregular breeding of certain Hawaiian sea birds may indicate a weakness both of environmental controls and inherent rhythm, conditions that may reflect the tropical origin and general distribution of these species. Fall and winter breeding, as in the two albatrosses, may indicate, though, a particularly strong inherent rhythm which dominates the usual environmental controls. Adequate evaluation of the relative strength of inherent versus environmental controls of breeding cycles in Hawaiian sea birds must probably await further study and experimentation.

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