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BREEDING BIOLOGY
OF THE
BLUE FACED BOOBY
ON GREEN ISLAND,
KURE ATOLL

CAMERON B. KEPLER

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OF THE BLUE-FACED BOOBY
Sula dactylatra personata
ON GREEN ISLAND, KURE ATOLL

PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB, NO. 8

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Breeding Biology of the Blue-faced Booby

Sula dactylatra personata

on Green Island, Kure Atoll

by

CAMERON B. KEPLER

CAMBRIDGE, MASSACHUSETTS

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This paper is a modification of my doctoral dissertation, submitted to the faculty of the graduate school at Cornell University in 1968. I thank the members of my graduate committee, Dr. W. C. Dilger, chairman, and Drs. W. T. Keeton and L. C. Cole, for their considerable help and encouragement. I thank Dr. Olin S. Pettingill, Jr. and his staff at the Laboratory of Ornithology for the substantial use of their facilities, including a photographic dark room, during the preparation of this monograph. Students at the laboratory contributed many very useful discussions. R. B. Clapp and P. W. Woodward, Pacific Program, read the entire manuscript and made many helpful comments. Special thanks go to my wife Kay, who spent uncounted hours helping proofread the manuscript and drafting the final figures. Her help and moral support were invaluable.

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INTRODUCTION

The work upon which this paper is based represents a small part of the investigations of the Pacific Ocean Biological Survey Program (POBSP).¹ Administered by the Smithsonian Institution, the POBSP is an extensive examination of the avifauna of a large segment of the Pacific Ocean bounded by latitudes 30° N. and 10° S., and by longitudes 180° W. and 150° W. Within this 11,137,000 km² area, regular at-sea observations have yielded much information on the migration and distribution of oceanic birds. Periodic expeditions to the Line and Phoenix Islands have determined the breeding phenology and ecology of seabird populations there. Farther north, Johnston and Kure Atolls have been permanently manned by POBSP staff. In this way the life cycles of many breeding seabirds on these atolls are being studied (see Humphrey, 1965).

Field work for the project was begun in 1963 and continues at the present time. I joined the POBSP in June 1964 and remained in the Pacific, except for one month, until December 1965. In addition to my stay on Kure, detailed below, I spent one month at sea, seven months on Johnston Atoll, and two months in the Line and Phoenix Islands.

The present paper is an outcome of the efforts of many Pacific Program members, extending from January 1964 through August, 1965. My work with Blue-faced Boobies began on 25 October 1964 and, except for a three-week absence from Kure in December, continued until 28 February 1965. After my departure, observations on the nesting activities were continued through the 1965 breeding season and the weekly census (see Appendix) was continued through April by A. H. Anderson. When I arrived in October the boobies had been followed through one breeding cycle and the entire population had been banded, either by POBSP staff or by Chandler Robbins and others from the U.S. Bureau of Sports Fisheries and Wildlife. The breeding outcome of all NAF pairs was documented. I could, therefore, compare the breeding activities of 1965 with those of known pairs in 1964. Many of the data in Chapters 3 and 4 result from this comparison. I gathered all the data for the behavioral sections of this paper between 25 October 1964 and 25 February 1965.

¹ Paper no. 45 of the Pacific Ocean Biological Survey Program, Smithsonian Institution.

CHAPTER 1

ENVIRONMENT

KURE ATOLL

Kure Atoll is the northwesternmost atoll of the Hawaiian Leeward Islands, a low-lying string of volcanic and coral atolls extending approximately 1,600 km northwest from the main Hawaiian Islands. Lying at 28°25' N. latitude, 178°10' W. longitude, Kure is 1,890 km northwest of Honolulu and is centered in the Pacific Ocean some 3,480 km southeast of Tokyo and 5,210 km west of Baja California, Mexico. The atoll has an almost circular fringing reef, with a diameter at its widest point of approximately eight kilometers and a circumference of 24 km. The only permanent island is Green Island, located in the southeast section of the lagoon. Transitory sandspits occur to the west of the main island, forming in early spring and often vanishing during winter storms.

Green Island (Fig. 1.1) is low-lying and crescentic in shape, with the long axis of the crescent extending from the west to the north. It is approximately 2.3 km long by 0.6 km wide at its widest point, perpendicular to the axis. There are 87 hectares of land, of which 57 are vegetated. Exposed eastern and southern shores are from 15 to 30 m wide, moderately sloped, and strewn with coral rocks. The northern beaches which face the lagoon are much wider (up to 60 m in places) and consist of fine sand. These latter beaches slope gradually to brush-covered (*Scaevola taccada*) dunes from two to 4.5 m in height. A flat six-hectare central plain averaging about two meters in elevation occupies the center of the land.

Within the past 10 years two major sources of disturbance have vastly altered the original appearance of the island. In 1959 a series of access paths to the central plain from the beach were bulldozed in an effort to improve the habitat for Laysan Albatrosses, *Diomedea immutabilis*, (Clay, 1961). More permanent changes began in 1960, with the construction of a Coast Guard Loran Station consisting of three buildings, water and fuel tanks, a 190 m Loran Tower, and a runway 1,220 m long by 60 m wide. The buildings cover about 2.4 hectares. Radial wires and guywires of the Loran Tower form a 259 m diameter circle over most of the central plain. A 21 m radar reflector tower stands on the west beach. Paths cut during tower construction and habitat "improvement" are now largely overgrown, but the remaining overhead obstacles to seabirds account for continual mortality.

CLIMATE

Weather data have been amassed in quantity from Midway Naval Station, 90 km east of Kure. Because no long-term weather data are available from Kure, Midway data will be briefly summarized below.

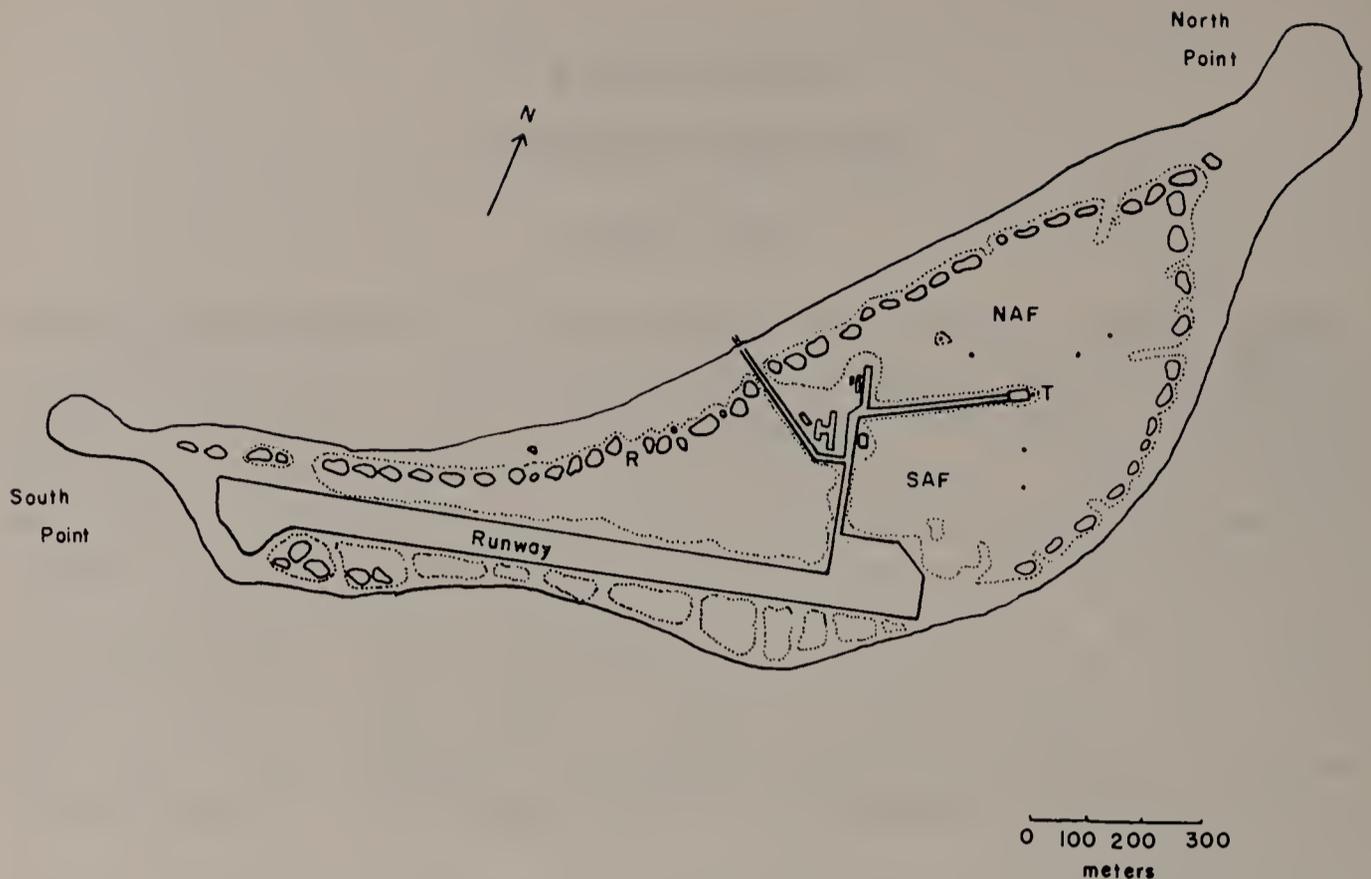


FIG. 1.1. Green Island, Kure Atoll, Hawaiian Leeward Islands (after Wirtz, 1968). Dotted lines enclose vegetated portions; solid lines delimit sand dunes. R refers to radar reflector tower and T to Loran tower. NAF and SAF stand for north and south antenna fields (see text).

All information is based on a summary of the years 1953-1963 by the Nav. Sta. Midway Forecast Handbook and Air Weather Service, MATS Climate Center USAF, as presented by Wirtz (1966). No appreciable difference has been found between Midway and Kure weather.

The climate of the area is typically marine. In summer the Pacific High is dominant, resulting in marine tropical easterlies (trades). In winter (especially November through January) the Aleutian Low extends south over Midway and Kure. The climate is then variously affected by marine Pacific (cold) air, or marine tropical trades. The resultant annual fluctuations in temperature, rainfall, wind force, and wind direction are represented in Figures 1.2 to 1.4.

Specific information on the weather of Kure Atoll has been kept by POBSP personnel during their stay on the island. Details for the 1964-1965 seasons are given in Figures 1.5 and 1.6. A discussion of the pertinent factors is presented below in the section on breeding biology.

FLORA

In 1923 the Tanager Expedition found 13 species of vascular plants on Green Island (Christophersen and Caum, 1931). Clay (1961) reported six additional species in October 1959. Lamoureux (1961) found 23 additional species, 22 of them weeds or cultivated plants introduced during and after the construction of the Coast Guard facilities. The flora now consists of 41 species, as one of Clay's six new plants is no longer present (see Lamoureux, 1961).



FIG. 1.2. Mode of monthly means for a ten-year period, 1953-1963, and the range of maximum and minimum modes of temperatures for Midway Atoll (after Wirtz, 1966).

Of importance to the present study are the plants found in the six-hectare central plain. This flat area is completely ringed by the hardy xeric bush, *Scaevola taccada*. *Scaevola* is the dominant species on the island, and forms a margin along the edges of the Blue-faced Booby colonies that can be penetrated only with great difficulty. It may be important to the birds by providing them protection against wind and wind-borne sand during winter storms. Plants on the central plain include:

<i>Eragrostis variabilis</i>	Gramineae
<i>Boerhavia diffusa</i>	Nyctaginaceae
<i>Lepidium o-waihiense</i>	Cruciferae
<i>Tribulus cistoides</i>	Zygophyllaceae
<i>Ipomoea indica</i>	Convolvulaceae
<i>Solanum nelsoni</i>	Solanaceae
<i>Verbesina encelioides</i>	Compositae

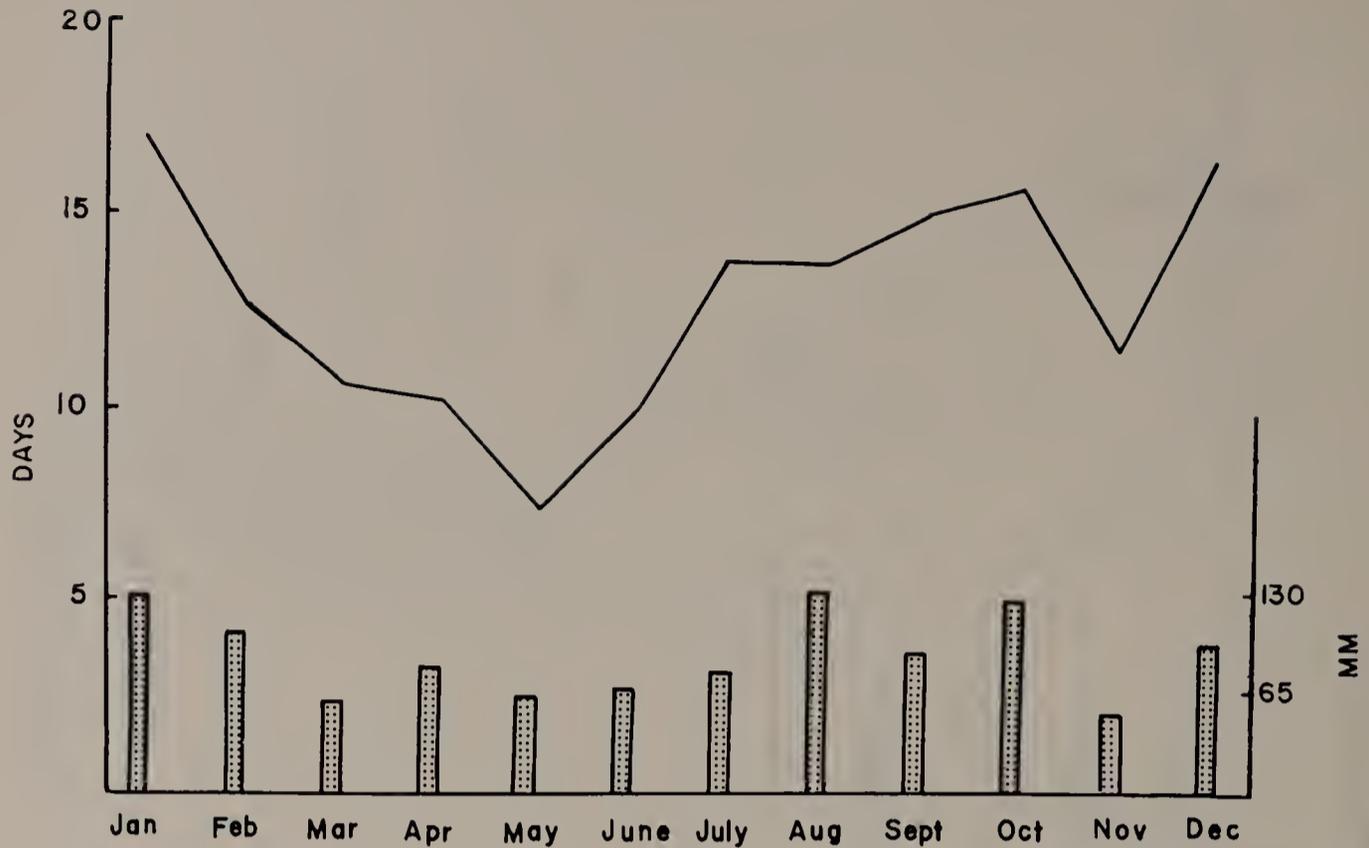


FIG. 1.3. Mean monthly precipitation (histogram) and mean number of days with measurable precipitation (line graph) for Midway Atoll, 1953-63 (after Wirtz, 1966).

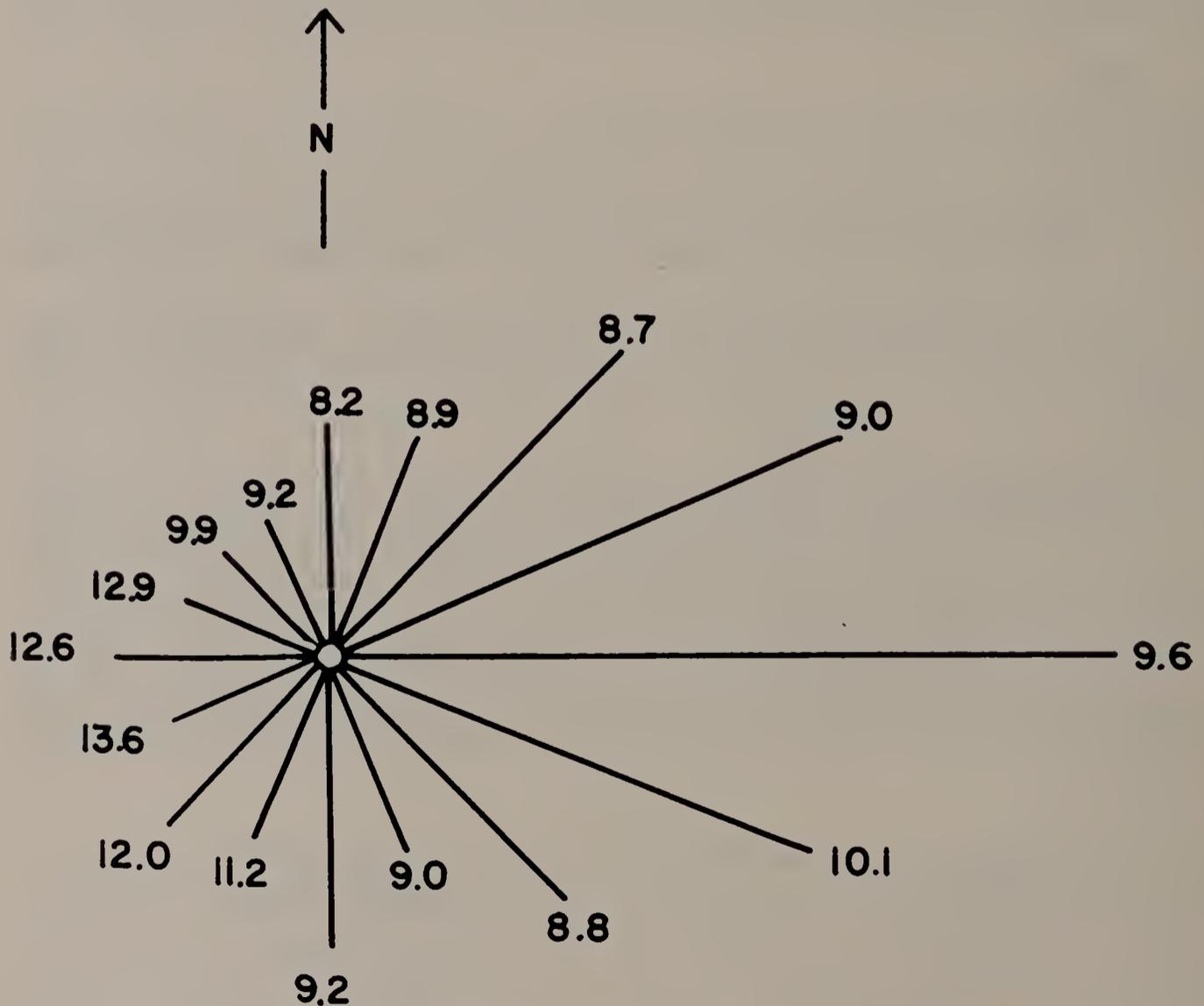


FIG. 1.4. Wind direction and speed at Midway Atoll, 1953-63. Length of directional line indicates percentage of observations from that direction; figure at end of the direction line is mean wind speed in knots (after Wirtz, 1966).

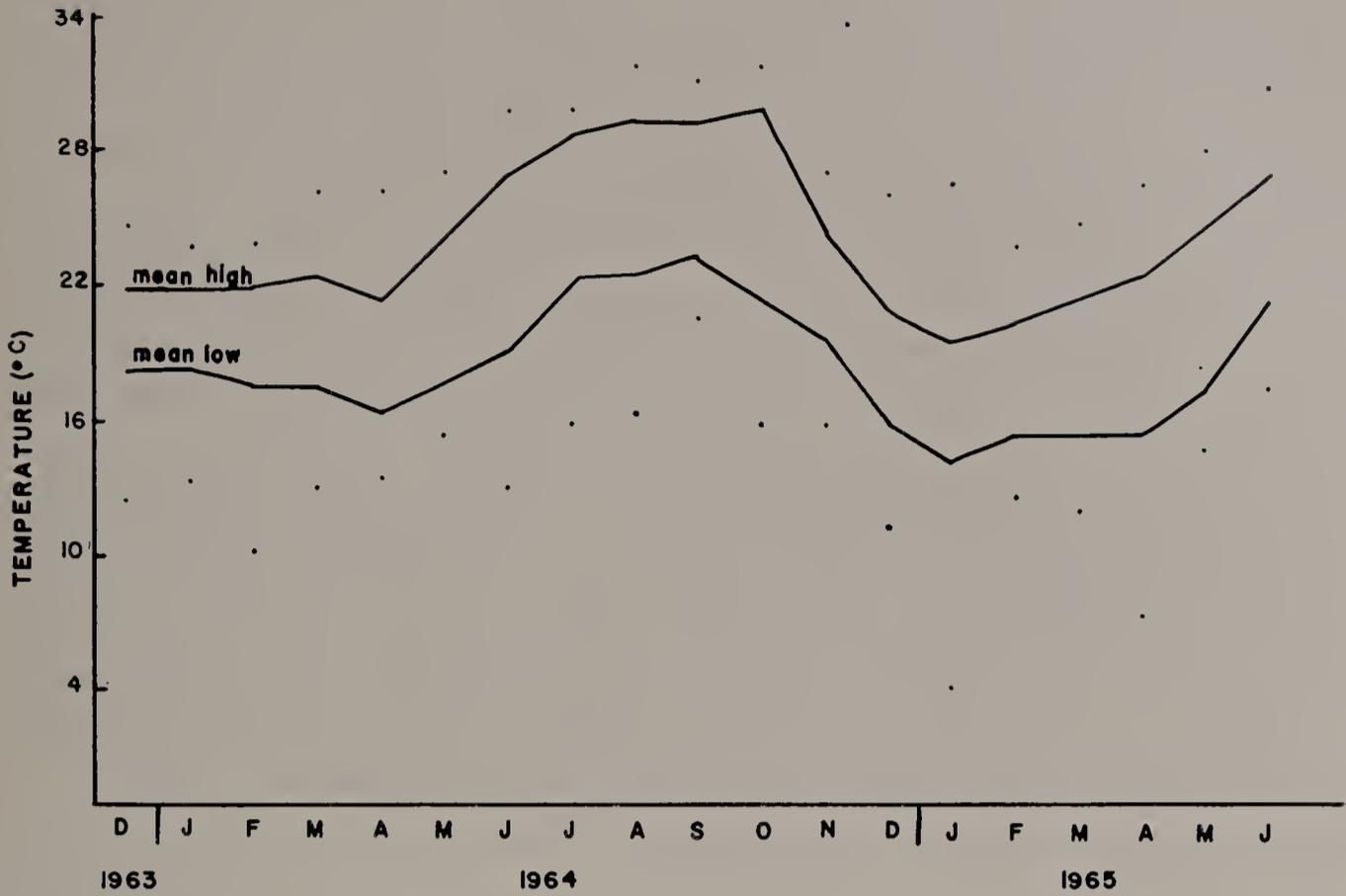


FIG. 1.5. Mean and extreme high and low temperatures, Green Island, December 1963-June 1965.

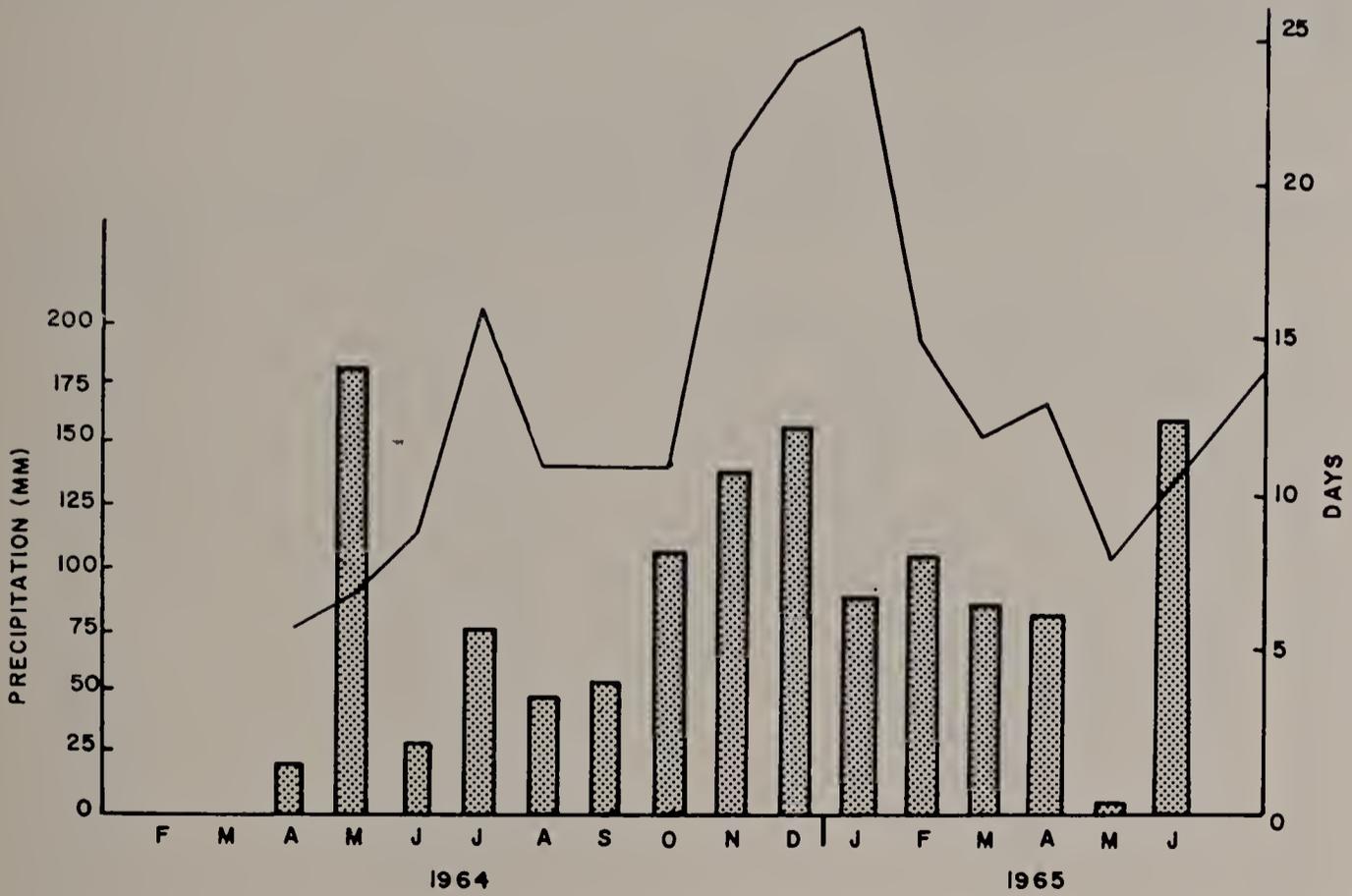


FIG. 1.6. Precipitation (histogram) and number of days with measurable precipitation (line graph, right legend), Green Island, April 1964-June 1965.

All but the last plant are native to the island. *Tribulus* is a dense, low-lying bush that has extremely sharp thorns which are often found embedded in the feet of birds frequenting the plain. *Boerhavia*, with its sticky seeds, is often seen adhering to the plumage of the seabirds. These native plants form a thick green mat during the winter months when the boobies breed. It is over this mat that the birds walk when courting and through which they must tear in order to make their nest scrapes. Twigs from these plants play important roles in the courtship ceremony and during agonistic encounters. Behavior that utilizes this vegetation will be discussed in detail in Chapters 5 and 6.

Verbesina, accidentally introduced from Midway, is a hardy, tall (up to two m) annual that poses a threat to the nesting seabirds of the central plain, especially the Blue-faced Booby and the Laysan Albatross. Since its introduction it has spread over thousands of square meters of the plain, growing so thickly that native vegetation is completely crowded out. Birds nesting in the open will not be able to breed if *Verbesina* continues to take over suitable nesting habitat.

FAUNA

The Hawaiian monk seal (*Monachus schauinslandi*) and the Polynesian rat (*Rattus exulans*) are the only native mammals on Green Island. Seals use the beaches of the atoll as hauling and calving areas. As many as 80 animals have been counted on Green Island at one time, especially during rough weather when sandspits in the lagoon are washed away. The rats occur seasonally in vast numbers and prey heavily on the breeding seabirds (Kepler, 1967). For an account of the ecology of this species, see Wirtz (1968).

TABLE 1.1
BREEDING BIRDS OF GREEN ISLAND, KURE ATOLL
(after Wirtz, 1966)

Name	Resident	Maximum population
Black-footed Albatross, <i>Diomedea nigripes</i>	Nov.-July	1,150
Laysan Albatross, <i>D. immutabilis</i>	Nov.-July	7,000
Wedge-tailed Shearwater, <i>Puffinus pacificus</i>	March-Nov.	3,500 ¹
Christmas Shearwater, <i>P. nativitatus</i>	March-Oct.	100
Bonin Petrel, <i>Pterodroma hypoleuca</i> ²	Aug.-April	2,500 ¹
Red-tailed Tropicbird, <i>Phaethon rubricauda</i>	Feb.-Nov.	2,200
Blue-faced Booby, <i>Sula dactylatra</i>	permanent	160
Brown Booby, <i>Sula leucogaster</i>	permanent	90
Red-footed Booby, <i>Sula sula</i>	permanent	550
Great Frigatebird, <i>Fregata minor</i>	permanent	1,600
Sooty Tern, <i>Sterna fuscata</i> ³	March-Aug.	5,500
Gray-backed Tern, <i>Sterna lunata</i>	March-Aug.	50
Brown Noddy, <i>Anous stolidus</i>	March-Dec.	1,350
White Tern, <i>Gygis alba</i>	permanent	30

¹ Estimate only.

² Unsuccessful breeder.

³ Newly established; colony growing annually.

Introduced to the island in recent years are dogs, maintained by Coast Guard personnel, and a squirrel monkey, released and resident without human aid from 1961 to 1967.

The most complete information available concerning the birds of the atoll is that collected by POBSP personnel. The only published reports on this seldom-visited area are the studies of Kenyon and Rice (1958), Udvardy (1961), Robbins (1966), and, recently, Clapp and Woodward (1968). The POBSP has recorded more than 50 species from the atoll, most of which are migrants and accidentals. The 14 breeding species are listed in Table 1.1. In addition, the following five shorebirds are regular migrants that over-winter: Golden Plover (*Pluvialis dominica*), Ruddy Turnstone (*Arenaria interpres*), Bristle-thighed Curlew (*Numenius tahitiensis*), Wandering Tattler (*Heteroscelus incanum*), and Sanderling (*Crocethia alba*). The remaining 31 species are accidental, and include ducks, shorebirds, gulls, alcids, and a few passerines (Wirtz, 1966; Clapp and Woodward, 1968).

Reptiles are represented by occasional Green Sea Turtles (*Chelonia midas*) and introduced geckos (*Hemidactylus frenatus*). Amphibians do not occur.

CHAPTER 2

TAXONOMY, DISTRIBUTION, AND MORPHOLOGY

TAXONOMY

Boobies are placed in the family Sulidae, one of six families comprising the order Pelecaniformes. The outstanding taxonomic feature of the order is the webbing together of all four toes (totipalmate), the hallux being turned forward and webbed to the second digit. Except for anhingas and some cormorants and pelicans, members of the order are oceanic.

Sulids are characterized by their obsolete nostrils; bare gular skin; long, stout, unhooked, serrate bills; wedge-shaped tails; pneumatic pouches under the skin of the neck and breast; stout stocky legs; and heavy bodies—all adaptations to their habit of plunge-diving, often from considerable heights, to obtain food. The nine species within the family fall naturally into two groups, the three temperate gannets and the six tropical boobies. Although different in appearance and behavior, the degree of relationship between them is disputed, some authors favoring a single large genus, *Sula*, to encompass them all (Nelson, 1964 and following; Thomson, 1964), others preferring two genera, keeping the gannets, *Morus*, distinct from the smaller boobies, *Sula* (Alexander, 1928; Peters, 1931; Murphy, 1936; Palmer, 1962; Van Tets, 1965; Simmons, 1967). The latter scheme is adopted here.

DISTRIBUTION OF THE SULIDAE

Gannets breed in temperate waters and have a definite breeding season followed by a post-breeding dispersion to lower latitudes. In contrast, the six boobies are tropical, with few populations breeding at latitudes of 30° or above. The Blue-faced Booby, Red-footed Booby, and Brown Booby have pan-tropical distributions, and are each broken into many isolated populations having subspecific designation. The Blue-footed Booby (*S. nebouxii*) and the Peruvian Booby (*S. variegata*) are found in the tropical eastern Pacific. Abbott's Booby (*S. abbotti*) breeds only on Christmas Island in the Indian Ocean (Gibson-Hill, 1947; 1950a,b). In addition to being smaller than gannets, most boobies are sexually dimorphic and some adults may be found within their colonies throughout the year.

DISTRIBUTION OF THE BLUE-FACED BOOBY

The Blue-faced Booby has a cosmopolitan distribution in warm oceanic waters. The distributions sketched below are taken from Peters (1931) and King (1967). The nominate race, *S. d. dactylatra*, is found in

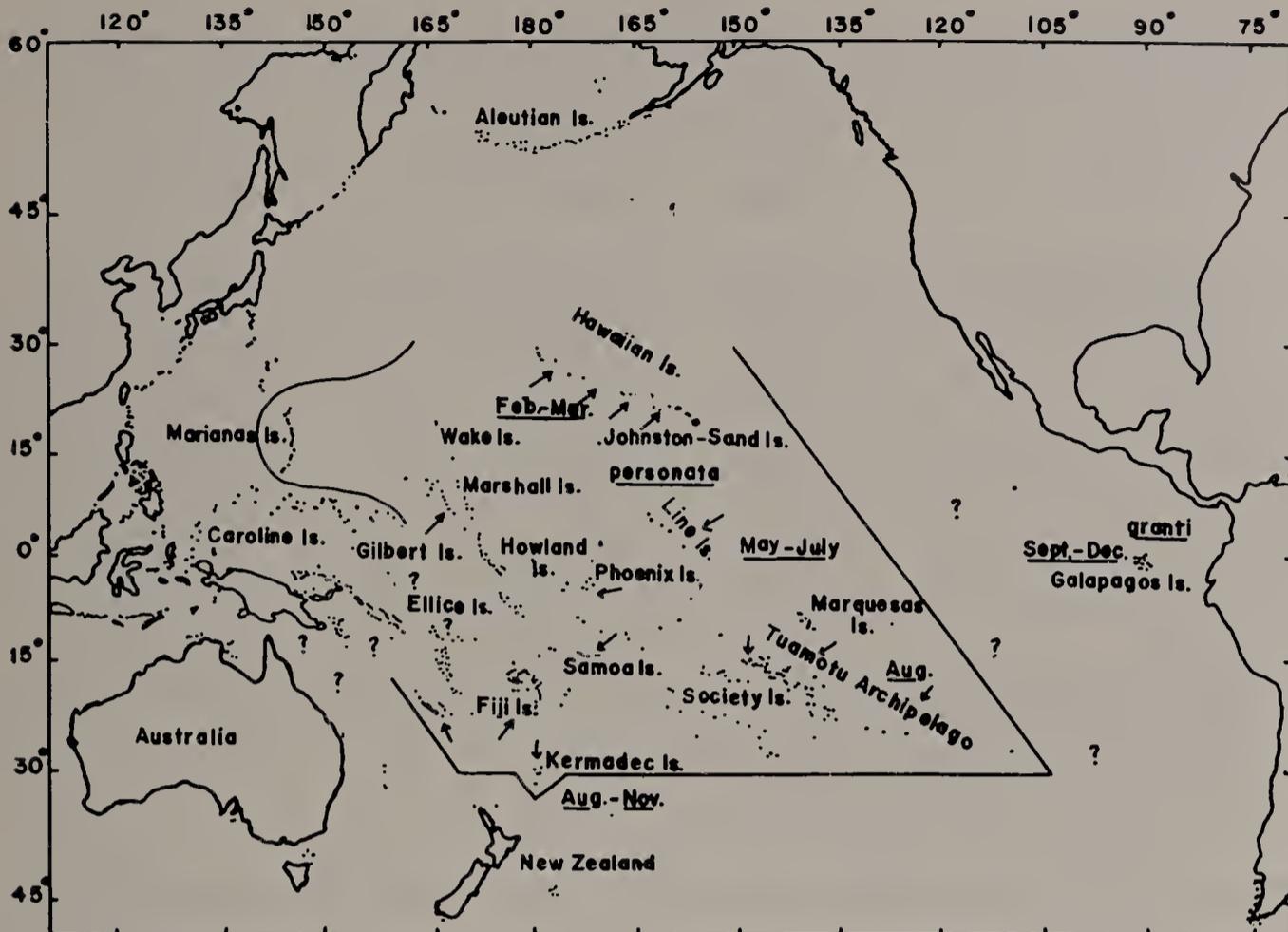


FIG. 2.1. Geographic distribution, breeding locations, and peak egg dates for *S. d. personata* and *S. d. granti*.

the Atlantic Ocean from the West Indies to Ascension Island. Three distinct races have been described from the Pacific Ocean: *S. d. californica*, restricted to the islands off the west coast of Mexico; *S. d. granti*, restricted to the Galapagos; and *S. d. personata*, distributed virtually throughout the rest of the tropical Pacific (see Fig. 2.1). The northern-most breeding colony of *S. d. personata* is on Kure Atoll, and the species ranges south to the Kermadec Islands (31° S. lat.), where a small colony breeds each year. In the waters around Australia it approaches, and may overlap, the range of a race that may not be separable from it. This race, *S. d. bedouti*, is found north of western Australia, breeding from the Cocos-Keeling Islands to the Banda Sea (Gibson-Hill, 1950a). A breeding record from Christmas Island (Indian Ocean) is believed to be incorrect (Gibson-Hill, 1950a). The remaining race, *S. d. melanops*, is found in the western Indian Ocean.

DESCRIPTION OF THE ADULTS

The Blue-faced Booby, largest of the six boobies, is sexually monomorphic in plumage but dimorphic in size. Adults are mainly white, with rectrices and remiges, and some coverts, black. The facial skin is blue-black, and forms a dark mask around the bill. The foot and leg color is variable, but is generally an olive-drab or bluish-gray in Kure birds. Females are significantly larger than males. Twenty-seven adults

TABLE 2.1
MEASUREMENTS OF 27 ADULT MALES AND 27 ADULT FEMALES, OCTOBER 1965

Character		Males	Females
Weight: ¹	mean	1,879.89 gr.	2,094.78 gr.
	range	1,503-2,211 ²	1,616-2,353
Culmen: ³ (from base)	mean	102.74 mm.	104.96 mm.
	range	97-107	98-109
Tarsus: ³	mean	63.56 mm.	65.15 mm.
	range	60-67	60-70
Middle toe: ³	mean	91.81 mm.	94.44 mm.
	range	80-99	88-102
Wing: ¹ (flat)	mean	439.81 mm.	456.22 mm.
	range	427-462	435-476
Tail: (from base)	mean	187.81 mm.	192.41 mm.
	range	170-215	173-205

¹ Differences between sexes significant at .001 level.

² Weights available from only 26 males.

³ Differences between sexes significant at .01 level.

of each sex were measured (see Appendix). These data are presented in Table 2.1. The only character not differing significantly between the sexes is tail length. The bills of both sexes are yellow, but in the breeding season that of the male is a richer, brighter color. The most striking difference between the sexes is the voice. Adult females, and immatures of both sexes, produce a series of hoarse honks and croaks, not unlike the sounds of a goose. The males utter a shrill, highly pitched whistle, and the advertising call is thrush-like in quality. Murphy found that this difference is the result of a different male vocal apparatus, appearing at sexual maturity, consisting of a "double sounding-box at the juncture of the trachea and bronchial tubes" (Murphy, 1936, p. 834).

PREVIOUS STUDIES

There are numerous reports on short visits to islands throughout the tropics that mention the occurrence of boobies. Two detailed studies of the biology of the Blue-faced Booby have recently been completed. Populations on Ascension Island (*Sula d. dactylatra*) were studied over an 18-month period by D. F. Dorward (1962a,b). More intensive work with *S. d. granti* has recently been concluded in the Galapagos (Nelson, 1967a). Nelson has produced a very thorough account of the behavior, and promises an equally intensive study of the ecology, of the Galapagos subspecies. My work (on *S. d. personata*) will be compared with that of these authors whenever possible. To facilitate cross-comparisons by future workers, I have used Nelson's (1967a) terminology and organized the behavior section in essentially the same way as his. Differences and similarities between the biology of these three races will be continually stressed.

CHAPTER 3

THE COLONY

INTRODUCTION

When not at sea, Blue-faced Boobies are usually confined to a relatively small portion of the atoll. I never observed them perching in the *Scaevola*, and they were rarely encountered on the beaches, although I visited these areas hundreds of times during the study. Individuals roost almost exclusively in the central plain, and restrict their nesting to this area. This central location is unusual, as most Blue-faced Booby colonies in the central Pacific are located at or near the periphery of their islands. Residents stop on the lagoon's sandspits and may roost on exposed portions of the reef at low tide. On 16 November 1964 I made a boat trip around the entire lagoon, finding four Blue-faced Boobies on a sandy islet within one kilometer of Green Island. Two of these were birds new to the atoll. They may have been stragglers from other atolls or possibly young from previous years returning for the first time. The other birds were color-marked residents.

POPULATION SIZE

Because Blue-faced Boobies are conspicuous and restricted to the central open areas of the island, censuses are believed to have included most (at least 95%) of the Kure population. As populations are highest at night, night censuses have been conducted by POBSP personnel (see Appendix). Over the two and one-half year census period, the average number of Blue-faced Boobies was about 140. The population, however, has steadily decreased during the study; the number found in corresponding months of successive years has been progressively lower. The highest recent population levels (1963) are lower than those in the past. Munter (cited in Wirtz, 1966) found 200 birds in March 1915, and Wetmore (1923) found approximately 200 pairs in April 1923. In November 1963, POBSP counts of 275 and 225 individuals are reported, but these numbers are so far above any other counts that I question their accuracy. Excepting these counts, no recent survey has recorded a population of more than 200 birds. The Fish & Wildlife Service also censused the boobies on Green Island (Robbins, 1966); these numbers appear on Figure 3.1 as dots with dates. I assume these counts were made during the day, as the numbers are very low. They may not be comparable to our counts because the number of birds observed is dependent upon the time of day when the census is conducted (see Fig. 3.2). The observed recent decline may be a result of the continued disturbance caused by Coast Guard personnel and POBSP scientific efforts; some birds also die by striking the guywires

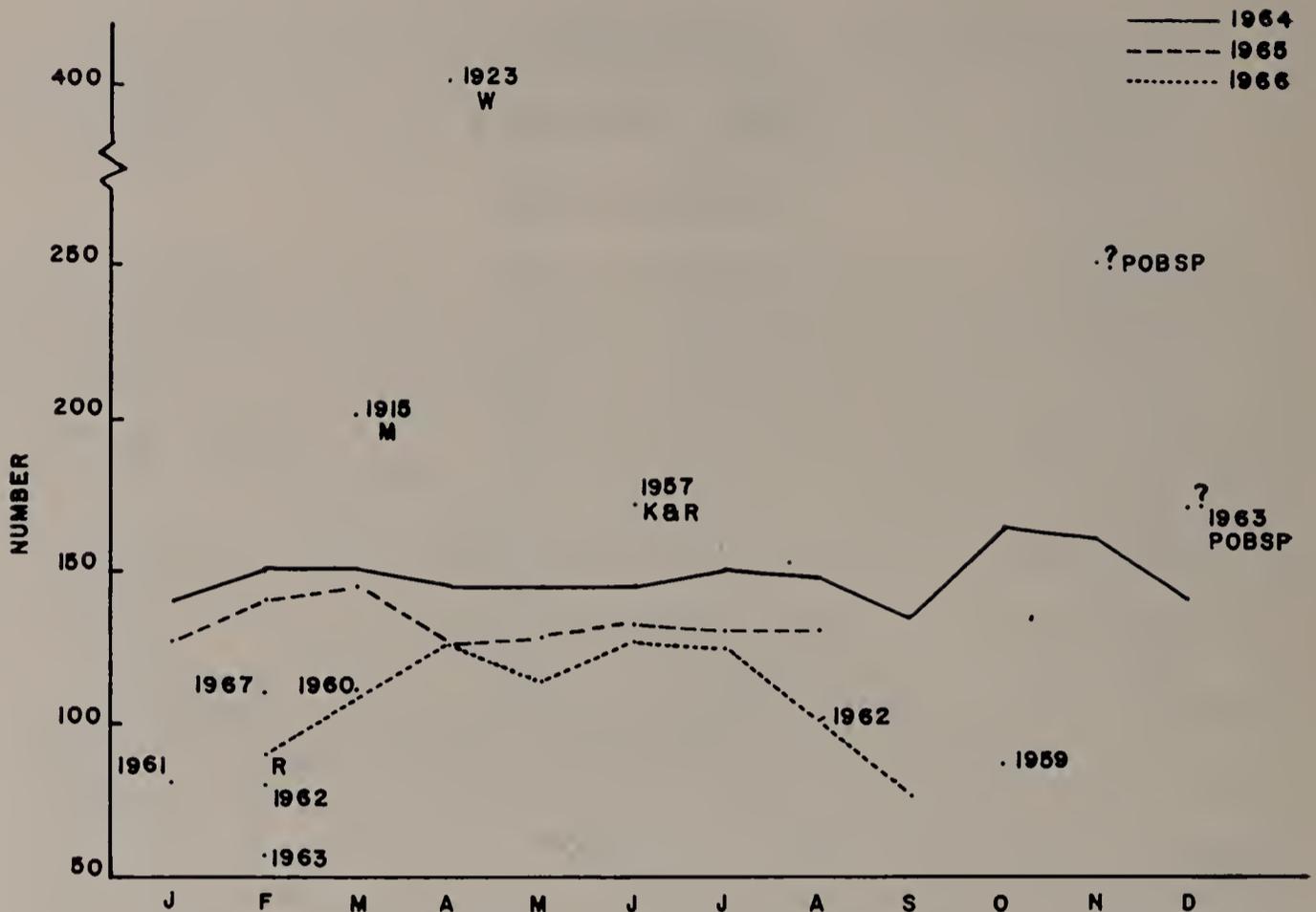


FIG. 3.1. Population fluctuations since 1915 (see text).

of the Loran tower each year. *Verbesina* has not invaded the colonies and is not, as yet, a factor in this decline.

The data suggest that there may be a regular annual fluctuation in the number of birds on the island. Numbers are high during February and March, when egg laying is at its peak, and lowest during the late summer (August–September) when young are flying and the nesting season is concluding. A similar post-breeding drop in population has been observed in Blue-faced colonies in the Line and Phoenix Islands (Roger Clapp, personal communication).

SUB-COLONIES

Within the island's central plain the birds are found in two discrete sub-colonies. The largest of these is located in the northern end of the plain, and consists of about 75% of the breeding population. A second sub-colony is located to the south of the main breeding area in an extension of the plain to the west. Both sub-colonies are under the Loran tower guywires, and have been named the North Antenna Field (NAF) and South Antenna Field (SAF) sub-colonies, respectively. The two sub-colonies are separated from one another by an often-used crushed coral road, the Loran tower, and a dense growth of *Scaevola taccada*. Although the sub-colonies are less than 90 m apart, there is almost no interchange of members between them. This was determined by painting birds (26 October 1964) in each sub-colony with a prominent patch of color on the breast—red for SAF birds and green for

NAF birds. Each sub-colony was regularly checked for inappropriately marked birds: NAF birds were examined at least once daily, SAF birds at least once weekly. During my stay only two birds were ever seen in the "wrong" sub-colony. One SAF bird was recorded once in the NAF. The other, a NAF female, left the NAF and paired with a male in a bare patch near the SAF. She subsequently left this mate and was thereafter seen in the SAF. Thus, in four months (26 Oct.-28 Feb.) only one bird made a permanent switch in location. This is notable because most of these observations were made between breeding seasons, a time when the maximum amount of movement would be expected. When breeding begins, adults seldom move far from a small territory within the colony.

The Kure colonies lack "clubs," the peripheral loitering and roosting areas for non-breeding birds. Clubs are a conspicuous feature of many Blue-faced Booby colonies. Dorward (1962a) found six separate locations in his huge colony of 9,000 birds where "near-adults," juveniles, and immatures gathered to roost. Breeding adults occasionally settled there as well. I have seen similar clubs in the Phoenix Islands in October 1965. Baker Island had only one breeding pair of birds, yet supported a club of about 15 adults. These birds roosted on the windward beach in an area unsuited for breeding. Likewise, Howland Island clubs were found on the windward beaches; breeding birds were found away from the beach, in the vegetated parts of the island. Enderbury Island contained about 550 Blue-faced Boobies on 2 October 1965. Approximately 100 of these were found nightly in two clubs in the center of the island. By contrast, during the 1965 breeding season on Kure, all birds in the colony were breeding or attempting to do so; there were no "unemployed" birds permanently on the island. All birds were in adult plumage. On one occasion a new female in adult plumage did arrive in the colony, but she was continually harassed by established pairs and finally disappeared. When a large population of non-breeders is present on an island, they are not tolerated within the colony and will associate aggression-free areas with roosting. As the birds are gregarious, "unoccupied" birds may come to gather habitually in such a location. When all birds have large breeding territories there is very little roosting outside of that area and clubs do not form.

DIURNAL FLUCTUATION IN NUMBERS

The number of birds present in the colonies fluctuates regularly through the day, with maximum numbers at night and minimum numbers in the morning between 09:00 and 11:00. Most birds spend the night in the colony (see Fig. 3.2). At first light the birds wake; a brief period of loud activity is followed by a gradual dispersion to feeding areas at sea. The NAF sub-colony may drop from 90 or more individuals at 06:30 (January to April) to less than 10 birds by 09:00. By 11-12:00 the birds begin returning to the colony and numbers build

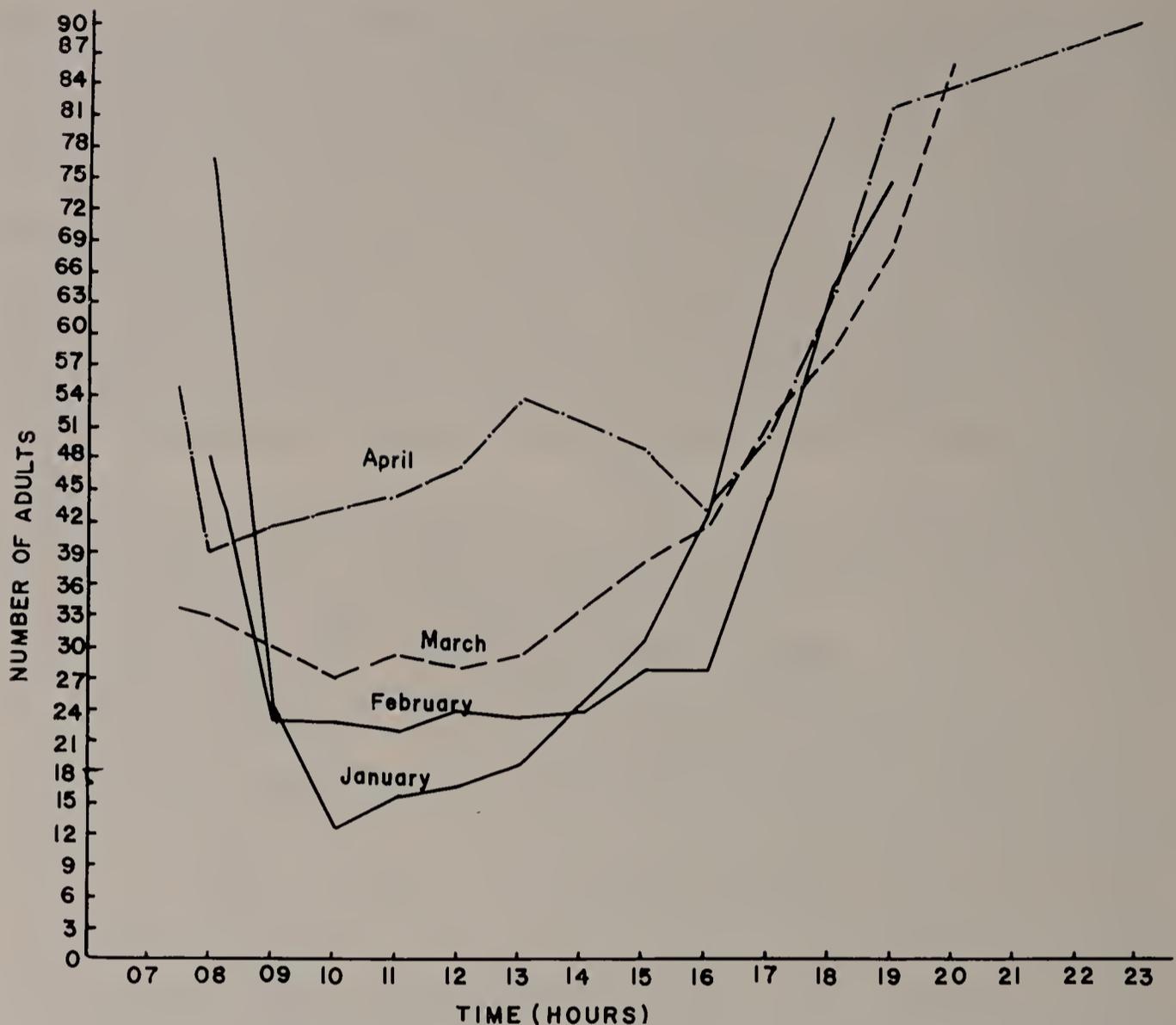


FIG. 3.2. Mean hourly fluctuations in numbers of adults, by month, in the NAF colony, January through April, 1965.

up through the day. Most birds have arrived by dark, but a few continue to arrive in the first hours after total darkness. As mentioned below, incubating birds that have been relieved late in the afternoon may fly to sea and return after dark, thus Blue-faced Boobies are able to locate their colony at night from the sea. We do not know whether these birds feed close to the island and find their way back by seeing land or hearing the surf, or whether they are able to navigate from greater distances using other cues.

The change in the relative numbers of birds present in the colony through the day from January to April is a function of the progression of the nesting season. The first eggs are laid in January and, as more pairs begin laying, the number of incubating birds present increases. In January less than 15% of the total number of birds were seen in the mornings. On several occasions in November and December I have seen the colony devoid of birds. In April the colony at all times of day contains at least 40% of the total population. These diurnal and seasonal changes may have a drastic effect on accurate censusing in Blue-faced Booby colonies. Any census data that do not include the breeding condition of the colony and the time of the census are almost useless.

TIME SPENT AT SEA

Birds spend a variable amount of time away from the island during the day. To determine the time that individuals remained at sea, an hourly census of the breeding sites of all marked birds was conducted once each week (see Appendix). Table 3.1 presents the duration of absences from the colony for 477 observations of non-breeding birds from 5 January to 31 March 1965. This can be compared with Table 4.8, which presents similar information for breeding birds. It was soon apparent that censuses of one day (dawn to late evening) were shorter than the feeding bouts of some birds; clearly, many birds remained away from the colony for more than 12 hours. In March censusing continued for two consecutive days on two occasions. Some birds remained away from the colony for longer periods. It should be borne in mind, therefore, that completed round trips could be recorded only for those that were embraced by our sample intervals. Longer feeding bouts are recorded simply as "minimum possible time away" from the colony: approximately one-third of the bouts were of this nature.

Most feeding bouts are very short in duration, averaging less than 10 hours for all those recorded, and 4.9 hours for males and 5.9 hours for females who completed their bouts during the observation period. These differences between the sexes are highly significant ($t = 3.276$; $P < .0001$). The longest bout was more than 36 hours; there were five

TABLE 3.1
TIME NON-BREEDING BIRDS ABSENT FROM COLONY, PRESUMABLY AT SEA,
5 JANUARY—31 MARCH 1965

Hours	Total time		Minimum possible time	
	Males	Females	Males	Females
1-2	76	38	7	4
3-4	26	11	2	—
5-6	31	19	6	2
7-8	59	47	12	9
9-10	23	28	19	23
11-12	—	3	10	9
13-14	1	—	1	—
15-16	1	1	1	—
17-18	—	—	—	—
19-20	—	—	2	1
21-22	—	—	1	—
23-24	—	—	—	—
25-26	—	—	—	1
27-28	—	—	—	1
.				
.				
.				
34	—	—	1	—
36	—	—	1	—
No. obser.	217	147	63	50
Mean time	4.91	5.91	9.41	9.59

bouts that exceeded 20 hours duration. On six occasions birds failed to leave the colony throughout the day (unless they left and returned within about 40 minutes, in which case their absence may have been undetected). Incubating birds may also remain in the colony for 24 or more hours (see Table 4.7). Of interest are the 114 bouts that took less than two hours. It is hard to believe that food is so abundant that the birds could fly from the island, locate fish and feed to capacity, and return in such a short time. These bouts occurred throughout the censusing, occurring simultaneously with much longer bouts by other birds, so a common local food supply seems unlikely. It is not an individual characteristic, as birds may have had an alternation of short and long bouts on subsequent census days. It is possible that no feeding occurs during these periods, and they are just short exercise flights. They could also represent the fortuitous discovery of an abundant food source by a small number of birds. Another possibility is that some birds are only moderately hungry when they leave, and fewer fish are required by them.

TERRITORY

All Sulids defend areas around their nests against conspecifics. The size of these defended areas is highly variable. In gannets the territory consists essentially of the nest site itself, and the distance around the nest that an incubating gannet can stab. Similar territories have been described for the Peruvian Booby and the Blue-footed Booby by Murphy (1936). The territory of the Red-footed Booby, a tree-nester, consists essentially of a nest and its adjacent branches, and stabbing distance in all directions, vertically as well as horizontally (Verner, 1961; and personal observations). This assures the breeding pair perching sites around the nest in addition to the nest-site itself. Brown Boobies have larger areas around their nests, and a defended territory will usually contain vantage points. Simmons (1967) considers the Brown Booby a spaced-out nester. The nests are usually "some yards apart." Nest sites may be compressed, however, when populations are high and favorable nest sites are scarce.

Nelson (1966a) discusses the relative breeding densities in the Sulidae, and lists six of the nine species in the following order, progressing from the dense to the dispersed nesters: *Morus bassana*, *Sula variegata*, *S. nebouxii*, *S. dactylatra*, *S. leucogaster*, and *S. sula*. The last three species have highly variable territory sizes in different colonies, and it is not as easy to assign them to a position among themselves as it is to list them relative to the other species. The variation in density described for the Blue-faced Booby is immense; some of this variation must reflect obligate territorial compression under crowded conditions in some colonies. The Boatswain Bird Island (Ascension) colony, containing 9,000 birds, 1,200-1,300 of which are breeding pairs, and having only seven acres (2.8 hectares) of available land, has a breeding density

of approximately 25 pairs per 100 square yards (83.6 m²). This is still a great deal less than the density of gannets observed by Nelson (1967a) at the Bass Rock, Scotland, where approximately 230 pairs per 100 square yards (83.6 m²) was the normal nesting density. The opposite extreme is well illustrated by a "colony" I observed on Baker Island, Pacific Ocean, in October 1965. One breeding pair had the entire island of nearly 2.5 km² to itself. Optimal territory size should be found in a colony where there is more suitable nesting habitat than is occupied by the birds, and with a large number of pairs aggregated into a small part of that area. Such a situation is found on Green Island, where 150 birds have approximately six hectares of suitable nesting habitat. The two sub-colonies cover only a small portion of the suitable area. The NAF sub-colony occupies about 8,800 m². Within this area 43 pairs were found in 1964, and 45 pairs in 1965, with a few pairs scattered beyond the bounds of the sub-colony. There were, therefore, almost 200 m² for each pair in the two seasons. This is more dispersed than colonies mentioned by Nelson in the Galapagos Archipelago, viz., 150 square yards (125 m²) per pair on Tower Island and 100 square yards (83.6 m²) per pair on Hood Island.

The Kure birds are not distributed uniformly over the entire available area within the sub-colony. Nests are often clumped, with large intervening areas of open space. For this reason, two other methods of determining the territory size were employed. First, the distances between nearest neighbors (nests) were determined for all nests within the main sub-colony in the two seasons. These distances varied from a minimum of 1.7 m to a maximum of 27 m. The average nearest-neighbor distance was seven meters in 1964 and 7.6 m in 1965. This means that actual density is slightly less than two pairs per 83.6 m².

The most accurate way to determine the spatial needs of the birds is to map their exact locations through time. This has been done. All known locations determined during hourly censuses and behavioral observations (see Appendix) have been plotted for five mated and five broken pairs randomly selected from the numbered birds, and for four bachelor males and one single female. Hundreds of point locations are available for some birds. The results of these determinations are given in Table 3.2. The table presents the bird's breeding status, the number of days and hours on which the bird was seen, and the size of the area(s) that the bird occupied. Single excursions to areas outside the territory were also recorded. Several generalizations can be made with respect to these data. First, the area defended and utilized by the birds is far less than would be predicted by simply measuring the number of birds per unit area in the sub-colony. Only four birds, an unmated female, one pair, and a "divorced" male, used over 83 m². The average area used by broken pairs, mated pairs, and bachelors is 50 m², far less than that predicted by density figures alone (i.e., 200 m² per pair). Most of the activity of the birds is thus restricted to less

TABLE 3.2
TERRITORY DATA DECEMBER 1964 TO APRIL 1965

Birds	Observations				Territory data ²	Excursions ⁴ (meters)
	Beh. Days ¹	Census Days	Hours	Dates		
Bachelor males						
01	31	15	49	28 Dec.-14 Apr.	353	none
02	17	14	67	31 Dec.-14 Apr.	27	4.5, 9
03	20	15	80	6 Jan.-29 Apr.	37	24
022	00	3	9	4 Jan.-10 Apr.	linear	—
Unmated female						
R22	11	16	63	29 Jan.-14 Apr.	Average 33	7.5, 13.5
Broken pairs						
R5	3	15	100	30 Dec.-14 Apr.	60	4, 20, 5
R6	3	15	100	30 Dec.-14 Apr.	29	20, 10.5, others
R7	4	11	69	29 Dec.-14 Apr.	29	none
R8	4	11	69	29 Dec.-14 Apr.	14	41, 13.5, 15
B3	1	14	92	29 Dec.-24 Apr.	41	7.5, 15, 22.5, 29
B4	1	14	92	29 Dec.-24 Apr.	46	none
R23	11	16	98	28 Dec. 24 Apr.	92	16.5, 15
R24	11	16	98	28 Dec.-14 Apr.	70	15, 12
Average						47.6

TABLE 3.2 (cont.)

Birds	Observations			Dates	Territory data ²			Excursions (meters)	
	Beh. Days	Census Days	Hours		Size (meters)	Total area used (square meters)			
Mated pairs									
R3-4	4	18	148	28 Dec.-14 Apr.	B.E.5 6 × 10.5	O.E.6 3 × 4.5	B.E. 41	O.E. 10	none
R11-12	28	17	105	29 Dec.-14 Apr.	4.5 × 6	1.5 × 1.5	14	2.3	7.5
R19-20	24	17	149	29 Dec. 14 Apr.	6 × 18	4 × 4.5	90	15	5, 3, 9, 4, 10.5, 6, 7.5
B15-16	0	17	175	1 Jan.-14 Apr.	5 × 11	2 × 5	51	9	none
R27-28	23	14	160	28 Dec.-14 Apr.	7.5 × 9	3 × 5	56	8	4.5, 4.5
							Average 50.4	8.9	

¹ Beh. Days: number of days locations recorded during behavioral observations, in addition to those on census days.

² Some used more than one territory successively.

³ Due to irregularly-shaped territories, totals are not multiples of the linear dimensions.

⁴ Single trips outside territory.

⁵ B.E.: size before egg laid.

⁶ O.E.: size after first egg.

than 25% of the areas covered by the sub-colony. Secondly, the territorial needs of the birds depend upon their status. Bachelor males occupied an area about 65% of that used by paired birds (mean of 33 m²). We shall later see that advertising males generally restrict their activity to a small area around their cleared platform. Pairs parade about a larger area as part of their courtship activities, and pairs that break up may use a succession of areas before finding new mates. In all cases, broken pairs were more likely to be found far from their original areas than mated pairs (Table 3.2). Two of the five mated pairs were never seen outside the limits of their small territory, and two others were found outside their area once and twice, respectively. All birds thus restrict most of their activity to the small territories that are defended. It is important to note that the territory size of all mated pairs shrank by at least 75% after the laying of the first egg. This means that courting pairs defend four times as much area as they will use when nesting is actually under way. The implications of this are considered at length in the discussion below.

The territories of the Blue-faced Booby are three dimensional entities. Birds walking toward, or flying over, the territory receive a variety of agonistic displays (see Chapter 5) or are attacked. More than 850 agonistic bouts were recorded. Over 75 of these were directed at birds flying overhead. The average height of these birds was two meters, although they ranged from one to seven meters. On seven occasions the entire NAF sub-colony called aggressively at a bird soaring over the colony; in these instances the exact numbers involved could not be determined.

INTERSPECIFIC TERRITORIALITY

Thirty-three aggressive encounters between Blue-faced Boobies and other species were observed between 17 November 1964 and 15 February 1965. Twenty-nine of these involved threats or attacks directed against Laysan Albatrosses. Only three other species were involved: several birds called at a Red-footed Booby flying overhead, one bird Yes/No Headshaked at two Ruddy Turnstones, and on two occasions Brown Boobies were chased vigorously or received Yes/No Headshakes. The Laysan Albatross is the most important species against which the boobies defend their territories, in terms of both the frequency and vigor of the encounters. In 11 instances the aggression involved an attack upon the albatross. In 10 of the encounters the albatrosses fled, often receiving pecks on their rump or flank. On one occasion the albatross stood, faced the booby, and gave a Head-up-and-whine, a display often given by an albatross after it has chased away another bird (Rice and Kenyon, 1962). This terminated the attack. In ten encounters the boobies Yes/No Headshaked at the albatross, and in six instances simply called at it. It is clear that albatrosses recognize the postures of the defending boobies, as in all but one case they responded to them by changing directions and moving away.

Laysan Albatrosses never initiated an aggressive encounter. In 18 encounters they were walking within the booby colony, either toward (six times) or past (12 times) the booby before it became aggressive. In 10 cases the albatross was flying over the colony, and once landed near a territorial pair and was quickly driven off. On one occasion a booby returning to the colony found a Laysan Albatross standing on his platform. The booby immediately landed beside the intruder, bit him viciously, and drove him from the territory.

It is clear that interspecific territoriality is an important part of the booby territorial system. Laysan Albatrosses are larger than boobies and prefer the same nesting habitat, viz., the open plain. They will nest under the dense *Scaevola* on occasion, or even on the beaches, but the latter area is occupied by the closely related Black-footed Albatross. Therefore, there is competition for nest sites between the albatrosses and the boobies. Unfortunately, I have no measure of Laysan Albatross nest density within the Blue-faced Booby colony, as opposed to density away from the boobies, but my strong impression is that there are many fewer albatrosses within the colony. It appears that interspecific territorial defense permits the Blue-faced Boobies to compete successfully for nest territories against the larger Laysan Albatrosses. In a review paper by Orians and Wilson (1964) on the subject of interspecific territorial defense, many cases of intergeneric or even interfamilial interactions are cited, but the authors do not record instances between larger taxa. They conclude that most cases of interspecific defense involve competition for food, but this cannot apply in this instance, as both species are pelagic feeders that do not use the same areas, as far as is known. The function of this territorial system is considered in the discussion below.

SITE ATTACHMENT BETWEEN SEASONS

It would be expected that Blue-faced Boobies would nest in the same territories each year. Nelson (1964d) mentions that "the sites and mates of Gannets are permanent." Rice and Kenyon (1962) and Fisher (1968) have shown the phenomenal site attachment of Laysan Albatrosses; in thousands of nests observed, most pairs regularly re-nested within two meters of their previous year's nest site. White Terns (Dorward, 1963) and Black Noddies (Ashmole, 1963) also tend to return to the same site each year; indeed, nest site specificity in seabirds is common and often taken for granted. I was, therefore, surprised to find that Blue-faced Boobies on Green Island showed very little proclivity to return to the same nest site from one year to the next; very few pairs even returned to the same territory. Table 3.3 presents site attachment data for 22 mated pairs and for 22 birds remating between the 1964 and 1965 season. In these 44 cases only three pairs and one remating bird re-nested within 7.6 m of the previous nest site. This means that 90% of the population moved from their territory of the previous year. Only three birds re-nested within three meters of the previous nest

TABLE 3.3
 DISTANCE 1965 NEST SITE MOVED FROM THAT OF 1964

Distance moved (meters)	Pairs remaining together	Birds remating	
		Females	Males
0.1-3	2	1	0
3.1-6	0	0	0
6.1-9	2	0	0
9.1-12	4	1	0
12.1-15	2	2	1
15.1-18	2	0	2
18.1-21	1	0	2
21.1-24	1	2	1
24.1-27	2	3	0
27.1-30	1	0	0
30.1-33	1	0	0
33.1-36	1	1	0
36.1-39	1	0	1
39.1-42	0	1	1
42.1-45	0	0	1
49	1	0	0
62	0	1	0
65	1	0	0
95	0	1	0
Total birds	22	13	9
Mean distance	19.8	28.4	23.8
S.D.	15.28	24.57	10.33

site. It is equally remarkable that 12 pairs (27%) moved over 30 m between the two seasons. The average move for mated pairs (19.8 m) is less than that of males (23.8 m) and females (28.4 m) from broken pairs. Although it appears that mated birds re-nest closer to old nest sites, the difference between them and pairs that switched is not statistically significant ($t = 1.366$; $.250 > P > .10$). However, because females respond to courting males by moving toward them (see Chapter 6), and the single female (R22) moved through an area twice as large as that observed in the pairs (Table 3.2), we would expect them to re-nest farther from old sites.

DISCUSSION

What are the primary functions of territory in the biology of the Blue-faced Booby? It is fortunate that studies of this species have been conducted in colonies as different in density as those found in Botswana Bird Island and Green Island. A comparison of the differences in breeding efficiency between the two colonies provides insight into some of the important functions of the territory. Dorward's colony was 10 times as dense as the Kure colony. Dorward records occasional nests with three eggs, and found single occurrences of clutches with five, six, and even seven eggs. Unattended eggs "lay all around." In a

tally of 96 nests, he found 69 nests with one egg and 27 with two (see Table 4.4). Dorward believed that most birds laid a clutch of two eggs but that egg-rolling between the nests and egg loss was so frequent that nests with two eggs were seldom found. In a total of 105 nests examined daily on Kure, no case of egg-rolling between nests was observed. Two-egg clutches are normal and were found in over 90% of the nests. Recall that the average distance to the nearest neighbor in the Kure colony was seven and 7.6 m in the two years. This increased spacing greatly reduces the probability of pair-pair interference with nesting. The high incidence of egg-rolling, scattered eggs, and clutches of abnormal size consistently seen in the Ascension colony could not occur in the Kure population. Spacing is, therefore, seen as an adaptation increasing the efficiency of nesting. The crowding observed on Boat-swain Bird Island is abnormal. Dorward cited evidence to demonstrate that Blue-faced Boobies originally nested on mainland Ascension, and were probably driven to the small offshore island with the introduction of man and his companion predators to the main island. The Blue-faced Booby population is now essentially restricted to this small area. The extreme territorial compression that has resulted has very adverse effects upon nesting success.

Another corollary of increased density is decreased food per bird if food is limited. Dorward (1962a) and Simmons (1967) strongly suggest that food is limited in the impoverished tropical blue waters surrounding Ascension. Both Simmons (for the Brown Booby) and Dorward report depressed breeding or die-offs attributable to food. Dense colonies would suffer more than expanded ones if they permitted larger numbers, as there would be less available "search area" per bird within easy distance to the colony. Thus birds would be forced to expend more energy searching for food in a limited resource that had to serve a larger number of birds. This directly affects the breeding success of the colony, for if birds must fly far to sea to feed, then they must leave their mates alone longer. They also bring back less food to the young, as a larger percent of what is caught is digested before they return. It is possible that the large territory size so typical of the Blue-faced Booby in the tropical blue waters of the oceans, and not seen in gannets, or in the boobies of the phenomenally rich waters of the Humboldt Current, is an adaptation to limit population size in depauperate waters.

Nelson (1966a) points out that with a lowered density there would be a reduced tendency for the birds to synchronize their breeding, as there would be a decrease in close contact and its resultant social stimulation. This would be adaptive if there is an irregular food supply because breeding would be temporally spread out, permitting a more efficient exploitation of food resources. This may function in most of the low latitude colonies, but it does not hold for the Kure population; on Kure there is a high degree of breeding synchrony with very large ter-

ritories. The question of how great a density is necessary for social stimulation, and how much stimulation from aggregated birds does occur, is tangential to the present discussion (see Darling, 1938, for a discussion of these points).

Certain breeding patterns are affected when birds must forage at sea for long periods of time. Incubation and chick-guarding spells will be longer, as mates must wait for their foraging partner to return before they leave. If, because of hunger or thirst, they are forced to leave before their mate arrives, then loss due to overheating (see Bartholomew, 1966) or predation by frigatebirds is common for eggs or young. On Kure the average time spent away from the nest by a foraging bird was from 4.5 hours (female) to 6.5 hours (males). No comparable data are available for either Ascension or the Galapagos, but I would predict that spells off the nest are longer there (since confirmed for the Galapagos by Nelson, personal communication). The average incubation spell for Kure birds is about 10 hours, contrasting with 32 hours for Ascension birds. Much of this difference may be due to the time required for feeding by the adults in the two colonies; this is discussed at length in the section on incubation. The impact that spacing may have on overall breeding success is discussed in Chapter 4. It is sufficient to mention here that nesting for the 1964 and 1965 seasons on Kure was five and six times as successful, respectively, as nesting on Ascension. Both hatching success and chick survival were also greater in the Kure population.

The above arguments support the contention that territory functions in reducing adverse pair-pair interactions during incubation, and may also act to decrease competition for food, especially during food shortage, by reducing the population through spreading out the birds within the colony. These considerations do not, however, adequately explain the prominence of interspecific territorial defense against the Laysan Albatrosses. There is little or no competition for food between these species. Competition between the birds is not restricted to nest sites; boobies defend the entire territory, even though they only use 25% of that area once the eggs have been laid. Thus the territory itself, and not the nest, is the defended resource. Prior to nesting Blue-faced Boobies engage in a large number of courtship displays that involve traversing large spaces. These are discussed at length in Chapter 6, but it should be mentioned here that pairs commonly walk six to 10 meters within their territories as they court. These strolls are very important components of the epigamic repertoire. Bachelor males attract walking females in the same manner. Under conditions of crowding the displays are often disturbed or even broken up by the activities of nearby birds. Therefore, the maintenance of a large territory for the uninterrupted performance of walking displays is essential. I believe that, in addition to buffering the pairs against interferences during incubation, the extra territorial space not used during incubation is an important

THE COLONY

display-ground for bachelors and mated pairs alike. Laysan Albatrosses are larger than boobies but are similarly patterned, being white birds with dark wings and mantle. If albatrosses were common within the display territory, it is easy to imagine an unending succession of interactions that would disrupt booby displays. Indeed, occasionally a walking Laysan Albatross temporarily halts Blue-faced Booby activity and normal movements do not resume until the bird has left the area. This idea has been dismissed as a possible function of interspecific territoriality by Orians and Wilson (1964, p. 737), who consider that "individuals of other species are, in general, no threat to pair formation and mating." The authors further maintain that food is the most usual unsharable resource in common to two competing species of birds. This is most likely true for land birds. It is well to consider, however, that the food argument is inappropriate to the present situation and perhaps not generally applicable to sea birds. The breeding environment may be an essentially hostile one for a bird adapted to a life at sea and such terrestrial "novelties" as overhead obstacles, entangling trees or bushes, extreme microclimatic conditions, landslides, and an area devoid of food may create difficulties for them. In such cases, the main resource in short supply may often be space. An important part of the space of Blue-faced Boobies is used as a display ground and any adaptation that can minimize disturbance to displaying birds in this area will be selected for. In this case, with large numbers of albatrosses breeding in the same habitat with the boobies (and this is a situation unique to the Hawaiian Leeward Islands), interspecific territoriality does effectively reduce such disturbance.

CHAPTER 4

BREEDING BIOLOGY

INTRODUCTION

Populations of Blue-faced Boobies in tropical waters may contain breeding individuals at any time during the year. In spite of this, there is a limited breeding season during which most, or in many cases all, of the birds breed. A comparison of these breeding peaks in the Pacific reveals interesting and perhaps very important trends (Fig. 2.1). Within the subspecies *personata* the northern populations (Hawaiian Leeward Islands) lay in February and March, equatorial (Line and Phoenix Islands) populations lay in early summer (King, 1967; Roger Clapp, personal communication), and southern populations (Kermadec Islands) lay in their winter, i.e., August through November (Falla et al., 1966; Sorenson, 1964). Dorward found that the Ascension Island birds (*S. d. dactylatra*) breed in mid-summer. In contrast, a third equatorial subspecies (*S. d. granti*) from the Galapagos, surrounded by the cold sub-Antarctic waters of the Humboldt Current, has a peak laying period that approximates that of southern populations of *personata*. The causes underlying this distribution of breeding seasons are unknown, but may involve food supply or climatic factors affecting adults, eggs, or young.

BREEDING CYCLE

Investigations of the breeding phenology of the Kure Blue-faced Boobies were begun by POBSP personnel in January 1964. During daily visits every new nest, egg, or chick was recorded. Eggs were marked and nests were numbered and staked (see Appendix). I continued this in 1965, adding the hourly check described above. From this information, as well as that gathered after I left the island, it is possible to analyze the sequence of breeding events for each year and to correlate the 1965 activities of most pairs with those in 1964.

Table 4.1 and Figure 4.1 summarize the main breeding events for the two seasons. There were fewer clutches in 1965 and a higher proportion of these were second attempts by pairs unsuccessful with their first nests. Overall breeding success was lower in 1965. The 1965 season began two weeks later in the year and showed no peak laying period, contrasting with 1964, when 60% of the clutches were begun within the 30-day period from 10 February to 10 March (Fig. 4.2). The mean laying date in 1965 was 26 days later than in 1964.

The delayed laying in 1965 was very pronounced. Known pairs (Table 4.2), as well as the colony as a whole, showed this shift. If a two-week shift occurs each year, observers in the past would have reported breeding at vastly different times than the present January to

TABLE 4.1
COMPARISON OF 1964 AND 1965 BREEDING SEASONS

	1964	1965
Number of nests	56	49
Number of renesters	2	9
First egg date	4-5 Jan.	20 Jan.
Last egg date	29 June	13 July
Duration of laying	177 days	174 days
Laying peak	late Feb.	none
Mean laying date	8 March	3 April
First chick date	21 Feb.	6 March
Success	64%	52%
Number of fledged young	34	25

April egg season. However, this has not occurred (Fisher, 1903; Dill, 1912; Kenyon and Rice, 1958; Robbins, 1966). Some irregular factor during or prior to the 1965 season would seem to have accounted for the differences between the two years.

SUGGESTED REASONS FOR DELAYED 1965 SEASON

Populations are sensitive to factors that affect their food supply. Food scarcity may be brought about either by a real depletion of food reserves, or by an event that renders food unobtainable. I was unable to assess the abundance of flying fish and squid, the boobies' principal food, during this study, but weather data are available. The value for wind speed in the first column of Table 4.3 (Beaufort 5 during the day) was chosen because at this speed the surface turbulence begins to increase appreciably, producing choppy conditions that could impair the feeding ability of plunge-diving birds. No rainfall data are available

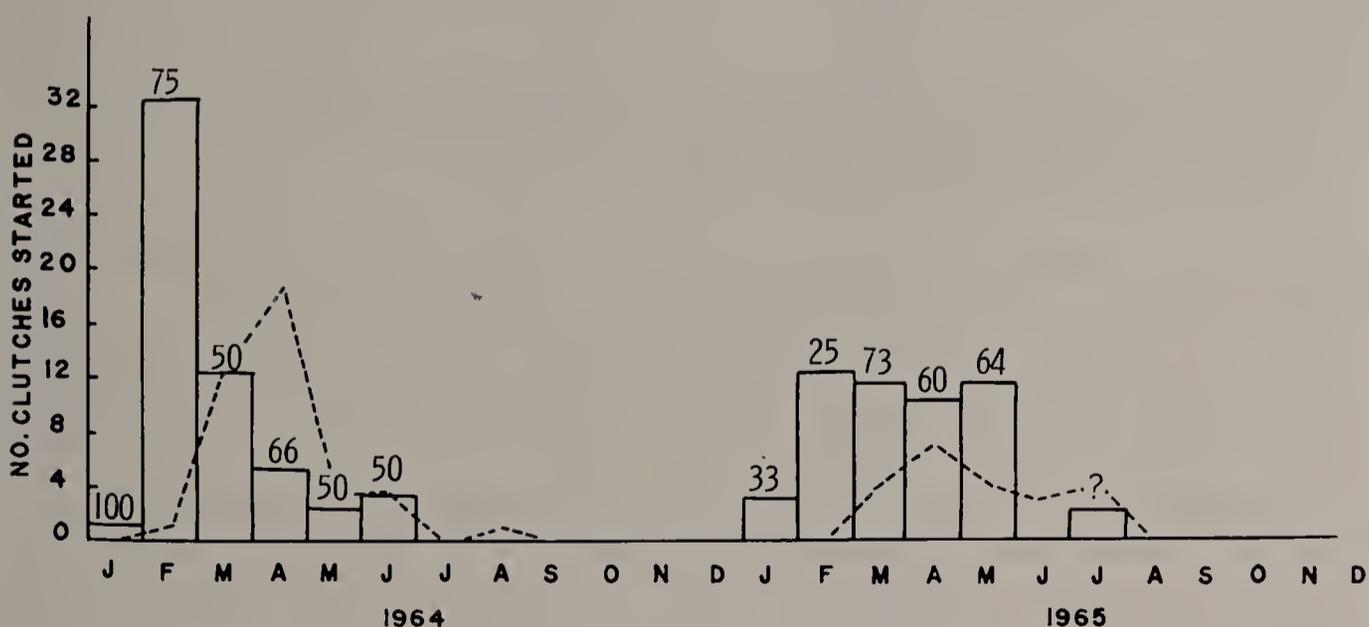


FIG. 4.1. Summary of 1964 and 1965 breeding seasons. Number of clutches started (histogram), percentage of successful clutches (numbers), and number of chicks hatched (line graph), in given month.

TABLE 4.2
INTERVAL BETWEEN FIRST EGG IN 1964 AND FIRST EGG IN 1965
FOR FOUR CLASSES OF PAIRS

Time between breeding Weeks (or days)	Pairs keeping 1964 mates in 1965		Pairs remating in 1965	
	S ¹	U ¹	S	U
47	1	—	—	—
48	—	—	1	—
49	—	—	—	—
50	2	—	—	—
51	3	—	—	1
52	—	1	1	2
53	5	1	—	—
54	2	—	1	—
55	—	—	—	—
56	2	1	2	—
(392-394)				
Mean				
(395-398)	—	—	—	1
57	—	—	—	—
58	1	1	—	2
59	—	—	—	—
60	1	—	1	—
61	—	—	—	1
62	2	—	1	1
63	—	—	—	—
64	—	—	2	—
65	—	—	1	1
66	—	—	1	—
67	—	—	2	—
Total pairs ²	19	4	13	9
Mean (weeks) ²	54.05	54.75	60.08	57.22
Variance	16.50	7.66	39.25	24.25
S.D.	4.05	2.77	6.26	4.92

¹ S (successful) and U (unsuccessful) refer to 1964 breeding outcome.

² Two-year total = 45 pairs; mean = 56.48 weeks.

from Kure before the 1964 season, so ten-year Midway averages have been used to provide a rough comparison with 1965 rainfall.

The two seasons differed only slightly in days with Beaufort 5 winds, with more Beaufort 5 days and higher average wind speeds in 1964. The year 1965 was consistently colder and had more than average rainfall. The most pronounced meteorological difference between the two seasons was the number of days with gale-force winds. No gales preceded the 1964 season. From 16 to 21 December 1964 a violent storm swept the northern part of the Hawaiian Leeward Chain, with winds of 52 knots recorded. The storm severed normal Navy flights from Midway to Kure for five days. I was on Midway when the storm began and had the opportunity to fly to Kure and back as the storm

TABLE 4.3
 WEATHER INFORMATION FOR MONTHS IMMEDIATELY PRECEDING AND DURING 1964 AND 1965 BREEDING SEASONS

	Days \geq B51		Days with gale winds \geq B7		Av. speed at 16:00 hrs.		Total rain (inches)		Av. min. temp. ($^{\circ}$ C.)	
	'64	'65	'64	'65	'64	'65	Midway ²	'65	'64	'65
Dec.	9	8	0	8	3.57	3.35	5.00	6.23	17.8	15.6
Jan.	1	2	0	2	2.90	2.80	4.00	3.63	17.8	13.9
Feb.	2	1	2	1	3.22	2.96	2.50	4.10	17.2	15.0
March	7	6	0	1	3.74	3.60	3.00	3.31	17.2	15.0

¹ Wind speed in Beaufort scale.

² Approximate 10-year averages at Midway. See text.

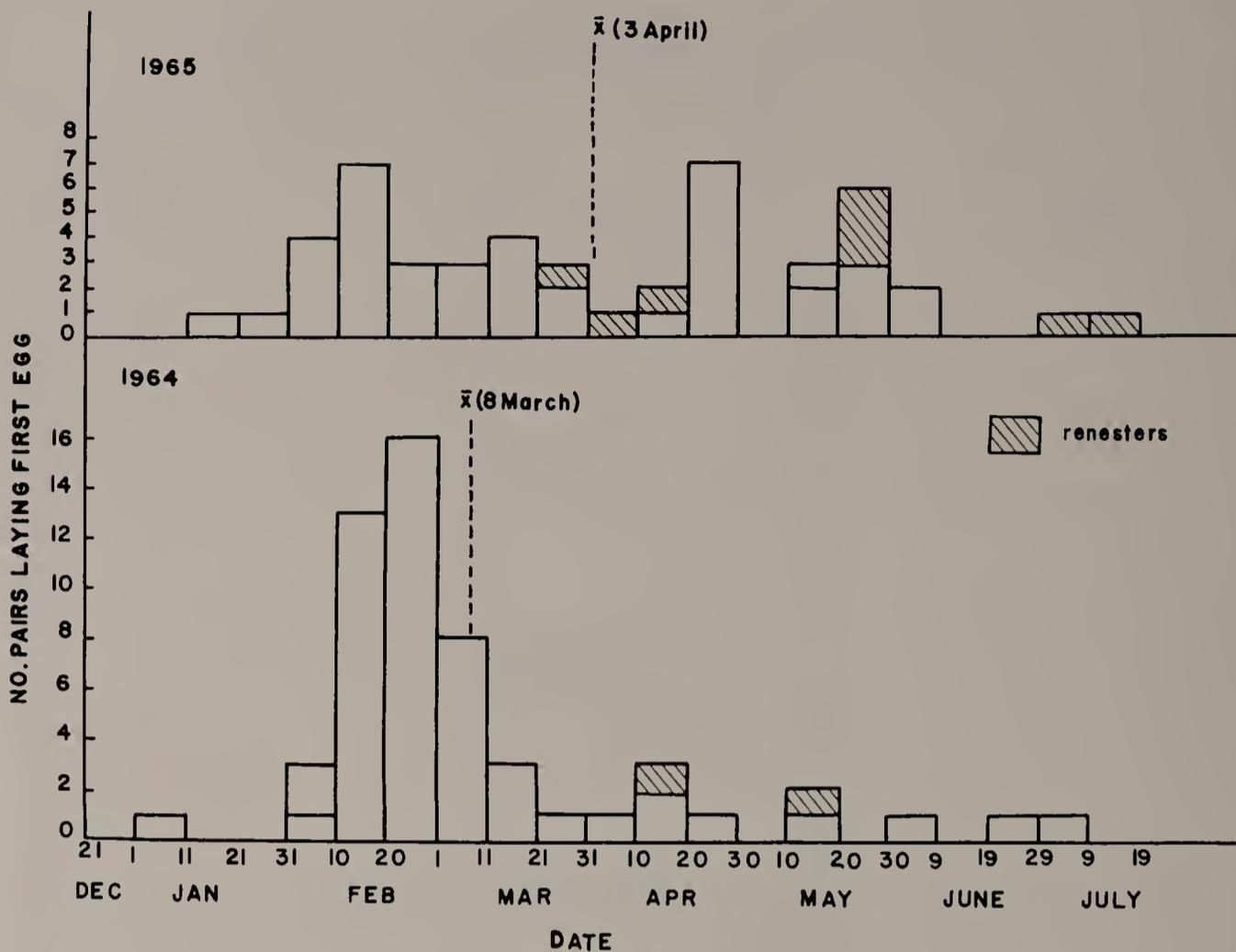


FIG. 4.2. Comparison of 1964 and 1965 egg laying periods.

gathered momentum. We were unable to land on Kure. The surface turbulence and excessive spindrift would have rendered it almost impossible for a Blue-faced Booby to feed effectively. There was no surface area free of foam. It seems likely that a period of six days during which boobies would, at best, feed with only minimal effectiveness could have a very profound effect on the breeding capacity of the birds. This would be compounded by the fact that energy demands would be exceptionally high for birds flying in such wind conditions.

Much has been written concerning factors that are responsible for breeding success in animals. The information dealing with the effect of the food supply on breeding phenomena in birds has been extensively examined by Lack (1966). He maintains that food supply determines the breeding potential in the birds he examined, either through density-dependent mortality of chicks, fledglings, or adults, or through insufficient food for the females prior to the breeding season. The latter point is of interest here. Lack shows that Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*) both lay at times that are not optimal for the later raising of young. For these species the nesting success of earlier breeders is higher than that of breeders later in the season, when most birds, in fact, lay. He concludes, therefore, that the amount of food available to the females prior to their nesting is what determines the time at which they lay. My observations on Kure are consistent with this hypothesis.

The situation may not be as simple as this, however. Fisher (1969) reports that the 1964-65 breeding season (i.e., 1965 season for boobies) was a very poor one for Laysan Albatrosses on Midway Atoll. He found that the breeding colony size was 50% less than in the preceding and following years. However, 41.5% of the absent birds returned to breed in the 1965-66 season, thus ruling out heavy mortality as a major factor in the decline. Since Laysan Albatrosses on Midway finish their laying by 15 December, the storm that I mention above could not have affected albatross laying. Fisher does not know the factors responsible for the depressed season, but they could have affected the boobies on Kure, only 90 km away, as well. If this is true, the gale may merely have compounded detrimental conditions already affecting the birds.

Figure 4.1 shows the percentage of nests started in a given month that produced fledged young. Of relevance to the present discussion is a comparison of nest success early in the season (January-February) with that later. In 1964 the early nesters were more successful, while the reverse is true in 1965. This, in addition to further evidence presented below, suggests that conditions in the poor 1965 year may have improved as the season progressed.

That food supply can have a profound effect on seabirds is well documented. The spectacular die-offs of millions of Guanay Cormorants (*Phalacrocorax bougainvillii*), Peruvian Boobies (*Sula variegata*), and Brown Pelicans (*Pelecanus occidentalis*), associated with the intrusion of the warm waters of the Equatorial Countercurrent into the Humboldt Current off Ecuador and Peru ("El Niño"), have been well described by Murphy (1936) and Hutchinson (1950). Similar seabird kills are recorded off the west coast of Africa during times of insufficient food (Hutchinson 1950). Dorward's chick die-off on Ascension Island (1962a) is also thought to have been caused by a lack of food. Simmons (1967) demonstrates that breeding in the Brown Booby (*Sula leucogaster*) on Ascension Island is determined by the available food resources. My evidence suggests that there was a similar process at work on Kure. The storm alone in December 1964 certainly reduced the availability of food at a possibly crucial time just prior to the 1965 breeding season. The presumed effects of these conditions, seen in almost every aspect of the 1965 season, will be detailed in the following sections.

INDIVIDUAL PATTERNS

The laying period for the colony extends over five months. It is important to consider how individual pairs fit into this cycle. How much time elapses between successive annual layings and what variables may affect this?

A successful breeding season for a given pair lasts about seven months. Incubation averages 43 days, and chicks begin flying at about 120 days. The juveniles are not independent when they begin to fly.

They can be found in the colony for a month or more after their first flights, during which time they are fed by the parents. Whether they forage at sea with the parents or by themselves is not known.

Although four birds bred in 1965 that did not do so in 1964, their mates were experienced birds. Thus at least one member of every 1965 pair had bred in the previous year. The average time for successive layings by these pairs was 56.5 weeks (see Table 4.2). We need to know whether the annual cycles of individual pairs are scattered at random around this mean, or whether there are sub-populations whose cycles are different. Two variables have been analysed: did either 1964 breeding success or pair maintenance from one year to the next affect the timing of the annual cycles?

Two fourfold contingency tables were used to test individual annual cycles against the above variables. The mean cycle time was used as a cutoff point in constructing the tables: successful vs. unsuccessful birds were grouped according to whether they took more or less than the mean time to reneest. The same procedure compared birds that retained their mates in 1965 with those that switched. Adjusted chi-square

$$\chi^2 = \frac{n \left(|n_{11}n_{22} - n_{21}n_{12}| - \frac{n}{2} \right)^2}{n_{.1}n_{.2}n_{1.}n_{2.}}$$

is computed with one degree of freedom.

The results show that there is no correlation between previous nesting success and the length of the annual cycle ($\chi^2 = 0.453$; $.250 > P > .10$). However, the hypothesis that there is no difference between the timing of the breeding cycle and the permanence of the pair bond is rejected ($\chi^2 = 6.46$; $.025 > P > .01$). Pairs that remained together bred sooner in 1965 than pairs that changed mates.

These results are identical to those found by Coulson (1966). His twelve-year study of the breeding biology of the Kittiwake (*Rissa tridactyla*) showed that females that retained their mates from the previous breeding season bred earlier and showed more consistency in the time of egg laying than did pairs that broke up. Increased breeding efficiency resulting from mate retention undoubtedly involves many factors. One possible consequence of mate retention is an increase in the behavioral efficiency of the established pair. Dr. W. C. Dilger (personal communication) has found that in African Lovebirds (especially *Agapornis roseicollis*) much more time and energy is expended in the courtship activities of newly formed pairs than of established pairs. Members of the pair must learn the individual peculiarities of their new mates and break down behavior associated with the maintenance of individual distance. A prolonged period is required before courtship, and its attendant nesting activity, will proceed as quickly and efficiently as in well-established pairs. Coulson (1966) noted in Kittiwake

wakes that a "depressive effect on the breeding biology induced by a change of mate was apparent for at least two breeding seasons after the change took place." This would be predicted by the above hypothesis. It is quite likely that the same model holds for the observed effect in the Kure Blue-faced Boobies.

CLUTCH SIZE

Table 4.4 compares the clutch sizes in the three most thoroughly studied Blue-faced Booby populations. The typical clutch in all races appears to be two eggs, yet the variation is considerable. Dorward's data are not strictly comparable because of the disruptive interactions between neighboring pairs discussed in Chapter 3.

The second egg is normally laid within five to six days of the first. The range between first and second eggs for 85 clutches was three to 15 or 16 days. The mean time between eggs was 5.6 days for both seasons ($n = 49$ in 1964, 36 in 1965). This falls within the five- to six-day range described for other colonies.

TABLE 4.4
CLUTCH SIZE IN THREE RACES OF *Sula dactylatra*

Race	Location	Reference	No. nests	1 egg	2 eggs	> 2 eggs	Mean
<i>dactylatra</i>	Ascension, Atlantic	Dorward, 1962a	96	69	27	—	1.3
<i>granti</i>	Galapagos, Pacific	Nelson, 1967a	209	84	125	0	1.61
<i>personata</i>	Kure, Pacific	Present study	105	11	94	1	1.9

¹ Calculated from Nelson's data.

INCUBATION

Incubation begins with the first egg. Blue-faced Boobies incubate by wrapping the webbing of their toes over the eggs. On very hot days the eggs are shaded (Bartholomew, 1966). Dorward (1962a) reports that the webbing is more vascularized during incubation than at other times of the year.

The incubation periods found for first and second eggs in two-egg clutches on Kure are presented in Table 4.5. The wide range in the periods exceeds that found by Dorward (42-46 days) in the Ascension

TABLE 4.5
MEAN INCUBATION PERIOD (DAYS) FOR FIRST AND SECOND EGGS, 1964 AND 1965

	No.	Range	Mean	< 43	≥ 43
Egg 1	58	40-49	43.78	13	45
Egg 2	48	38-47	42.76	20	28
Total	106	38-49	43.32	33	73

$\chi^2 = 3.68$; d.f. = 1.

colony. It has been thought that the incubation time for each egg is the same, as the range in days between hatchlings has appeared the same as that between the two eggs (Dorward, 1962a; Nelson, 1967a). A four-fold contingency table to test whether first or second eggs on Kure require more or less than the average time (43 days) to hatch has been constructed (Table 4.5). The hypothesis of no difference is not rejected by these data ($\chi^2 = 3.68$; $.10 > P > .05$). However, the wide variation in hatching times from pair to pair obscures the relationship between first and second eggs in a given clutch. If the incubation time for each egg in a clutch is analyzed (Table 4.6), the null hypothesis of no difference in incubation periods is rejected at the .01 level. Four times as many first eggs required more time to hatch than did second eggs.

A bird may spend from one hour to more than 44 hours on the eggs. I was unable to determine the longest attentive period, but it could easily match an interval of over 70 hours once found by Nelson in the Galapagos. Table 4.7 gives values for 47 complete bouts and for 48 bouts in which the total time was not determined. Nests were checked hourly, except between 22:00 and dawn, for a 44 hour period. The average incubation bout is less than half that found by both Dorward (32 hours on Ascension) and Nelson (30 hours for males, 24.7 hours for females on the Galapagos). The average spell on the nest was more than two hours longer for the males, but the longest individual bouts recorded were those of females.

It is generally thought that the length of the incubation bouts gives a good indication of the amount of food available to the birds, and the distance this food is from the island. The incubation bouts on Kure were very short compared to those measured by Dorward and Nelson and surprisingly short when compared to the incubation bouts of other seabirds. Laysan Albatrosses and Black-footed Albatrosses have shifts of over 22 days (Rice and Kenyon, 1962, and personal observations). Ashmole and Ashmole (1967) recorded the attentive periods of seven species of seabirds from Christmas Island (Pacific Ocean), and all were longer than those of Kure Blue-faced Boobies. Five species (Red-tailed Tropicbird, Christmas Shearwater, Phoenix Petrel (*Pterodroma alba*), Sooty Tern, and White Tern) had shifts averaging more than three days, and the diminutive Black Noddy (*Anous tenuirostris*) and Blue-gray Noddy (*Procelsterna cerulea*) had bouts averaging 17.5 and 20 hours, respectively. The short periods recorded for the Kure boobies indicate that they must have an abundant source of food close to the island.

Perhaps a better indication of food availability is the time spent at sea by incubating birds when relieved by their mates. Short absences should indicate plentiful food near the colony; long absences could indicate a food supply farther from shore or one that is nearer but less abundant. The periods that birds remained away from the colony are given in Table 4.8. These values are very short, further indicating

TABLE 4.6
 INCUBATION PERIODS (DAYS) FOR FIRST AND SECOND EGGS
 IN TWO-EGG CLUTCHES, 1964 AND 1965

Nest No.	Egg 1	Egg 2	d_1	rank
1964:				
2	48 or 49	38	(10.5)	30
5	44	45	-1	-9½
8	43	43	0	
10	45	43	2	22½
11	44	43	1	9½
12	44	43	1	9½
13	43	42	1	9½
17	44	43	1	9½
18	44	42	2	22½
19	44	42	2	22½
24	43	42	1	9½
26	46	45	1	9½
27	43	42	1	9½
28	42	41	1	9½
29	42	42	0	
33	44	42	2	22½
36	44	43	1	9½
38	41	43	-2	-22½
40	46	43	3	28
43	43	42	1	9½
53	42	42	0	
1965:				
1	45	44	1	9½
2	44	41	3	28
6	44	44	0	
10	44	42	2	22½
17	47	44	3	28
18	45	47	-2	-22½
20	43	44	-1	-9½
23	40	41	-1	-9½
32	45	43	2	22½
33	43	42	1	9½
34	43	42	1	9½
39	45	45	0	
41	42	43	-1	-9½
1a	43	43	0	
19a	42	41	1	9½

$$T = \sum - \text{ranks} = 83$$

H_0 : hatching time egg 1 = hatching time egg 2.

Acceptance Region, $\alpha = .01$, $n = 30$ (ties not counted), for Wilcoxon two-sample sign-rank test: $T \geq 109$. Critical values from Table 2, Wilcoxon and Wilcox, 1964.

that food was not particularly limited during the study period. It is unfortunate that such data are not available from other colonies. Future workers might consider this relatively simple technique of evaluating the food resources of other populations.

Table 4.9 shows the times at which incubation change-over occurred. Most change-overs take place in the afternoon and evening, although

TABLE 4.7
LENGTH OF INCUBATION BOUTS, 1965

Sex	No.	Hours											Mean			
		0-4	5-8	9-12	13-16	17-20	21-24	25-28	29-32	33-36	37-40	41-44				
Complete Bout	24	4	5	7	4	1	1	2	0	0	0	0	0	0	0	11.16
	23	8	5	6	1	2	0	1	0	0	0	0	0	0	0	8.41
Incomplete Bout ¹	22	8	5	6	0	2	0	0	0	0	0	0	1	0	0	—
	26	3	5	8	3	2	1	0	1	2	0	0	0	2	2	—

¹ Either beginning or end of bout not observed.

TABLE 4.8
TIME MATES OF INCUBATING BIRDS ABSENT FROM THE COLONY,
PRESUMABLY AT SEA, 23 JANUARY-31 MARCH 1965

Hours	Completed trips		Minimum possible time ¹	
	Males	Females	Males	Females
1-2	7	14	—	—
3-4	7	8	—	1
5-6	3	7	—	—
7-8	4	3	1	1
9-10	4	1	3	5
11-12	4	4	3	2
13-14	—	—	1	—
.				
.				
29-30	1	—	—	—
33-34	—	—	1	—
37-38	—	—	1	1
41-42	—	—	1	—
No observ.	30	37	11	10
Mean time	6.50	4.47	—	—

¹ Departure or arrival time uncertain.

some (9%) occur after dark. This is similar to the other subspecies studied. Relieved birds may remain with the mate or fly directly to sea (Fig. 4.3). Most birds relieved during the morning and afternoon fly to sea within one hour. However, in the late afternoon, the birds could be overtaken by darkness if they remain at sea too long. As a consequence, birds do not leave the colony if less than roughly one-half hour remains before sunset. This raises intriguing questions as to what stimuli the birds are responding to in late afternoon, and what method they have for assessing the time remaining for fishing.

Most (16 of 18) birds that left the colony within two hours of sunset returned the same night. All birds relieved at night remained with their mates until dawn.

In Table 4.10 the sex of the incubating bird is recorded for 1,556 nest visits in 1965. There is a tendency for males to predominate on

TABLE 4.9
TIME OF INCUBATION CHANGE-OVERS

Time	No.	Percent
22:01-06:00	8	5.6
06:01-12:00	38	26.6
12:01-18:00	63	44.0
18:01-20:00:		
light	21	14.7
dark	13	9.1
Total	143	

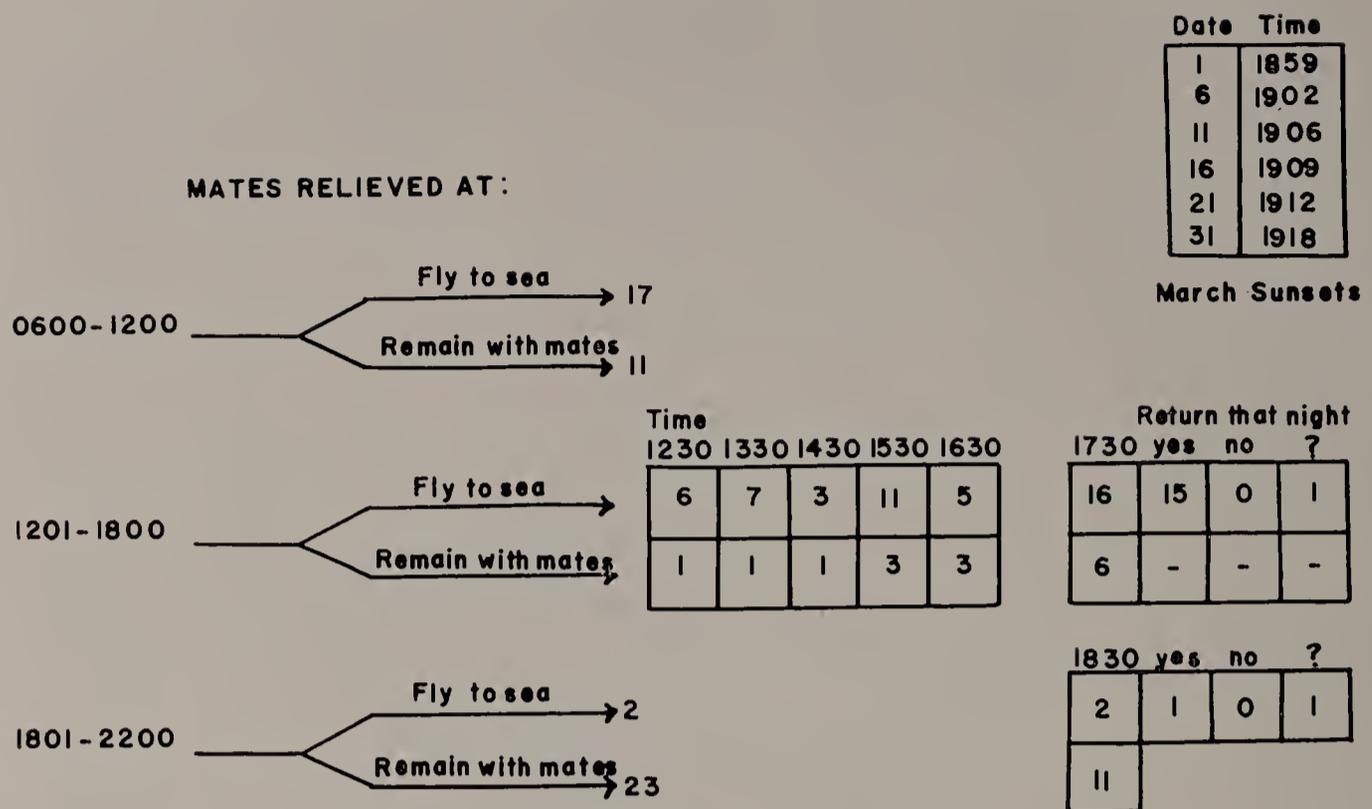


FIG. 4.3. Proportion of relieved incubating birds flying to sea at various times of day, March 1965.

TABLE 4.10
NUMBER OF MALES AND FEMALES OBSERVED INCUBATING DURING DIFFERENT
TIMES OF DAY, JANUARY-MARCH 1965

Time	No. observations	Males	Percent	Females	Percent
06:01-12:00	609	247	40.6	362	59.4
12:01-18:00	699	301	43.1	398	56.9
18:01-22:00	158	97	61.4	61	38.6
22:01-06:00	90	49	54.4	41	45.6
Total	1,556	694		862	

the eggs at night, and for females to predominate during the day. Males spend more time at sea than females (see Table 4.8), and females have more long bouts (Table 4.7).

From the data in Figure 3.2 we could predict that courting and breeding pairs would be together at their nest during the early evening and night. This is documented in Table 4.11. Most courtship, pair-

TABLE 4.11
TIME OF DAY WHEN PAIRS TOGETHER IN COLONY

Time	No. observations	Pairs together	Percent
06:01-12:00	609	61	10.0
12:01-18:00	699	91	13.0
18:01-22:00	168	101	60.1
22:01-06:00	76	58	76.3
Total	1,552	311	20.0

TABLE 4.12
HATCHING SUCCESS OF FIRST AND SECOND EGGS IN TWO-EGG CLUTCHES,
1964 AND 1965

	No. clutches	Egg 1		Egg 2	
		Hatched	Percent	Hatched	Percent
1964	50	36	72.0	27	54.0
1965	39	17	43.5	22	56.4
Total	89	53	59.6	49	55.1

maintenance, and agonistic behavior occurs in the last hour before dark, often after sunset. This makes it possible for an observer to concentrate his observations of behavior during a period when intra- and inter-pair activity is at its height.

Hatching success for first and second eggs in two-egg clutches for the two breeding seasons is shown in Table 4.12. There is no difference ($\chi^2 = .2067$; $75 > P > .50$) in the number of first and second eggs that hatched.

ABANDONMENTS

Every year some pairs abandon their eggs, either before they would normally hatch, or well past the normal incubation span. Twenty-two such nests (21.6% of all nests) were observed in the course of this study (Table 4.13). Abandonments have been categorized according to whether or not a normal incubation spell (43 days) was attempted. If a full spell was completed, or exceeded, the birds were presumed incubating inviable eggs. If, however, less than 43 days were spent incubating, the failure is considered to have been a behavioral one. Behavioral failings accounted for 64% of the abandonments.

From the table we can see that in 1965 there were two and one-half times as many early abandonments as in 1964. This may be yet another effect of the pre-season storm which, as we have seen, may have accounted for the delayed breeding season, irregular timing in the pairs, and lower overall breeding success.

The mean incubation time for infertile eggs attended to beyond the normal period is 92.75 days. The birds may thus remain on their eggs for one-fourth of the year, or more than twice the normal incubation span. We would expect that such long attendance at the nest would preclude a second nesting attempt, but one bird did renest after 106 days on the eggs of the first nest (Figure 4.4).

RENESTING

Pairs that fail to hatch their eggs or rear their young may renest. Eleven pairs did so in 1964 and 1965. There was a marked difference between the two seasons (Tables 4.14 and 4.15). In 1964 only 10.5% of the initial failures renested but in 1965 the figure rose to 42.8%. In

BREEDING BIOLOGY

TABLE 4.13
EGG ABANDONMENTS, 1964 AND 1965

Year	No. observ.	Early abandonments			Mean	Percent renesting	No. observ.	Late abandonments			Mean	Percent renesting
		Incub. period (days)	Incub. period (days)	Incub. period (days)				Incub. period (days)	Incub. period (days)			
1964	4	26	38	78	28.25	50.0	5	91	91	98.20	0.00	
		31	18	103				109				
1965	10	5	40	106	14.00	40.0	3	69	69	83.66	33.33	
		15	30	76								
		8	22									
		7	5									
		5	3									
Total	14				18.07	43.0	8		92.75	12.5		

TABLE 4.14
NESTING SUCCESSES, FAILURES, AND RENESTINGS, 1964 AND 1965

Year	Initial success	Initial failure	Number renest	Percent renest	No. offspring from renesters	Percent contribution to population
1964	32	19	2	10.5	2	5.8
1965	19	21	9	42.8	6	24.0

1965 a majority of the first nests failed (52.5%). This was probably one factor resulting in the high number of renesting birds. It appears that birds that lose either eggs or chicks are equally likely to attempt a second nest.

The differences between the two breeding seasons have been repeatedly stressed. The differences in renesting patterns between 1964 and 1965 are striking. The two young produced by second nests in 1964 represented only 5.8% of the total production for that year. In contrast, the six young produced by renesters in 1965 represented 24% of the young. The high number of renesters, and the resultant contribution to the population of their young, are important factors that may have resulted from the climatic disturbances preceding the 1965 season. Renesting can be seen as a highly advantageous behavior that functions in adverse times to implement later nesting at times more favorable for the colony. In 1965, 66.6% of the renesters successfully raised their young, compared to a success of 47.5% for the first nests.

In all cases birds renesting retained the same mates. The average time between the loss of a nest and the beginning of the next was 30.45 days. There is moderate spread in the data (S.D. = 10.5 days); however, this assumes more meaning when we consider that these renesters represent pairs that have a wide variation (S.D. = 36.95 days; M = 71.7 days) in the times they had been incubating or brooding prior to the break-up of the nest (Fig. 4.4). One pair had been incubating only five days when the nest broke up, while another had remained on eggs for 106 days. Three pairs had successfully hatched at least one chick, and had attended them from one to 23 days. The uniform renesting time after nest loss argues for a very uniform physiological system underlying the reproductive timing of the pairs. With so few birds renesting no attempt was made to analyse the endocrine changes that accounted for the observed temporal synchrony.

TABLE 4.15
RENESTING AS FUNCTION OF STAGE AT WHICH NEST FAILED, 1964 AND 1965

Year	Total failures	No. losing eggs	No. renest	Percent	No. losing chicks	No. renest	Percent
1964	19	13	2	15.4	6	0	0.0
1965	21	18	6	33.3	3	3	100.3
Total	40	31	8	25.8	9	3	33.3

Nest No.	Days on first nest	Renesting date	Renesting time from:	
			1st egg	Nest loss
22-50	26	16 April 1964	56	30
39-53	49	11 May 1964	66	17
1-1a	50 (c-2)	6 April 1965	57	27
5-25	21	25 March 1965	44	23
8-46	106	2 July 1965	136	30
12-39	68 (c-23)	24 May 1965	94	26
14-14a	8	28 February 1965	36	28
15-47	76	13 July 1965	135	59
16-42	58 (c-1)	28 May 1965	88	30
19-19a	7	17 April 1965	40	33
28-41	5	28 May 1965	37	32
Average:			71.7	30.45

c = number of days chick attended.

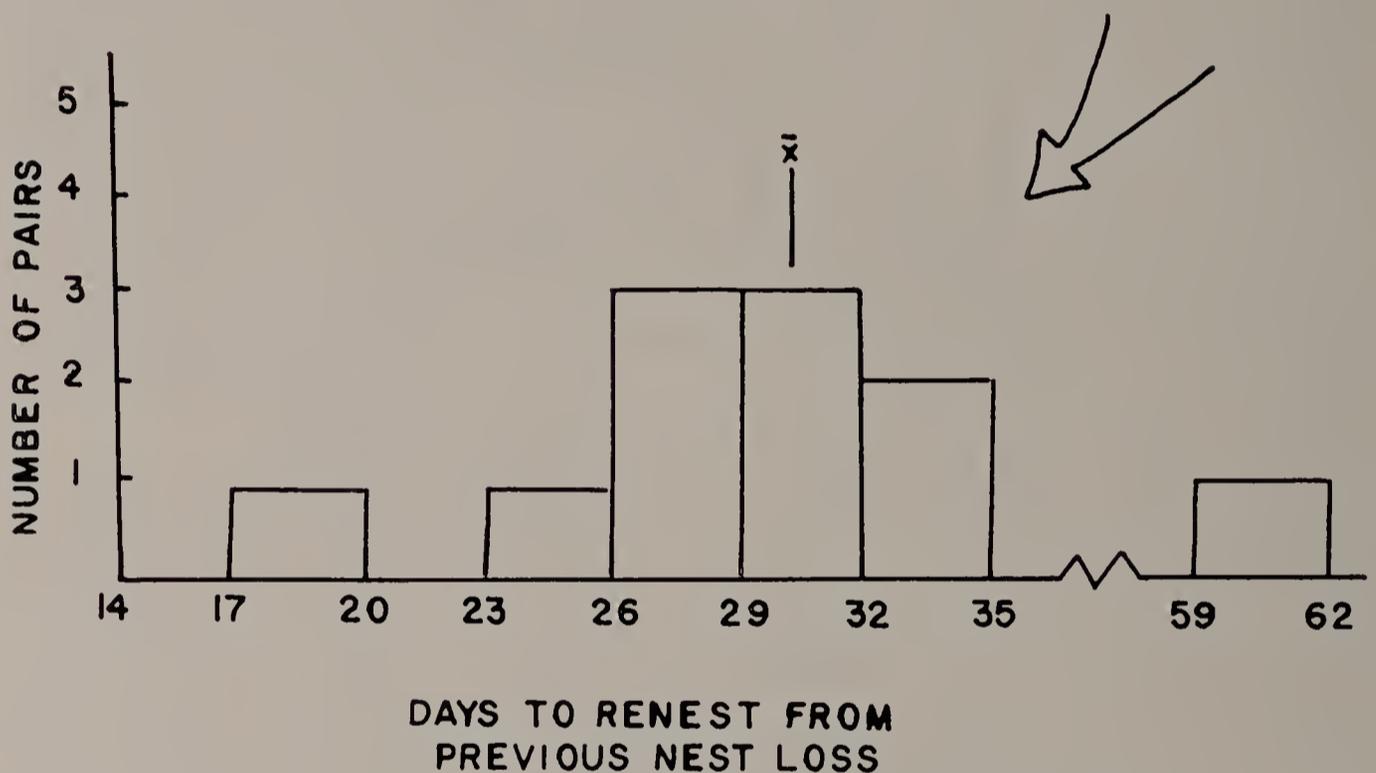


FIG. 4.4. Phenology of renesting pairs, 1964 and 1965.

ASYNCHRONOUS HATCHING AND DIFFERENTIAL SURVIVAL OF CHICKS

It is a well-noted fact that although two eggs is the normal clutch size in most Blue-faced Booby populations, only one chick is ever raised (Beck, 1902; van Bemmelen and Hoogerwerf, 1940; Brygoo, 1955, Dorward, 1962a; Fisher, 1904; Gibson-Hill, 1950; Murphy, 1936; Nelson, 1967a; Palmer, 1962; Reithmüller, 1931, and others). The eggs always hatch asynchronously. On Kure, three to seven days elapse between the appearance of the first and the second chick. The mean is 4.8 days (Table 4.16), approximately one day less than the normal time interval between the laying of the first and second eggs (5.6 days).

The first chick has several days in which to grow prior to the hatching of the second egg. Second chicks, smaller than their siblings, usually die or disappear soon after hatching. On Ascension Island, Dorward

TABLE 4.16
TIME BETWEEN HATCHING OF FIRST AND SECOND CHICKS IN TWO-EGG CLUTCHES

Year	No.	Interval in days							No.	Mean
		<3	3	4	5	6	7	>7		
1964	23	0	3	7	7	4	2	0	23	4.8
1965	14	0	1	4	7	2	0	0	14	4.7
Total	37								37	4.8

(1962a) found only one second chick that survived for a substantial length of time (34 days) with its sibling. Brygoo (1955) found 18 of 19 nests with two eggs, but only one of 31 nests with two young on Tromelin Island in the Indian Ocean. The two young in this case appeared to be about 30-40 days old, an exceptional age for twins. As Dorward suggests, this may have been a nest into which a chick from a nearby area had wandered. Not to be ruled out, however, is the rare chance of the survival of both chicks.

My results are very similar to those of Brygoo and Dorward. In 31 nests where the first chick was alive when the second egg hatched, all but one of the second chicks died or disappeared (the second chick survived because the first died). The average survival time for second chicks was 3.3 days (not including the survivor, see Table 4.17). The apparent reason for the death of most chicks is starvation or exposure. My experience on Kure is essentially the same as Dorward's. Second chicks were found outside the nest either dead or alive. If living young were replaced, they soon were expelled again. I agree with Dorward that the older chick probably expelled the weaker younger one, although I never witnessed this. Fratricide has also been reported, among Pelecaniformes, for the African White Pelican (*Pelecanus onocrotalus*) by Vesey-Fitzgerald (1957).

There are three possible explanations, not mutually exclusive, of why the chicks disappear. Great Frigatebirds on Kure gather their nesting materials, on the wing, from the plain in which the boobies nest. They have never been observed preying on seabirds, but could easily do so if chicks were unguarded. Dorward considers Ascension Frigatebirds

TABLE 4.17
FATE OF SECOND CHICKS HATCHED IN NESTS CONTAINING FIRST CHICKS

Year	No.	Fate			Days survived											Mean
		M ¹	D ²	F ³	0	1	2	3	4	5	6	7	11	15		
1964	20	5	15	0	1	4	3	6	2	0	0	2	1	1	3.8	
1965	11	3	7	1	1	3	2	1	1	2	0	0	0	0	2.4	
Total	31														3.3	

¹ M: missing.

² D: dead.

³ F: fledged.

(*F. aquila*) to be important predators of displaced chicks on Boatswain Bird Island. A second explanation is that the parents eat their own chicks. This has never been observed in the Blue-faced Booby, but I have seen a disturbed Brown Booby eat its chick on Johnston Atoll. The third, and most likely, explanation is that excluded young are eaten by Polynesian rats (*Rattus exulans*). Elsewhere (Kepler, 1967) I have demonstrated that these rats prey on other seabirds nesting on Kure. They have been observed feeding on the regurgitated remains of fish in the Blue-faced Booby colony and would eat any chick not defended by its parents.

ADAPTIVE SIGNIFICANCE OF THE TWO-EGG CLUTCH

The above considerations do not imply that second eggs only rarely gave rise to fledged young. First chicks occasionally died before the second egg hatched. Similarly, first eggs in many clutches failed to hatch or were cracked or lost early during incubation and the second eggs in most cases produced fledged young (Table 4.18).

Nelson (1966g), considering Dorward's data cited above, concludes that the two-egg clutch in the Blue-faced Booby is maladaptive and perhaps a holdover from a distant time when two eggs were advantageous. He bases his statement on the fact that two chicks are never raised by one pair of adults. However, the two-egg habit is not necessarily selectively disadvantageous if two young are never raised. The important considerations are whether or not the second egg gives rise to fledged young and whether clutches with two eggs are more or less successful than those with only one egg. Table 4.18 clearly shows that second eggs *do* produce chicks. Indeed, 22% of all young produced over the two-year period resulted from the second egg. Table 4.19 compares the breeding success of one-egg clutches with that of two-egg clutches. In the two-year period only two of 10 one-egg clutches gave rise to fledged young, whereas 57 of 90 two-egg clutches did so. Fisher's Exact Probability Test has been used to evaluate these differences: the hypothesis of no difference is rejected ($p = .01$) by these data. Two-egg

TABLE 4.18
CONTRIBUTIONS OF SECOND EGGS TO THE PRODUCTION OF FLEDGED YOUNG,
1964 AND 1965

	Number of occurrences			
	'64	'65	Total	
First egg fails, second egg yields fledged young	4	6	10	
First chick dies before second egg hatches, second egg produces fledged young	1	1	2	
First chick dies after second egg hatches, second chick survives	0	1	1	
Total second eggs producing fledged young	5	8	13	22%
Total first eggs producing fledged young	29	17	46	78%

TABLE 4.19
DIFFERENTIAL BREEDING SUCCESS WITH VARYING CLUTCH SIZE¹

Year	One-egg clutch				Two-egg clutch				Three-egg clutch			
	No.	F ²	U ³	Percent fledged	No.	F	U	Percent fledged	No.	F	U	Percent fledged
1964	4	2	2	50.0	49	32	17	65.3	0	0	0	0.0
1965	6	0	6	0.0	41	25	16	61.0	1	0	1	0.0
Total	10	2	8	20.0	90	57	33	63.3	1	0	1	0.0

¹ Three two-egg clutches and one one-egg clutch not included as breeding outcome uncertain when study terminated.

² F: young fledged.

³ U: eggs failed or young not fledged.

Probability of observed difference, Fisher's Exact Probability Test, = 0.01069.

clutches are significantly more successful than those with only one egg, and nearly one-fourth of the chicks raised came from second eggs. Any adaptation that can even slightly increase the net production of young, without detriment to the birds in some other way, will be selected for. In this case, the second egg effectively buffers against either inviability of the first egg or early death of the first chick. In the Kure population, therefore, the two-egg clutch is still highly adaptive, and does not appear to be a relict characteristic which previously was adaptive and which presently is in the process of being lost.

Dorward (1962a) first suggested that the "buffer" effect of the second egg was a sufficient explanation for the persistence of the two-egg clutch, but he lacked evidence for this. Recently, Simmons (1967) supported this idea, suggesting that the slight effort involved in producing the second egg, which is only 4% of the body weight (Stonehouse, 1963) is offset by the advantage conferred upon pairs that can continue breeding without interruption if one of the eggs fails, or if the first-hatched young dies prior to the hatching of the second egg. Lack (1966) takes the opposite view, suggesting that two eggs are retained because Blue-faced Boobies can occasionally rear two chicks under favorable conditions. Lack's position has no support, as there is as yet no evidence that two chicks are raised, in spite of an ever-increasing amount of published information on the species (Dorward, 1962a,b; Bartholomew, 1966; Nelson, 1966a,e,g, 1967a; Simmons, 1967; present study). The advantages described above provide a satisfactory explanation for the adaptive significance of the two-egg clutch.

FOSTER CHICKS

In the 1965 season six pairs whose nests had failed were given foster eggs or chicks. These six nests were recorded as failures in the previous sections, and the eggs or young are not included in any of the population figures. Foster eggs were second eggs taken from nests with newly hatched young. Foster chicks were second chicks taken from nests in

TABLE 4.20
SURVIVAL OF FOSTER EGGS AND CHICKS, 1965

Nest No.	Days on eggs	Given	Accept?	Raised to fledgling?	Remarks
7	53	1 day chick	Yes	Yes	
9	54	1 day chick	Yes	Yes	
11	35	1 egg	Yes	Yes	
14a	46	1 egg	Yes	Yes	
16	53	1 egg	Yes	No	Renested;
27	40	4 day chick	Yes	Yes	reared own chick

which the first chicks were present. The first chicks from all donor nests fledged, and these nests are recorded as successes in previous sections.

Table 4.20 presents the data for the foster eggs and chicks. All pairs accepted whichever was given to them; there was no recognition of either their own eggs or young. The three pairs given young accepted them, either before (nest 27) or after (nests 7 and 9) they had incubated for the normal period. The presence of a chick in the nest elicited the appropriate behavioral response from the parents. The actual process of hatching is, thus, not necessary for the development of proper parental behavior.

BREEDING SUCCESS

Breeding success for the two years was determined only for nests with known outcomes. Three nests in 1964 and one in 1965 contained young chicks when the study terminated, and are not included in the final calculation of nesting success. The five foster chicks that survived in 1965 have also been omitted; the pairs to which they were given are scored as failures. Since some of these pairs might have renested if left alone, the percent surviving shown in Table 4.21 may be slightly low. Data from Ascension Island (Dorward 1962a) are included for comparison. Comparable data are not yet available from the Galapagos.

Kure success was five to six times that found on Ascension. The

TABLE 4.21
BREEDING SUCCESS AT GREEN ISLAND COMPARED WITH THAT AT
BOATSWAIN BIRD ISLAND, ASCENSION ISLAND

	Year	No. clutches started	No. clutches hatching chick	No. chicks fledged	Percent surviving of total laid
Green Island	1964	56	43 (77%)	34 (79%) ¹	63.5
	1965	49	30 (61%)	25 (83%) ¹	52.0
Boatswain Bird Island, Ascension Island ²	1958	699	272 (39%)	68 (25%)	9.7

¹ Fate of three chicks in 1964 and one chick in 1965 undetermined.

² Figures for two colonies lumped and total successes calculated from Dorward's (1962a) data.

greatest difference is in the number of young that survived after hatching. Dorward reasons that a large chick die-off was the result of food shortages, which are common in the "tropical blue" waters of the equator. Kure birds are breeding in sub-temperate waters that may not show irregular food shortages of the kind reported from the tropics. Also of paramount importance to colony success in these two areas are the vast differences in colony size and spacing, as has been detailed in Chapter 3. The continual egg rolling found in the Ascension colony was completely lacking on Kure and chick starve-offs did not occur. The spacing-out that was so pronounced on Kure could not occur on Ascension.

Looking at the Kure data, we can see that the failure of the eggs to hatch accounted for most of the nest mortality in 1965 while there was no difference between the rate of egg loss and chick loss in 1964. The survival of the young between hatching and fledging was slightly higher in 1965.

EFFECT OF MATE RETENTION ON SUBSEQUENT BREEDING

The 1965 season has been analysed in terms of the breeding records of individual 1964 pairs. The overall contribution of 1964 birds to 1965 nests is shown in Table 4.22. In the table, arrows should be read "yields." Thus the first line shows that 23 pairs in 1964 keep their mates, yielding 23 pairs in 1965; five of these pairs renested after the loss of their initial nest, resulting in 28 nests producing 17 fledged young. Total nest success in this group was 74%, and their contribution to the total production of 1965 was 68%. Pairs that remained together during the two seasons produced more young than did pairs that broke up ($\chi^2 = 16.350$; $P < .001$). This may be in large part due to the familiarity of the pair members and their resultant behavioral efficiency.

EFFECT OF BREEDING SUCCESS ON SUBSEQUENT BREEDING

Success in one year may influence breeding in the following year and may also affect mate retention. The data have been arranged (Table

TABLE 4.22
COMPOSITION AND CHICK PRODUCTION OF PAIRS IN 1965 AND THEIR RELATION
TO 1964 PAIR BONDS

1964	1965	Percent nest success	Percent contribution	
23 kept mates →	23 pairs, 5 renest = 28 nests →	17 chicks	74	68
19 broke up →	17 pairs, 4 renest = 21 nests →	8 chicks	42	32
10 disappeared →				
4 unknown →				
56 nests	49 nests	25 chicks	100%	

TABLE 4.23
INFLUENCE OF BREEDING SUCCESS ON PAIR STABILITY AND SUBSEQUENT BREEDING SUCCESS

1964		1965	
32 Successes	—————→	21 chicks from 32 nests:	66% success
19 (59%) remained mated	—————→	15 chicks from 19 nests:	79% success
13 (41%) broke up	—————→	6 chicks from 13 nests:	46% success
10 Failures	—————→	4 chicks from 10 nests:	40% success
4 (40%) remained mated	—————→	2 chicks from 4 nests:	50% success
6 (60%) broke up	—————→	2 chicks from 6 nests:	33% success

4.23) to permit an analysis of these variables. The null hypothesis that success in one year does not effect mate retention is not rejected ($\chi^2 = .5085$; $.50 > P > .250$). Although pairs that were successful in 1964 were more successful the following year than those that had failed, the hypothesis of no effect is again not rejected by the data ($\chi^2 = 1.149$; $.50 > P > .250$).

We can also analyze 1965 outcomes both in terms of mate tenacity and 1964 breeding performance. In all cases (Table 4.23) the results are those that we would predict *if* the two variables exerted an influence on breeding outcomes. Of those pairs successful in 1964, highest success was achieved the following year by pairs that retained their mates; of those pairs unsuccessful in 1964, lowest success was registered for those that switched. The most successful 1965 birds were those that were both successful in 1964 and kept their mates, while the least successful were those that failed in 1964 and switched. The null hypothesis of no effect, however, is not rejected ($\chi^2 = 2.516$; $.250 > P > .10$) by these data.

SUMMARY: INTERACTIONS BETWEEN THE TWO BREEDING SEASONS

1. Pairs that remain mated reneest sooner in the following year than pairs that break up ($P \sim .01$).
2. Pairs that remain mated from one year to the next have a higher breeding success in the second year than do pairs that break up ($P < .001$).

DESCRIPTION OF THE YOUNG

The data upon which the following discussion is based were collected by POBSP personnel prior to my arrival on the atoll. A listing of these workers is given in the Acknowledgments. The Appendix discusses the methods used for obtaining the measurable data upon which the figures and discussion are based. Figures 4.5 through 4.8 are presented courtesy of the POBSP.

The young hatch nearly naked and helpless (Fig. 4.5). A very sparse white down is distributed over the body, but affords no protection to the young, which must be constantly brooded or shaded by the adults (see Bartholomew, 1966). Down covers the flanks and lower back by the second week, and by 21 days the young are normally completely

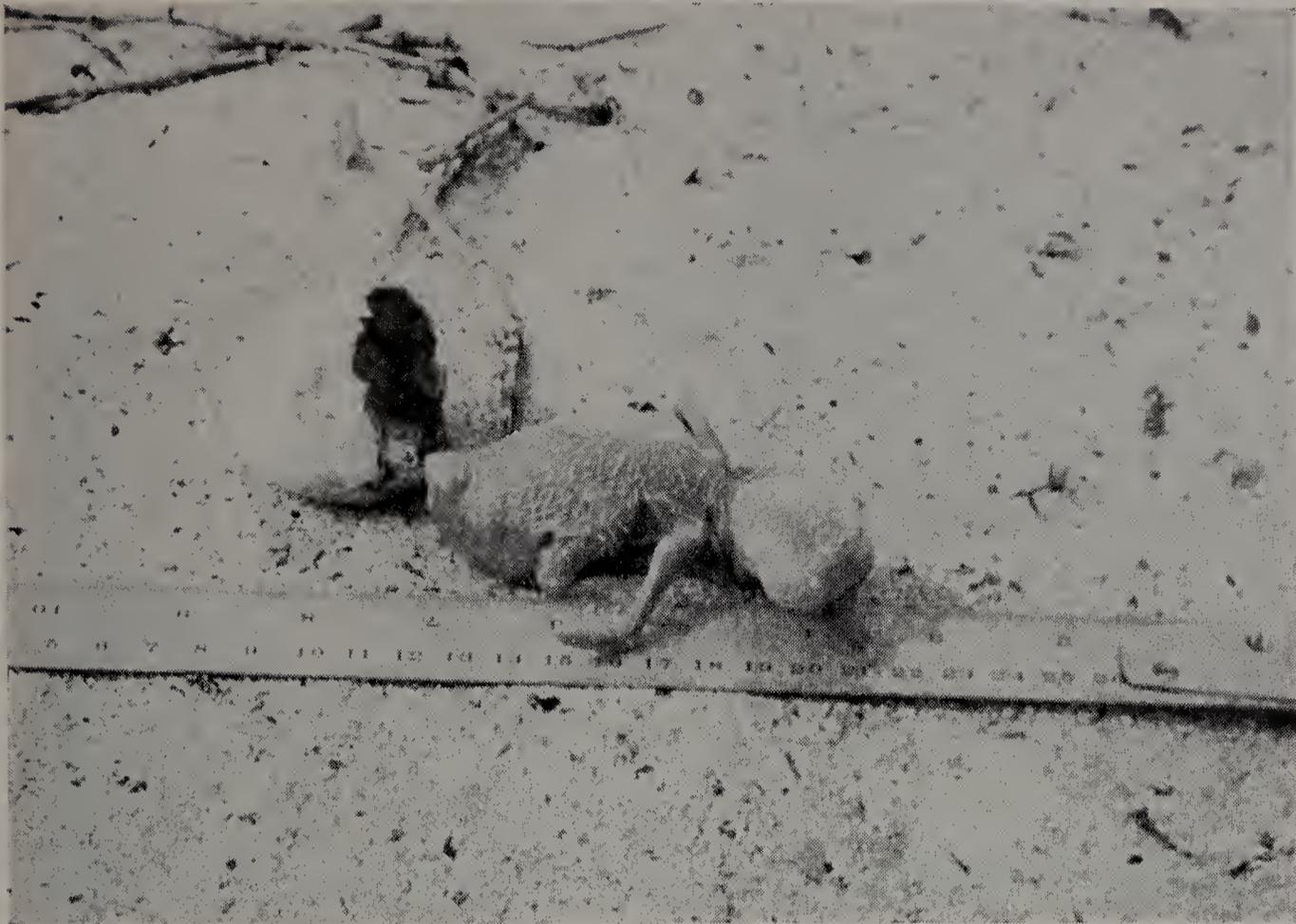


FIG. 4.5. Hatchling



FIG. 4.6. Downy young at 35 days.

covered, except for naked patches on the neck, with a loose white down. The down thickens in the next week, so that at about 30 days the growing chick is heavily covered except for the neck. At 35 days of age even this region is covered, and the bird has a very dense, fluffy white appearance (Fig. 4.6).

Between 26 and 35 days (average for 11 birds = 31.3) the egg-tooth is normally lost, although in one case it was present on a chick 40 days old.

The primaries begin erupting in the sixth week; the earliest age at which primaries were seen was 44 days. By 50 days of age most birds show primary development, shortly after which the tail feathers begin their growth. At about 70 days the primaries, secondaries, and tertiaries, as well as tail feathers, are prominent, but the chick is still essentially downy. The scapulars begin growing at about 70 days. By 80 days of



FIG. 4.7. Young at 70 days.



FIG. 4.8. Juvenile plumage, 112 days

age the young show a development of the wing and tail coverts and the feathering of the upper back may form a wide strip from wing to wing. The head, neck, flanks, belly, and lower back, and the leading edges of the wings remain downy (Fig. 4.7).

The growth of the juvenile plumage accelerates from about 90 to 105 days of age, and by 100 to 105 days it is normally completed. The juvenile plumage is much darker than that of adults, the only pure white areas being the breast, belly, and flanks. The head and neck are brown, often mottled with white; the wings and tail, and their coverts, are also dark brown. The back is mottled brown and white (Fig. 4.8). The plumage appears complete by 105 days, but the flight feathers at this time are not fully grown (Fig. 4.9), so the chick in juvenile plumage is still flightless. At about 120 days of age the flight feathers have completed their growth, and the juveniles begin to fly. A flying bird is easily recognized by its clean legs and feet, the encrusting guano of the early stages having washed off at sea.

GROWTH

The growth of the Blue-faced Booby chicks is highly allometric (Figs. 4.9 to 4.13). In each of the figures the character under consideration is

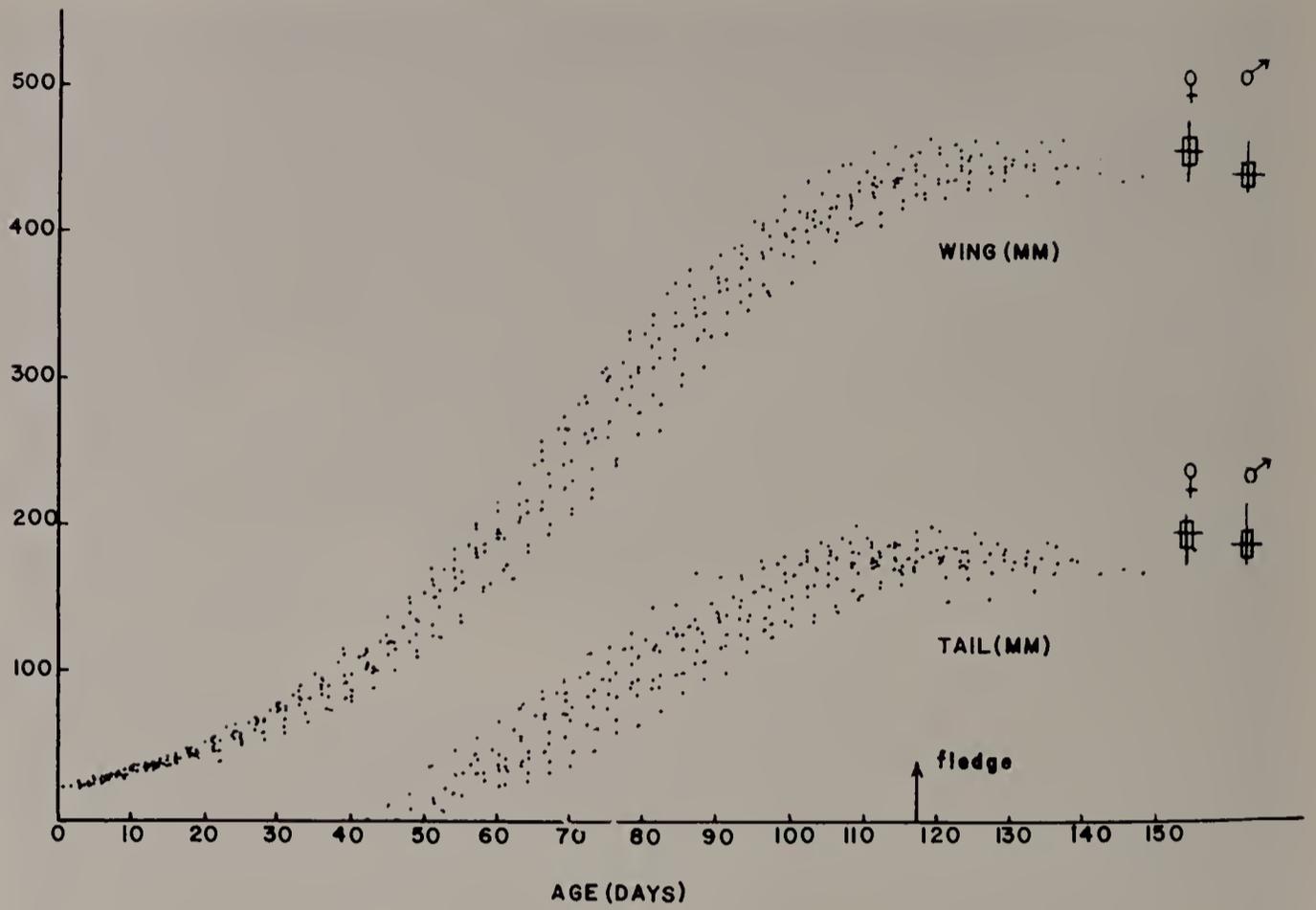


FIG. 4.9. Growth of the wing and tail in ten chicks.

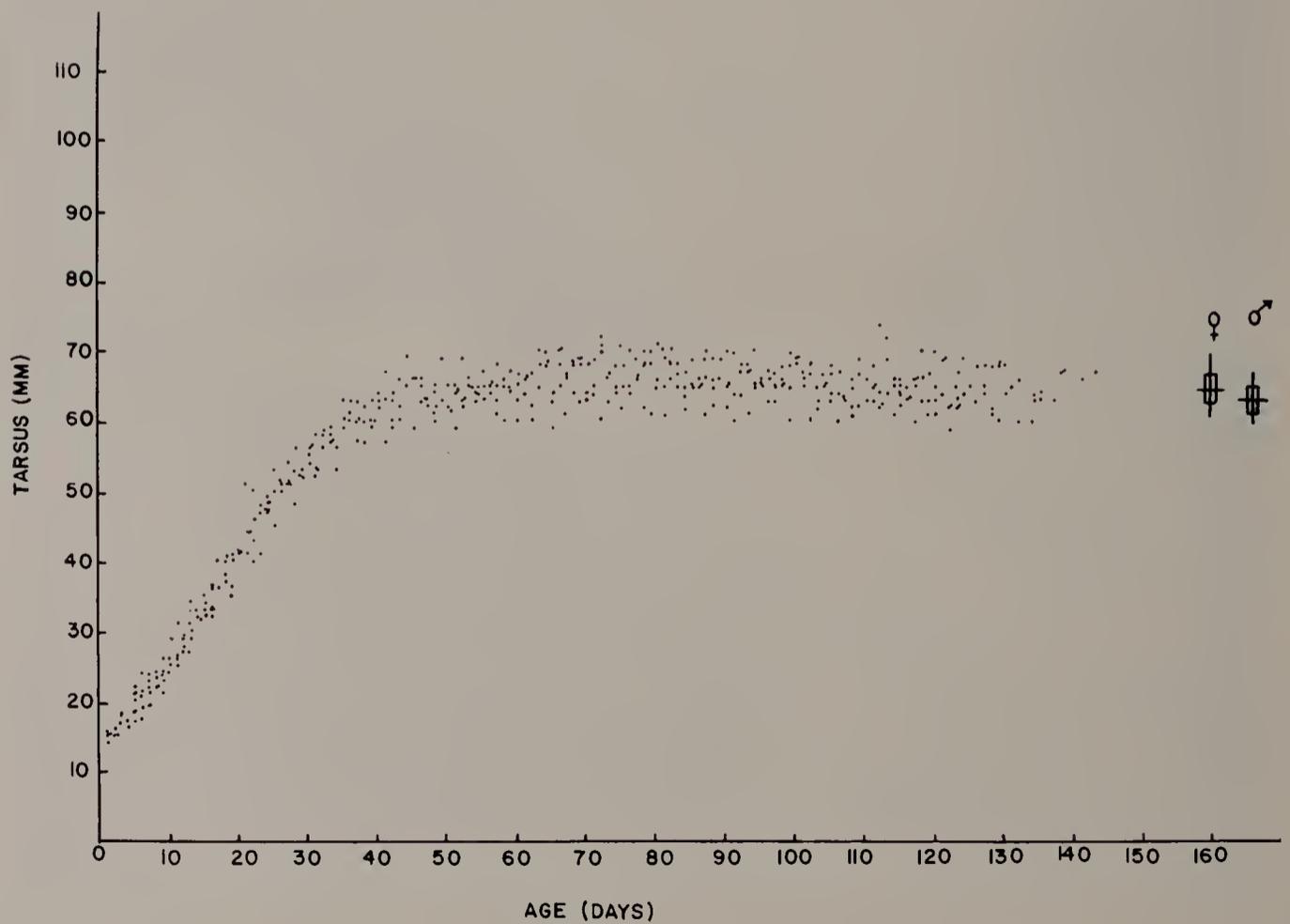


FIG. 4.10. Growth of the tarsus in ten chicks.

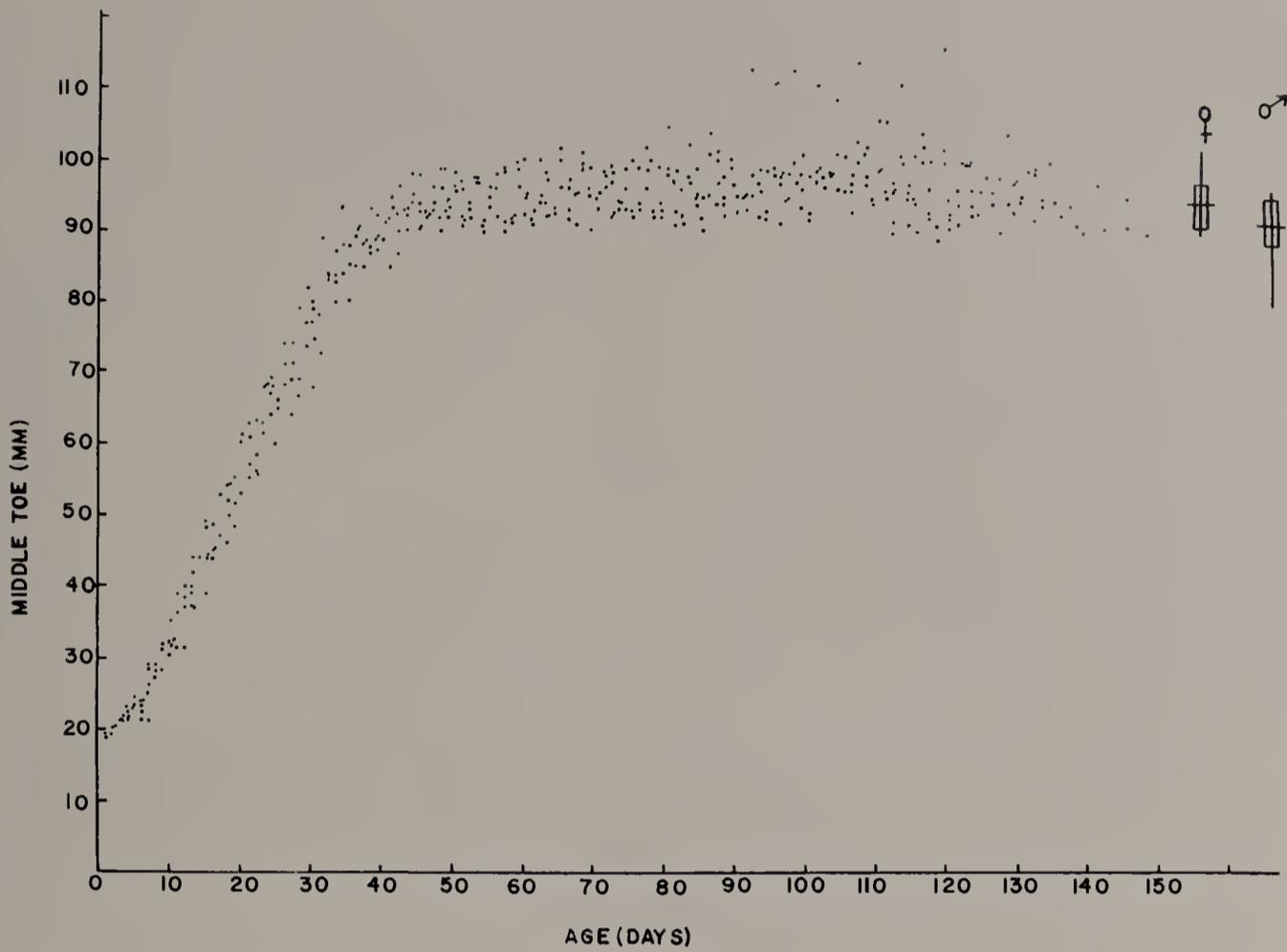


FIG. 4.11. Growth of the middle toe in ten chicks.

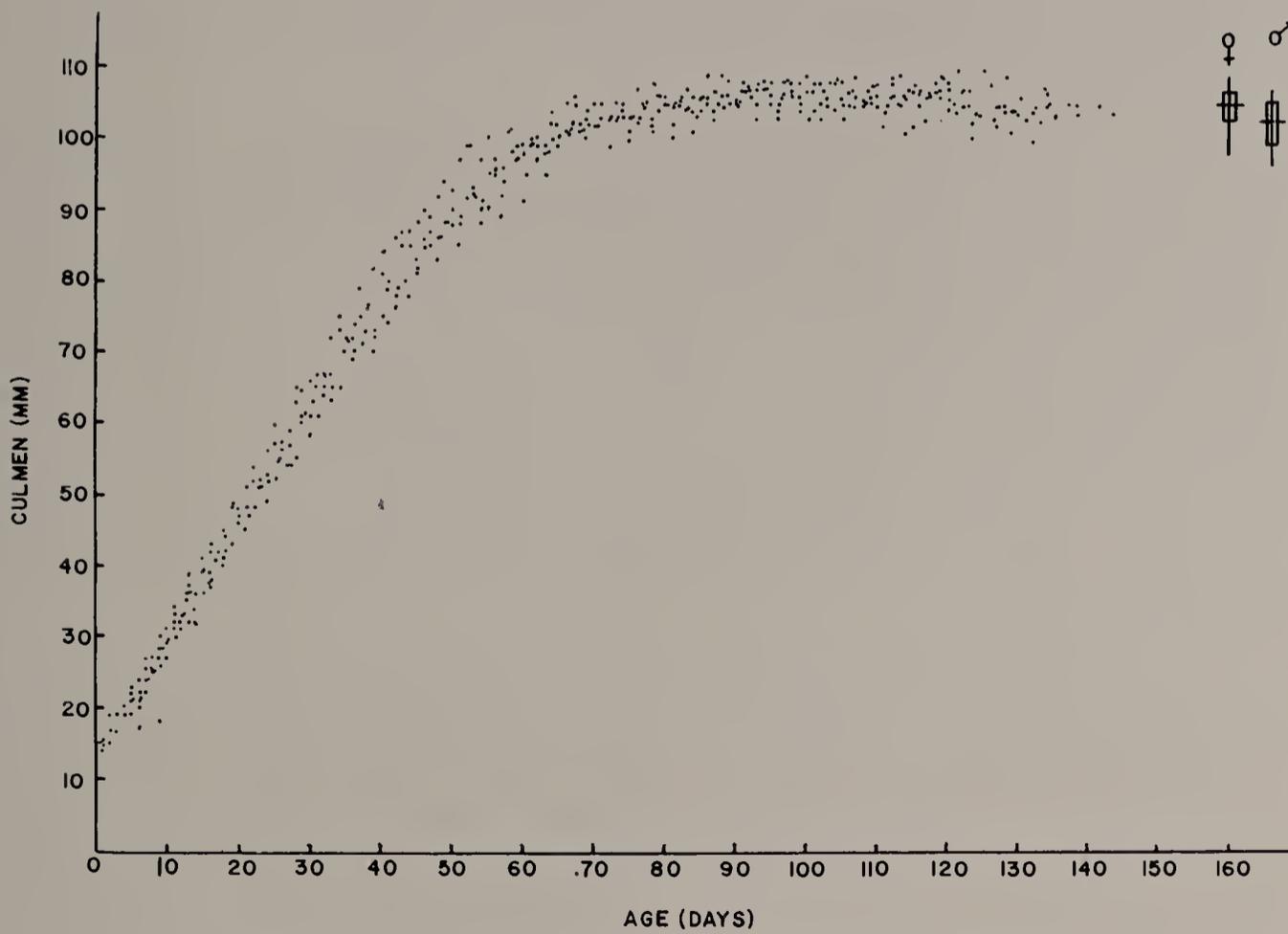


FIG. 4.12. Growth of the culmen in ten chicks.

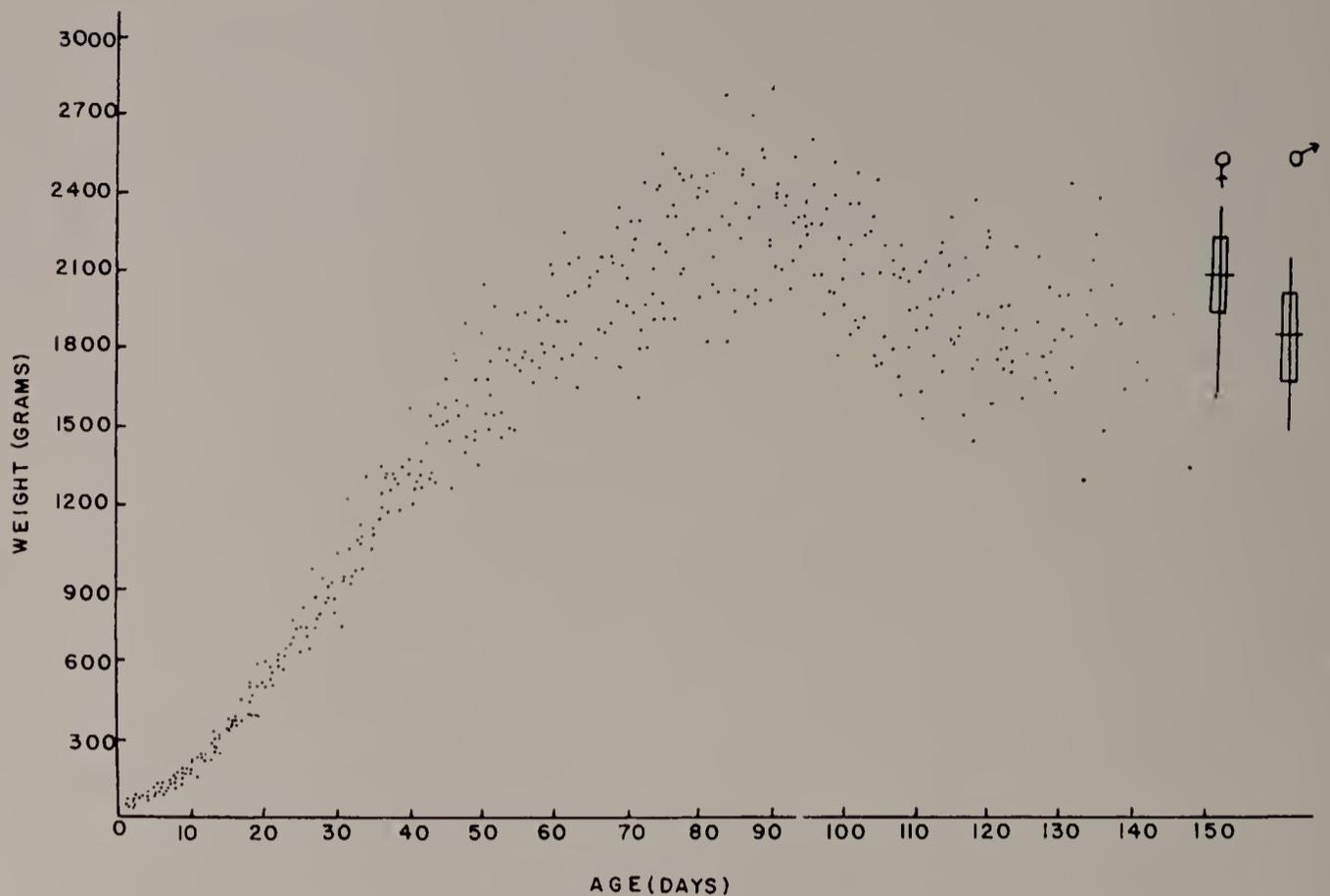


FIG. 4.13. Weight gain in ten chicks.

plotted against age for 10 chicks randomly selected from 19 chicks on which full growth and development records were kept. The range, mean, and standard deviation for 27 adults of each sex (26 males only for weight) are presented on each figure for ease in comparing the developing young with adults.

The most striking early growth occurs in the legs and feet (Figs. 4.10 and 4.11). At 45 days of age both middle toe and tarsus are of adult size. The culmen (Fig. 4.12) is fully grown by the 10th or 11th week, some 30 days later than found by Dorward (1962a). At this time most young have also grown to or beyond the adult body weight (Fig. 4.13). The spread in the data for weight is due to the sporadic feeding of the young. A chick just fed on one day would weigh more than it would before feeding the following day. No attempt was made to correct for this bias. It is clear, however, that the chicks reach a maximum weight exceeding that of the parents at about 80 to 90 days, and that weight decreases beyond that point. Dorward found the same phenomenon on Ascension.

The primaries and tail feathers do not reach adult length until about 120 days (Fig. 4.9), the time at which the juveniles begin flying. This differs strikingly from the Ascension birds, whose wings reached full development by about 100 days, 20 days before fledging. On Kure, as opposed to the Ascension birds, the young begin flying as soon as their wings are fully developed; the average flying ages for five chicks whose exact date of first flight is known was 117.6 days, with a range from 115

to 124 days. Flying juveniles may remain in the colony for an additional one or two months before leaving entirely. Once they leave, they do not normally return again until they are in breeding plumage, presumably at two or three years of age.

CHAPTER 5

SPACING-OUT BEHAVIOR

INTRODUCTION AND TERMS

In this and the following chapter the behavior of *Sula dactylatra personata* will be described and compared with that of other races. Previous contributions to the knowledge of the behavior of this species have been made by Dorward (1962b), who briefly described the displays of *S. d. dactylatra* on Ascension Island, and Nelson (1967a), who produced a more detailed study of *S. d. granti* in the Galapagos. All references to these authors will refer to the above two papers unless otherwise cited. Display names and their order of presentation follow Nelson. See the Appendix for a description of the methods I employed in this phase of the study.

Although behavioral terminology is now becoming fairly well established, differences in the use of the same terms by different authors necessitate very brief definitions of a few of the words that will frequently appear below. "Agonistic" will refer to behavior that is basically hostile or aggressive in character, and which serves to increase distances within the colony; fear and fleeing are also considered agonistic. "Epigamic" will refer to distance-decreasing displays occurring between opposite sexes, which function in bringing individuals into close proximity or preparing them for copulation. "Display" is used to mean any combination of postures and vocalizations consisting of a form similar in, and recognizable by, all individuals that perform them. Such displays contain signal value. I am purposely loose in definition here, as Yes/No Headshaking, although clearly a display, is highly variable and defies attempts to reduce it to one or two stereotyped postures. Courtship displays in this species are quite stereotyped and fit more closely to the concept of highly rigid, ritualized form. By "bout" I mean each single occurrence of the display in question, to be distinguished from "encounter," which refers to an interaction between birds, involving one or more display bouts.

Birds on their territories utilize a variety of behavioral displays to increase the distance between them and other birds within the colony. I shall first describe the normal resting posture of a territorial bird and the Alert posture that is employed during any disturbance. A description of the aggressive displays will follow, proceeding from highest to lowest intensities. Nelson lists these in the following order: fighting, Jabbing, Wing-flailing, Mutual Jabbing, Yes/No Headshaking, and aggressive calling with the neck extended. To this list I shall add Chasing, which may occur when one bird is much more aggressive than another.

RESTING POSTURE

Birds within their territories are seldom inactive. However, when they are not interacting with mates or territorial rivals, or performing maintenance activities, they stand in a relaxed manner (Fig. 5.1). As this is a basic position different in appearance from the displays, it forms a logical basis for comparison.

Form. The plumage of a resting bird is neither elevated nor unduly sleeked. The tail is relaxed and normally continues the line of the back posteriorly. The wings are folded against the side and the head is pulled slightly down toward the body, producing an S-shaped curve in the neck. The bill is rarely inclined and normally will be declined slightly toward the ground. This position may be maintained for a considerable time, but activity nearby will usually produce a corresponding action in a resting bird.

ALERT

The Alert posture (Fig. 5.2) occurs during territorial encounters, pair interactions, and in response to any disturbance within the colony. The Alert differs from a resting posture in that the neck is stretched vertically, and the bill is level or nearly so. An Alert bird may scan the colony, maintaining the horizontal aspect of the bill as it rotates the head, or may direct its gaze at the source of disturbance. The Alert allows the bird to monitor the environment and prepares it for the



FIG. 5.1. Resting posture.



FIG. 5.2. Alert posture.

immediate situation. It also has signal value: an Alert gaze by one bird may result in epigamic or agonistic behavioral responses by others. These signal functions will be discussed in their proper context in the following sections.

FIGHTING

Nelson states that fighting was rarely seen in the Galapagos colonies. When fights occurred they involved members of the same sex, the birds interlocking their bills and pushing (not pulling) with their necks extended. The interlocking of bills was never seen in territorial conflicts on Kure, although 754 intraspecific agonistic bouts (excluding bouts of calling) were recorded. Fighting is, thus, extremely rare on Kure and most territorial conflicts are resolved by posturing alone.

JABBING

Fighting consists of jabbing and seizing an opponent. Jabbing without seizing (Fig. 5.3) is much more frequent and occurs when a



FIG. 5.3. Pairs Jabbing, an encounter before either pair began laying.

single bird or pair defends its territory against intruders, or between members of a courting pair before a pair bond is established. Jabbing between members of an incipient or newly formed pair has been termed "Mutual Jabbing" by Nelson, in distinction to "Jabbing" between site-holding birds and intruders. The latter situation, however, is almost always mutual as well. I shall use Nelson's terminology, restricting the term Jabbing to agonistic territorial encounters. The reciprocal nature of Jabbing should always be borne in mind, and perhaps the term "Sparring," introduced by Dorward, would be a preferable term for these encounters. Since Nelson does not discuss this important agonistic display, I shall consider it in detail.

Form. Jabbing birds face one another on the borders of their territories. Jabbing is ordinarily preceded by, and interspersed with, Yes/No Headshaking (see below). Pairs oppose each other in such a way that males face males, and females face females. Under normal circumstances (see Table 5.1) only males jab, and the females Yes/No Headshake, Wing-flail, or call. Jabbing birds lean forward, thrust the neck forward, and open the bills widely. The heads may shake laterally. Bill contact, when it occurs, can be heard from a considerable distance—up to 21 m on one occasion. The wings are lifted from the back and extended, the tail is raised, often to an angle of 70 to 80 degrees, and the rectrices are widely spread. The feathers of the head and neck are raised. When the head and neck are extended, the body is held low, so that the neck projects upwards from the body, giving a U-shaped appearance to the bird (see Fig. 5.3). The opposing birds stand two to three feet apart, so that by leaning forward and jabbing they seldom reach farther than the bill of the opponent when he too leans forward. Birds farther apart jab the air and an intense encounter in which the birds call, Wing-flail, and jab may never result in bill contact. Individual Jabbing bouts rarely last more than 15-20 seconds and the birds

TABLE 5.1
 FREQUENCY WITH WHICH MALES AND FEMALES ARE INVOLVED IN AGONISTIC
 ENCOUNTERS, EXCLUSIVE OF MUTUAL JABBING

Active Birds	Jabbing	Chasing	Wing- flailing	High- intensity Yes/No	Yes/No	Total
Pair vs pair						
Male-male	27	5	11	18	159	220
Female-female	1	0	0	2 ⁵	1	4
Male-female	3	1	1	2	11	18
Pair-pair	2	0	3	1	4	10
Pair vs single bird						
Pair-female	3 ¹	0	11	4 ⁵	8 ³	16
Pair-male	4	2	0	2	29	37
Male-male	0	0	0	0	0	0
Female-male	0	1	0	0	0	1
Single birds						
Male-male	2	7	1	2	6	18
Female-female	0	0	0	0	0	0
Male-female	7 ²	1	3 ⁵	0	17 ⁴	28
Total	49	17	20	31	235	352

1 One female had mate on eggs.

2 Three females had mates on eggs.

3 Five females had mates on eggs.

4 Thirteen females had mates on eggs.

5 All females had mates on eggs.

may Yes/No Headshake or call between one bout and the next in a prolonged encounter.

Males are involved in Jabbing encounters more frequently than females (see Table 5.1). The sexes involved in Jabbing in pair-pair bouts were observed 33 times: in 27 of these (82%) only the males jabbed and in only two (6%) did the pairs jab. Equally uncommon were jabs between different sexes (3 = 9%) or by the females alone (1 = 3%). All other distance-increasing displays are also performed primarily by the males, a fact that will be discussed in more detail below.

Context. The causes of 63 observed Jabbing bouts between conspecifics were determined. All of these initially involved an approach to a territorial boundary by intruding birds. The 21 separate kinds of behavior seen to elicit Jabbing have been lumped into three basic activities and presented in Table 5.2. Direct intrusion by a bird or pair toward a territory holder accounted for all but two of the Jabbing bouts witnessed. Those events within the context of a prolonged encounter were the direct result of bouts originally started by territorial intrusion. The two cases of redirection also owe their origins to territorial trespass, as the birds redirecting had both initially intruded into a territory, engaged in Jabbing with the territorial birds, and then

TABLE 5.2
BEHAVIOR INITIATING JABBING BOUTS

1. Territorial intrusion	44
Territory or holder approached without any display	13
Territory or holder approached with agonistic display	10
Intruder stands on edge of territory	13
Intruder stands on edge of territory and Yes/No Headshakes	8
2. Occurs during a prolonged encounter	17
Follows a pause after previous Jabbing	11
One bird looks, walks, or faces away from another	6
3. Bird in Jabbing bout attacks another bird (redirection)	2
Total	63

moved off and attacked another individual. Intruders walked at, hopped at, or ran at territorial birds and those locomotory activities were on ten occasions accompanied by Yes/No Headshaking, Wing-flailing, or Jabbing. Birds Jabbing paused regularly and activities at that time included calling, looking at each other, or Yes/No Headshaking, followed by another Jabbing bout. Birds looking away during an encounter were on six occasions jabbed at and this initiated another Jabbing bout. It is clear that there is a very strong aggressive component operating in all Jabbing individuals. Birds walking toward a territory, often with the territory holder headshaking and calling, are certainly aggressively motivated, as are territorial birds that react by walking directly toward intruders. Fear, however, must also be important. Bouts never led to overt fighting, and in many encounters the opposing birds never made contact. The raised feathers of the head and neck indicate fear (Nelson, and below). In boobies, looking at an opponent is aggressive (see under Yes/No Headshaking), and is intimidating to the recipient of a gaze in agonistic encounters. In six bouts Jabbing occurred only after one bird turned or faced away from another, an action usually functioning as an appeasement display. This differs from the normal inhibition of further attack by appeasement described for most higher vertebrates, e.g., Kittiwakes, *Rissa tridactyla* (Cullen, 1957), Herring Gulls, *Larus argentatus* (Tinbergen, 1960), dogs and wolves, *Canis* spp. (Lorenz, 1957), and Blue-faced Booby chicks (Dorward). In other contexts, especially Yes/No Headshaking, facing-away does result in the inhibition of further agonistic posturing. It may be that in Jabbing bouts the aggressive drive is so high that the normal appeasement of facing-away fails to inhibit attack. The response in these cases was swift; the antagonist immediately lunged and jabbed at the bird turning away, thus promoting a further Jabbing bout.

Jabbing encounters normally end when one or both of the antagonists walk away from the area. In the 63 bouts discussed above, 33 ended in this way. Seventeen of the bouts were followed by Yes/No Head-

shaking; on five occasions intruders were driven off, in five bouts the birds stopped jabbing without moving away, and two of the bouts were succeeded by a redirected attack on other birds. Of the 33 encounters in which the ending was not marked by further aggression (i.e., birds walked away), it was surprising to find that in 30 of these cases it was the *territorial* birds that walked away from the encounter, not the intruders. In all cases, the intruders failed to move into the territory after the bout was terminated. Thus the display does function in inhibiting further approach; so well, in fact, that the territorial border is "safe" without the presence of the territorial birds, who are free to continue their own activities. Yes/No Headshaking from a distance is in these situations sufficient to maintain the spatial relationship determined by the Jabbing encounters.

Function. Jabbing occurs only at very high-intensity encounters between territorial rivals and ordinarily involves adjacent pairs. When recurrent over a period of many days, or even weeks, Jabbing ordinarily occurs in the same location. It thus may serve to accurately delineate the territorial margins, something other agonistic displays fail to do. As pairs gain familiarity with each other's territories the frequency of Jabbing encounters decreases and Yes/No Headshaking is more common.

CHASING

Chasing is best considered a special form of Jabbing, in that it consists of similar behavior and occurs under circumstances of territorial intrusion. The essential difference is that one bird has little aggression and much fear. Therefore, instead of standing its ground, it turns and runs or flies from the more aggressive bird, who may pursue, jabbing and calling. Ordinarily no contact is made between the birds. It was common to see marked birds land in parts of the colony away from their territory. Such birds were very conspicuous, maintaining an Alert position as they scanned the colony, the wings often held loosely from their sides. Headshaking or calling by nearby birds under these circumstances were ordinarily sufficient to cause the birds to fly from the spot. I recorded 17 chases between conspecifics and, as mentioned in Chapter 3, on 11 occasions Blue-faced Boobies chased Laysan Albatrosses. In only two of the 17 chases between conspecifics did the chasing bird actually bite the subordinate bird. It is important to note that in these circumstances a territorial bird will bite or peck a bird that is facing away from it.

WING-FLAILING

Nelson mentions that this display is typical of high-intensity aggressive situations, and is normally performed in conjunction with Jabbing or Yes/No Headshaking. This was true of the Kure birds as well. In 26 observations of Wing-flailing occurring outside of a Jabbing bout, it

TABLE 5.3
 CONTEXTS IN WHICH WING-FLAILING OCCURS AND RESPONSE OF BIRD
 TO WHICH IT IS DIRECTED

Cause		Response by recipient of display	
Intruder nearby	9	Yes/No Headshaking	12
Part of headshaking	6	Moves away	6
Intruder moves at	2	None	3
Looked at	2	Jab	2
Nearby interaction	3	Call	1
Between Jabbing bouts	4	Defecate	1
Total	26		25

accompanied other agonistic displays on 20 occasions: Yes/No Headshaking (13), lunging forward (4), and hopping at another bird (3). It occurred without these activities on four occasions, two of them when a bird hopped away from a conflict (walking is the normal locomotion when on land). Wing-flailing is normally performed by Jabbing birds. It consists of a rapid flick of the wings upward and outward, so that they are completely extended, then quickly returned to the body. Nelson considers Wing-flailing to be an intention movement to fly at an intruder. On Kure it accompanied locomotion on five (20%) occasions, but two of these involved locomoting away from the other bird. Thus, it may well involve an intention to fly, but not necessarily toward the other bird.

Table 5.3 lists the apparent causes and effects of Wing-flailing. The close relationship between Jabbing and Wing-flailing may be seen by comparison with Table 5.2. Territorial encounters can be settled from a distance by Wing-flailing in conjunction with other displays, as is seen in the table: six (25%) of the targets of Wing-flailing left the area, two of them flying. Only three birds failed to respond overtly and all others reacted with agonistic behavior, thus extending the duration of the encounter.

YES/NO HEADSHAKING

This display (Fig. 5.4), originally called Head-wagging by Dorward, is by far the commonest distance-increasing display used by Blue-faced Boobies. On the 754 agonistic bouts recorded, 648 (86%) involved Yes/No Headshaking. The display occurred in 33 different contexts, and the targets of headshaking responded in 28 different ways. The display is thus both common and complex and, as would be expected, has a wide variety of forms, or intensities, depending upon the circumstances eliciting it.

Forms. The basic position from which Yes/No Headshaking is given is similar to that of the normal resting posture. The head is pulled down and back toward the body, producing the characteristic S-shaped curve to the neck. The bill, however, is inclined from the horizontal. Dorward's original descriptions of the head movements accompanying



FIG. 5.4. Yes/No Headshaking.

the display are still the best, and apply equally well to the three subspecies so far studied. He notes (p. 226) that "the head was turned from side to side and the bill simultaneously wagged up and down rapidly within a narrow range, as if the bird were indicating a slow 'no' and a vigorous 'yes' at the same time." At very low intensities the arc through which the bill is swung is very large (usually between 180 and 270 degrees), the bill almost hitting the tail as it swings from side to side. The tail may be slightly cocked as well and the display is loosely oriented at the object eliciting it. The "yes" component is almost or entirely lacking when the broad sweeping "no" is given.

At moderate intensities, the arc through which the bill is swung decreases, and the frequency of the "yes" component increases. The display is, therefore, more directed toward an opponent, both by virtue of the decrease in the "no" arc and the directedness of the "yes." The tail is usually cocked up, but, as in low-intensity bouts, need not be, and the wings are held loosely against the sides.

When encounters are prolonged, or intruding birds approach, a

high-intensity head-shaking is given which incorporates elements of the other agonistic displays mentioned above. The "yes" component is very prominent, increasing both in amplitude and frequency. The wings are very loose and Wing-flailing commonly occurs. Interspersed with the Yes/No Headshaking are forward thrusts, even though an opponent may be a meter or more away. The wings may be held in an extended position from the body. The bill remains closed at low-intensities but is open to a variable extent (to about 2.5 cm) during high-intensity encounters. Calling may occur at any time but is more frequent at high-intensity. The arc through which the bill is swung ("no") may decrease to as little as 60 to 70 degrees and the display is oriented directly at the antagonist. The feathers of the head and neck are often raised.

Context. In Table 5.4 the wide variety of events eliciting Yes/No Headshaking have been reduced to 14 main categories. This list en-

TABLE 5.4
BEHAVIOR ELICITING YES/NO HEADSHAKING

Cause	Intensity of Yes/No Headshaking:					
	High		Low to moderate		Total	
	No.	Percent	No.	Percent	No.	Percent
Territory or bird approached with agonistic display	11	17.5	17	2.9	28	4.3
Bird(s) near territory Yes/No Headshake	20	31.8	131	22.4	151	23.3
Bird(s) near territory call, Wing-flail, or jab	3	4.8	25	4.3	28	4.3
Bird(s) fly over area and land(s)	3	4.8	10	1.7	13	2.0
Territory or bird approached w/out agonistic display	7	11.1	77	13.2	84	13.0
Follows a pause between agonistic bouts	6	9.5	73	12.5	79	12.2
Bird(s) stand(s) on edge of territory	6	9.5	88	15.0	94	14.5
Bird looked at or toward *	4	6.3	60	10.3	64	9.9
Bird(s) fly over area	1	1.6	48	8.2	49	7.6
Another Yes/No Headshaking bout in area	1	1.6	18	3.1	19	2.9
Spontaneous	1	1.6	7	1.2	8	1.2
A male lands and he Yes/No Headshakes	0	0.0	15	2.6	15	2.3
A bird walks or turns away from Mate Yes/No Headshakes or jabs at something else	0	0.0	10	1.7	10	1.5
	0	0.0	6	1.0	6	0.9
Total	63		585		648	

compasses the observations of 648 separate headshaking bouts during the study period. The high-intensity bouts have been tabulated separately. In only eight of these bouts were there no apparent stimuli and in 15 others the display was given by a male just landing on his territory. All other bouts were preceded by the activities of a nearby bird. Of these only six were initiated by a mate giving the display to other birds outside the territory. Most of the Yes/No Headshaking bouts were elicited by an approach to the territory (17.3%), flight over the territory (9.6%), presence of bird(s) on the territory border or nearby (14.5%), Yes/No Headshaking or other agonistic encounters (12.2%) or stares at the bird (9.9%). It is clear that the display is an agonistic one occurring in hostile situations and in this respect does not differ from the display in other races. Nelson found Yes/No Headshaking between incipient or established pairs, but this was not common on Kure. Nelson's greater familiarity with Sulids may have enabled him to see low-intensity encounters more frequently than I. Mild headshaking bouts did occur between incipient pairs, particularly when one bird moved at another (see Chapter 6).

The display was given 64 times (9.9%) when one bird was looked at by another. This was a striking and conspicuous stimulus, and commonly occurred between adjacent territory holders. It was not unusual to see one bird standing on his territory, peering slowly around the colony. If I watched a nearby male I could often determine the direction in which the peering bird was looking, for as soon as he had turned and pointed his gaze at the other male, the bird looked at would headshake in response. The prominence of the bill is an extremely conspicuous feature of many other displays as well. Mated pairs perform elaborate displays that effectively turn the bill away from their mates.

Nelson noted that Yes/No Headshaking commonly occurred *in vacuo* in males that held territories in hollows or among bushes, such birds mounting vantage points and performing the display. These bouts were concentrated in early morning or late evening hours and a large number of birds would simultaneously perform them. In this aspect it is roughly analagous to song in passerines, which advertises the presence of territorial males. This rarely occurred on Kure, ostensibly because such territorial sites did not exist in the open plain. Other males were constantly in view, and the combined activities of these birds provided innumerable stimuli for the display.

The contexts in which high-intensity Yes/No Headshaking occur are very similar in most respects to those resulting in the display at more moderate intensities. A comparison of the number of responses in these contexts is very revealing, however. Situations that more frequently gave rise to high-intensity displays are listed first in Table 5.4, followed by behavior resulting more frequently in bouts of lower intensity. It is clear that in all contexts the high-intensity bouts resulted

more frequently from situations that were clearly more aggressive. The first type of behavior, i.e., when a territory holder or a territory is approached by a bird giving agonistic displays, is completely hostile, and it is not surprising that high-intensity Yes/No Headshaking was almost six times more frequent than lower intensity headshaking in these circumstances. In contrast, the last six kinds of behavior listed are all of low aggressive valence and elicited a high-intensity response on only three occasions.

Function. In 375 of the bouts the reactions of the targets of Yes/No Headshaking are recorded; these data have been presented in Table 5.5. The most common response to Yes/No Headshaking is a return headshake; in 54.7% of all bouts the initial display was met with further agonistic behavior. As mentioned above, however, a wide variety of outcomes was seen and second in importance to aggression was a cessation of further hostilities or trespassing. In 51 (13.6%) bouts the antagonist faced, turned, or walked away from the headshaking bird. More significant, however, is the fact that in only 15 bouts (4.0%) did the recipient of headshaking move farther toward the territory, whereas 17.3% of the bouts were begun when one bird approached another. Thus, while Yes/No Headshaking generally initiates further interactions, it ultimately restricts trespass into a territory by other birds. When headshaking fails to inhibit trespassers, higher intensity displays, especially Jabbing, do so. As mentioned above, headshaking by birds having left a Jabbing bout was sufficient to prevent further intrusion. Nelson's analogy to passerine song is a good one, the display clearly advertises the presence of territorial males. It should be mentioned, however, that the advertising is directed at potential ri-

TABLE 5.5
EFFECTS OF YES/NO HEADSHAKING ON BIRDS AT WHOM THE DISPLAY IS DIRECTED

Reaction by recipient of Yes/No Headshaking	Intensity of Yes/No Headshaking:					
	High		Low to moderate		Total	
	No.	Percent	No.	Percent	No.	Percent
More Yes/No Headshaking, jabs, or calls	36	69.2	166	51.4	202	53.9
Faces, turns, or walks away	5	9.7	46	14.2	51	13.6
No action or alert	4	7.7	40	12.4	44	11.8
Interacts with mate	4	7.7	25	7.7	29	7.7
Walks at, runs at	0	0.0	15	4.6	15	4.0
Looks at	1	1.9	13	4.0	14	3.7
Runs or flies away	0	0.0	8	2.5	8	2.1
Irrelevant activities	0	0.0	6	1.9	6	1.6
Chased or driven out	1	1.9	2	0.6	3	0.8
Bird stops	0	0.0	2	0.6	2	0.5
Headshaker driven out	1	1.9	0	0.0	1	0.0
Total	52		323		375	

vals; the display does not serve the dual function of advertisement to females as well, which is characteristic of passerine song. The attraction of the mate is performed by an entirely different display (Sky-pointing or advertising).

CALLING

Blue-faced Boobies show a striking sexual dimorphism in their calls (see Chapter 2). Calling is very common, occurring in all agonistic situations. It is also given by both males and females in very low-intensity agonistic situations and need not occur with other displays. No attempt has been made to tabulate separately all encounters in which calls occur. At any time of day the hoarse honks of the females and shrill whistles of the males may be heard. In many cases the stimulus evoking the call could not be determined; ordinarily, calls are given in any situations in which other agonistic behaviors are also appropriate. Females indulge in calling far more frequently than they do in any other agonistic display.

ROLE OF THE SEXES IN AGONISTIC DISPLAYS

The defense of the territory in Blue-faced Boobies is performed almost entirely by males. All the encounters for which the sexes of the opposing birds are known are presented in Table 5.1. Fully 98.9% of these involved males, whereas slightly less than one-third included females. More striking, however, is that in only four (1.1%) of the 352 encounters was the territorial defense performed exclusively by females, and in two of these the mate of the defending female was incubating at the time. This was also true of 32 of the 114 encounters in which females participated. Unmated females were never seen to defend a territory against other birds, as they have no territory to defend, and wander through the undefended portions of the colony forming temporary liaisons with bachelor males. By contrast, unmated males regularly defend small territories against all rivals, and advertise from these areas, which are very stable and are not, except under unusual circumstances, entered by adjacent pairs. The males, thus, select the territories and, as we shall see in Chapter 6, also select the nest site itself.

REDIRECTION

“Redirection” is defined as directing an appropriate behavior at an inappropriate object. Redirection is very common in birds and many examples of redirected aggression have been cited. Perhaps the most familiar of these is the grass-pulling behavior of Herring Gulls described by Tinbergen (1960). Redirection was observed 19 times during agonistic encounters between Blue-faced Boobies on Kure, although it has not been described from other colonies. A generalized picture of the context of these bouts will follow a series of descriptions of the activity. Although all these bouts were very obvious to the observer,

they may not appear so to the reader unless a few representative examples are described.

Male R25, after a Yes/No Headshaking bout with male O2, turned and fled from the dominant bird. Male O2 chased R25, overtook him, and pecked him on the neck, forcing him from the territory. As O2 turned back toward his platform, R25 turned after him, but stopped, leaned down, seized the stem of growing *Tribulus cistoides* and tugged at it vigorously, shaking it rapidly as he did.

R2 high-intensity Yes/No Headshaked, Wing-flailed, called, and Jabbed for 11 minutes with O4 and R22, a temporary pair. The pair, after a vigorous Jabbing bout with R2, turned away from the male and walked 12 m to attack R20, another male.

Males R7 and R21, one meter apart, Yes/No Headshaked (moderate and high-intensity) and Wing-flailed for eight minutes. They then Yes/No Headshaked at a Blue-faced Booby and a Layson Albatross that flew overhead. Shortly afterwards, after more headshaking, they Yes/No Headshaked at two Ruddy Turnstones that flew over. This was the only occasion in which any shorebird received an aggressive display from boobies.

The three examples were chosen to demonstrate the forms that redirection may take. The contexts are all similar; they involve either high-intensity or prolonged encounters. Redirection followed Yes/No Headshaking (13), high-intensity Yes/No Headshaking (3), chasing (2), and jumping at another bird (1). Only three types of response were observed: pulling at attached plants (*Tribulus cistoides*, 15; *Solanum nelsoni* 1), attacking neighboring birds (2), and Yes/No Headshaking at irrelevant birds (1). In all cases of pulling plants, the movement was vigorous and usually involved a rapid shake of the stem. In one 15-minute agonistic encounter involving three males, all the birds pulled at attached *Tribulus* on at least one occasion, and a total of nine pulls was recorded during the encounter.

DISPLACEMENT

“Displacement” is defined as performing a behavior inappropriate to the given situation. On two occasions pairs interacted in an abnormal manner following agonistic encounters with other birds. Both encounters involved a courtship behavior known as Symbolic Nest Building, in which pairs repeatedly mandibulate twigs and stones on their nest platforms. The movements are normally unhurried. However, in the two encounters in question the males performed very exaggerated Symbolic Nest Building movements. In the first, B12, after a prolonged high-intensity Yes/No Headshaking encounter with another male (O5), ran back to his mate and proceeded to mandibulate twigs, picking them up and placing them down very rapidly. On the other occasion, pair R9-10 usurped the platform of a bachelor male (O2). In the midst of a prolonged agonistic encounter with O2, and another nearby male as well, the pair began Symbolic Nest Building

on the stolen platform; the movements of both birds were noticeably affected. The frequency of twig mandibulation was abnormally high and the movements appeared very stiff, much in contrast to the more fluid performance normally seen. It is clear that normal courtship behavior was in these instances seriously affected by the previous agonistic encounters. The mandibulation of free twigs appears to be related to redirected stem pulling. The behavior has lost its overt aggressive character, however, and is performed in an epigamic context. Whether this behavior is "inappropriate" to the situation could perhaps be debated. The important point is that a behavior performed in an epigamic context is strongly modified by previous agonistic interactions with other birds.

ANTI-PREDATOR RESPONSES

Blue-faced Boobies have no colonial behavior comparable to mobbing, which is characteristic of gulls and terns. Instead, all birds react to danger as individuals. When approached during the day by men they will flee, if not incubating or brooding. An incubating bird will stand over its eggs, raising the feathers of the neck and head (fear). If approached to within about three meters the bird will raise the scapulars and breast feathers as well, and may lunge forward and call before leaving the eggs. Such a bird looks about the colony with jerky movements of the head. If one member of the pair is awake and the other asleep, the alert bird may simply walk away leaving its mate easy prey. I have walked up to sleeping birds and held my hand over their heads for periods up to 30 seconds while the mates watched quietly from a safe distance. There thus seems to be no mate-defending behavior.

An alarmed bird will call loudly. This simple mechanism seems to be the only way in which one bird can warn others of danger. This is especially effective at night. At 00:15 one morning I entered the periphery of the NAF sub-colony and disturbed one bird. It immediately called and as a result several nearby birds awoke and called as well. This continued until calls were heard from birds out of sight and over 90 meters away.

Polynesian rats are serious predators on Kure seabirds. Although they have been observed to prey on Laysan Albatrosses, Red-tailed Tropicbirds, Sooty Terns, Brown Noddy Terns, and perhaps Bonin Petrels, they have never been seen preying on boobies. On one occasion I did find two dead rats near a pair, and so assume that boobies have no trouble defending against them. On many of the Phoenix and Line Islands, cats have been introduced, but Blue-faced Boobies still nest there. Dorward (1962a) believes, however, that cats do prey on Blue-faced Boobies on Ascension (the Atlantic race is smaller), but the POPSP has found no evidence of extensive booby damage due to cats in the Pacific. It is reasonable to assume, however, that any larger predators, especially canids, would be able to prey upon Blue-faced Boobies; man, of course, finds them easy prey.

CHAPTER 6

BEHAVIOR OF THE PAIR

INTRODUCTION

Male Blue-faced Boobies begin a new breeding season by advertising to nearby females. When females approach them, several interactions may take place, depending on the relationship of the birds. Mutual Jabbing may occur between incipient pairs, whereas mated pairs normally perform a number of types of behavior associated with the manipulation of nesting materials in a cleared area selected by the male. A variety of displays, some of them involving walking about the territory, are closely linked with this activity on the nest platform; copulation always occurs on the platform. The epigamic behavior from advertisement to post-copulatory displays is discussed below.

SKY-POINTING OR ADVERTISING

Sky-pointing is a display performed almost exclusively by males. Its function is to attract females which are visible; it is homologous in form to a flight-intention movement of the same name in gannets (Nelson, 1967a). In this paper Sky-pointing always refers to the epigamic display.

Form. (Figs. 6.1, 6.2). As the name implies, a Sky-pointing bird stretches the neck vertically and gazes at the sky. Although the neck is vertical, the bill rarely points directly up and normally assumes an angle of about 45° . It is normally opened one centimeter or less. The tail is cocked up from 45° to 60° , or even 70° , and the wings are lifted from the back and rolled forward but not extended (as they are in the Blue-footed Booby). Thus the humeri extend upward, lifting the folded wings so that the upper secondary coverts and primaries present a board pattern of black and white behind the head and neck of the bird. The display is oriented directly at the female eliciting it. A single shrill flute-like or thrush-like whistle, unlike any other booby vocalization, is given by the male at the height of the display, after which the bird relaxes the head, neck, wings, and tail, and alert gazes at the female or bends down to mandibulate materials in front of him (see Table 6.3). Nelson noticed a ruffling of the head and neck feathers in his colony's Sky-pointing males but this was not observed on Kure, even though many photographs were taken of the behavior.

The Sky-pointing display of the Kure population of *S. d. personata* is different in form from that described for *S. d. granti* by Nelson. If the plates and drawing by Nelson are typical postures, the tail of *granti* is much less elevated, and the bill more nearly vertical, than it is in *personata*. Few Kure birds were recorded with the bills held so nearly vertical (approximately 60°) or the tail so flat during their ad-

vertising. Sky-pointing in *personata* is more similar to that of the Atlantic race (*dactylatra*) described by Dorward.

Sky-pointing is directed both to birds on the ground and those flying overhead. Ordinarily a bird flying overhead will receive only one display unless it circles back over the calling bird. Birds on the ground, however, received a series of advertising displays. The average number



FIG. 6.1. Sky-pointing or advertising. Side view.



FIG. 6.2. Sky-pointing or advertising. Front view.

given to females on the ground is five ($n = 641$), although this varies from one to, in one very prolonged encounter, 52. The average time between displays is 7.4 seconds ($n = 292$). In this study no female was observed Sky-pointing, although 859 advertisements were recorded. Dorward observed females advertising on 12 occasions (total observations not given).

Context. Dorward and Nelson have essentially restricted their considerations to ground-to-ground display. Several generalizations have been proposed that apply well to terrestrial encounters but fail substantially to account for ground-to-air displays. The two contexts are treated separately below.

ADVERTISING TO BIRDS ON GROUND

A total of 144 encounters, embracing 644 separate Sky-pointing bouts, were observed. Of these, 140 encounters were directed toward nearby females, while four were directed toward males. Females ranged from one to 18 m (average 5.6 m) from the males. In only four of these encounters were females nine or more meters from the males, which agrees with Nelson's statement that males do not advertise to "distant" females. Both mated and unmated males advertise. Table

TABLE 6.1
RECIPIENTS OF ADVERTISING BY MATED AND BACHELOR MALES

Calling males	Sky-point directed to:				Total
	Mated females	Unmated females	Males	Unknown females	
Bachelors	27	39	4	15	85
Mated	55 ¹	0	0	1	56
Unknown	3	0	0	0	3
Total					144

¹ Fifty-three to own mate.

6.1 demonstrates that they are selecting females of substantially different status. Bachelors call to mated or unmated females. They normally call to mated females when the latter are alone, although calls are occasionally directed toward females that are with their mates. Mated birds, however, call almost exclusively to their own mates: in 56 encounters observed only three were directed to the "wrong" female. Bachelor males hold territories near those of mated pairs; invariably it is the female of a nearby territory that receives the display. Dorward may be incorrect in stating that "unmated males obviously recognized unmated females" and that "unmated males never displayed at mated females on the ground." If this is true, there is a marked difference in the discrimination of the bachelors in the two colonies.

On four occasions males advertised to other males. These advertisements were performed by bachelor males, and only one call was given (compared to an overall average of five) in each case. It thus appears that males, although they do make mistakes, can recognize the sex of birds on the ground.

The behavior of the female directly preceding advertising was recorded for 264 bouts (Table 6.2). In 224 (84.9%) of these the female was looking at, or walking toward, the calling male, the former being the most common stimulus initiating the bout. Between bouts advertising males closely watch the female; if she is looking away from or lateral to him he does not usually advertise (see Table 6.2), but normally does so when she swings her head toward him. The wings can be

TABLE 6.2
BEHAVIOR OF FEMALES ELICITING SKY-POINTING IN MALES

Behavior	No.	Percent
Look at male	129	49
Walk at male	80	30
Walk at in Pelican Posture	15	6
Look lateral to or away	15	6
No response	6	2
Other	19	7
Total	264	100

TABLE 6.3
BEHAVIOR ASSOCIATED WITH ADVERTISING (SKY-POINTING)

Behavior following advertising	Nelson (1967a) (No. = 130)	Present study (No. = 123)
Touching nest material	46%	41%
Peering	27	21
Looking at ground	0	13
Pelican Posture	7	4
Head-fling	10	2
Alert	0	6
Other	101	13

¹ Doing nothing.

seen to roll forward, and the head lift, as the female gazes nearer to him. If she suddenly swings her head away, without pointing her bill at him, he may resume the Alert posture, peering at the female. On several occasions two males advertised to the same female, Sky-pointing alternately as she shifted her attention from one to the other.

After Sky-pointing the males may touch nest material, peer at the female, or engage in a variety of other activities, generally without moving from their position. This behavior associated with advertising is presented in Table 6.3, along with the results of a comparable study made independently by Nelson. Although it is difficult to know how comparable these observations may be, there is, nonetheless, a striking similarity between Nelson's findings and my own. The major activities are the same in both races. The activities listed under "other" in the table include looking around (4%), looking away from the female (2%), and walking at (4%), or away from (3%) her.

Function. The actions of birds preceding and following ground-to-ground advertising encounters are presented in Tables 6.4 and 6.5. The activities of bachelors are treated separately from those of mated males. Mated birds were standing or moving apart before the display in 79% of the encounters. In 86% of the cases the pair moved closer together after the display. Ordinarily it is the female that moves toward the calling male (73%), but in 11% of the cases males moved toward the female

TABLE 6.4
BEHAVIOR PRECEDING GROUND-TO-GROUND SKY-POINTING DISPLAYS

	Mated males (No. = 52)	Bachelors (No. = 61)
Male and female apart	54%	23%
Male moves from female	19	7
Female moves from male	6	0
Male lands in colony	4	3
Female lands in colony	2	18
Nearby pair interact	0	31
Another male Sky-points	0	8
Other (see text)	15	10

TABLE 6.5
MOVEMENTS OF MALES AND FEMALES DIRECTLY FOLLOWING SKY-POINTING

	Advertising males:	
	Mated (No. = 52)	Bachelors (No. = 60)
Female moves toward advertising male	73%	23%
Male moves toward female	11	8
None	6	35
Broken up Yes/No Headshaking	6	8
Female moves away from male	2	17
Male and female move toward each other	2	0
Female walks to mate as another male advertises	0	5
Male moves, but not toward female	0	4

if she failed to move first. Dorward, however, found that males never moved from their stations unless driven off. It is possible that such site tenacity is much more important in a very crowded colony. Males advertise from a cleared area in the vegetation-covered central plain. These "platforms" are used as nest sites and it is to them that the females are attracted. In mated pairs advertising is clearly a density-decreasing display and allows the male to select the site to which he draws the female. As described below, the pairs' epigamic behavior centers on their cleared platforms.

Both the stimuli eliciting Sky-pointing and the effected response differ sharply for bachelor males: 61% of all encounters were initiated by the interaction of nearby pairs. Bachelors directed their calls to females on the ground that were moving, either interacting with their mates or landing nearby. Sky-pointing is slightly mimetic for bachelors (8%), but not for mated males. In 31% of the cases the bachelor and the female decreased the distances between them; however, in 69% of the encounters the spatial relationships remained unchanged (43%) or actually increased (26%). Mated females on four (5%) occasions moved toward their own mates when a nearby bachelor called.

ADVERTISING TO FLYING BIRDS

During the study period 215 Sky-pointing displays were directed to birds flying overhead. This was a common and conspicuous part of the colony activity in January and February, being particularly pronounced in bachelor males, who accounted for 180 (93%) of the 194 identified calling birds. Mated males were seen advertising to flying birds only 14 times; only two of these were directed towards their mates. This contrasts strongly with the behavior observed by Dorward, who states (p. 223) that ". . . unmated males . . . Very occasionally . . . displayed to a bird flying overhead, . . ." Males normally advertised to birds directly above them, but often birds over 30 m away, and on one occasion approximately 75 m away, received Sky-pointing displays.

Dorward was not sure whether advertising males recognized indivi-

duals, or even the sexes, of birds flying over and Nelson assumed that such birds were all females. My marking scheme (see Appendix) readily permitted sex identification. Of 153 birds receiving the display, 95 (62%) were males and 58 (38%) were females. Bachelors also advertised to three Blue-faced Booby pairs and to Brown Boobies and Laysan Albatrosses on six occasions each. The latter displays were all by bachelors that appeared to have a very low threshold for advertising and displayed to almost every bird that flew over. From this it appears that there is no recognition of the sex of flying birds. However, it may be advantageous for bachelors to advertise to any birds approaching them from a distance. As the birds fly rapidly, a bachelor that failed to advertise until a bird was directly overhead, or even several meters away, and perhaps recognizable, could not display at all, because the flying bird would quickly move past. Thus, the appearance of a lack of sex recognition could be an artifact of a display system that maximizes a bachelor's chances of advertising to an appropriate bird.

BEHAVIOR OF PAIR UPON MEETING

This section deals with the behavior of a pair meeting after a temporary separation. The discussion is based upon 74 observations of birds, mostly mated pairs, moving together after landing, parading, or Sky-pointing. Pairs normally re-establish contact by staring (or gazing) directly at each other. Staring occurred in 57 (77%) of the contacts and in 53 of these the stares were reciprocal. The stare is a modified Alert posture, with a pronounced leaning toward the mate. In 17 of these gazes the birds overlapped their bills, and twice the bills were seized.

Nelson found that in all Sulids aggression normally accompanies landing at the nest site. In his study of the greeting ceremony (considering mainly landings), Nelson finds that Mutual Jabbing is very common. This occurs when mutually gazing pairs rapidly shake their heads, loudly hitting their bills together. Mutual Jabbing was relatively infrequent on Kure, occurring in only four (5%) of the encounters. It followed staring as a second or third event five times (in 64 further activities). It is, thus, infrequent in the established pairs on Kure. The remaining 13 contacts resulted in a variety of activities, including Symbolic Nest Building (7), walking behind the female by the male (3), circling by the male (1) or female (1), or headshaking (1). The mutual gaze is never maintained for more than a few seconds. It gives way to Symbolic Nest Building, reciprocal allopreening, or a wide variety of other activities.

BEHAVIOR OF PAIR ON THEIR TERRITORY

Pairs interacting on their territories normally center their varied activities near an area cleared from the dense mat of vegetation covering the central plain. This area, cleared by the birds, is called the

“platform.” As some pairs possess and use two platforms, the term is preferable to “nest site” or “nest scrape.” Symbolic Nest Building is restricted entirely to the platform and it is there that males advertise. Territorial parading ordinarily begins and ends there and copulation always occurs on it. The bulk of the activities, including most of the motile displays, are restricted to an area within about three meters of this cleared site. After the eggs have been laid portions of the formerly guarded territory beyond this distance are not utilized by the birds (see Chapter 3).

HEAD FLINGING

Nelson distinguishes two forms of this movement, an “upward” and an “oblique” head fling, each consisting of a sharp fling of the head given from an Alert position. As the names imply, the bill is jerked vertically in the former and obliquely, with the head titled sideways, in the latter. The two forms were not distinguished in the present study. Nelson noticed this display following aggressive behavior directed outwards from the pair. I noticed the movement infrequently, mainly in epigamic contexts. It occurred occasionally during Sky-pointing encounters (Table 6.3) and rarely during Symbolic Nest Building. It was performed more often by females (10 times) than by males (once) during Symbolic Nest Building, where it accounted for 6% of the miscellaneous behavior. Nelson also found that females performed this display more frequently than males.

TERRITORIAL PARADING

Members of a pair, singly or together, may leave the platform and walk about on their territory in the Pelican Posture. These walks, common before the eggs are laid, are normally performed by males. In a sample of 21 walks, 14 were by males, four by females, and three by the pair. Parading birds rarely moved farther than three meters from the platform; walks of six meters were recorded once for each sex. The bird remaining on the platform normally manipulates twigs; walking males often gather them. Mutual gazing followed by Symbolic Nest Building commonly follows these walks. Many walks lead directly to advertising. These have been treated at length above.

PELICAN POSTURE

This conspicuous display (Fig. 6.3) is associated with walking or running. It is characterized by three distinct modifications of the normal gait. In common with *S. d. dactylatra* on Ascension and *S. d. granti* in the Galapagos, there is a regularly repeated tucking or bowing of the head as the bird walks, with the result that the bill tip approaches or touches the feathers of the upper breast. The large feet are lifted high in an exaggerated series of steps, almost hitting the flanks as the bird moves or steps in place. The Kure birds are unique in that the tail



FIG. 6.3. Pelican posture.

is cocked almost vertically. As mentioned above, tail raising also figures prominently in Sky-pointing in this population. It is reasonable to expect differences among geographically isolated populations. Tail positions are important in the displays of many pelecaniform birds (van Tets, 1965) and appear to be a relatively plastic behavioral character within the order.

Table 6.6 presents the situations in which Pelican Posture occurs. During agonistic interactions it occurs with equal frequency when birds are moving either toward or away from a territorial rival. It is more common in birds moving toward their mates in epigamic en-

TABLE 6.6
CONTEXTS IN WHICH PELICAN POSTURE OCCURS

Context	Activity and sex of bird giving display						Total
	Move at		Move away		Move "about"		
	Male	Female	Male	Female	Male	Female	
Agonistic	33	7	38	3	12	2	95
Epigamic	48	27	25	9	62	6	177
Total	81	34	63	12	74	8	272

counters. It was also commonly seen in birds "moving about" on their platform (circling, circling each other, and in-place stepping); this accounted for 68 (38%) of the postures given in epigamic contexts. Females give the Pelican Posture more often in pair-pair (42 times, 24%) than in agonistic (12 times, 13%) interactions, which is to be expected in lieu of the predominant role of the males in territorial defense.

Birds performing the Pelican Posture bring the bill down away from the bird with which they are interacting. This lateral displacement is slight, but it occurred every time I noted the exact bill-tip position ($n = 22$). In this it resembles Bill Hiding, an appeasement behavior seen only in Blue-faced Booby chicks when they are attacked by adults (Dorward); it may have developed from this (Nelson). It appears that Pelican Posture maintains its original appeasing function by removing the bill from either mate or antagonist while moving toward them. It may be particularly important in facilitating the close approach of one bird to its mate.

SYMBOLIC NEST BUILDING

During the course of the breeding season the pair spends hours bringing twigs and dirt clods to its platforms (Figs. 6.4, 6.5). This is the



FIG. 6.4. Symbolic Nest Building. Male (right) presents clod to female.



FIG. 6.5. Symbolic nest building. Typical posture as pair mutually mandibulates items on platform.

most common and conspicuous epigamic activity. It is most frequent in late evening when both birds have returned to the colony. Twigs vary in length from five centimeters or less to 60 cm. Birds also bring clumps of grass and coral pebbles. Males brought 282 of the observed 351 (80%) items to their platforms.

The birds normally walk or lean away from their mates when they gather materials (Table 6.7). Items brought to the platforms are placed with elaborate and exaggerated care; the bill is opened widely and

TABLE 6.7
POSITION OF GATHERER OF NESTING MATERIALS RELATIVE TO ITS
MATE DURING SYMBOLIC NEST BUILDING

Bird gathering leans:	Males	Females
Not determined	153	59
Away from mate	97	7
Behind mate	17	0
In front of mate	11	1
Toward mate	3	2
Over mate	1	0
Total	282	69

TABLE 6.8
LOCATION OF PLACED MATERIALS RELATIVE TO MEMBERS OF
PAIR DURING SYMBOLIC NEST BUILDING

Items are placed:	Males	Females
In front of mate	136	8
By the foot of mate	32	0
Over head of mate	7	0
Beside or under mate	6	0
On top of mate	5	0
Beside self	0	1
In front of self	23	33
Total	209	42

slowly retracted. Males were observed placing 209 of their items; 186 (89%) were put in front of or near the female (Table 6.8), and of these 25% were "presented" to her. Presenting items consists of jabbing or poking them at the female's head or holding them high in front of her. Females never took these items from the males, although Nelson noticed that this did occur in the Galapagos.

The behavior of females differs sharply from that of males in that they gather far fewer items, rarely (one instance) present them to their mate, and normally (34 of 42 observations, 81%) place them in front of themselves. In these respects the role of the sexes is essentially similar to that of other Pelecaniformes, the male gathering and the female working the materials into a nest (van Tets, 1965). However, in Blue-faced Boobies no nest is ever constructed. Although hundreds, or even thousands, of items are gathered, they are rapidly dispersed. Nelson concludes from his study, and the present study fully supports his contentions, that the twigs gathered are normally too short, and the clods, pebbles, etc. are useless, for incorporation into a structured nest. Nest building movements are lacking. Nelson argues that the behavior, not functioning as a nest building activity (and hence "symbolic") has been or is being emancipated from its original function.

Birds placing items on their platforms necessarily come into very close contact (Table 6.9). Simultaneous mandibulation of items is very common and during such encounters the birds may rub flanks or heads. A male will lean across the outstretched neck of the female and may rest his bill on her head. The pair regularly stands and mutually gazes, touching bill tips or even seizing bills as they do (this is common when the pair is disturbed as well). Mutual stares may lead to reciprocal allopreening (*sensu* Cullen, 1963) of the head and neck (though never any other body region) or Mutual Jabbing. In-place parades and circling are common, and brief movements away, often accompanied by an appeasing Bill-up-face-away (see Nelson for discussion) posture are normally interspersed with bouts of Symbolic Nest Building. It is highly likely that repeated proximity and body contact help synchro-

TABLE 6.9
BEHAVIOR DURING SYMBOLIC NEST BUILDING

Activity	Observations
(Gathering items—for comparison only)	(351)
Mutual mandibulation	52
Mutual stare	39
Cross or touch bill tips	27
Reciprocal allopreen	25
Pelican Posture in circle	25
Head-fling	11
Male touches female's head with bill	11
Seize bills	9
Circles mate	9
Wing shake	6
Mutual jab	6
Total	220

nize the sexual cycles of the pair and ultimately prepare the birds for copulation, which occurs during Symbolic Nest Building.

The mandibulation of nesting materials is not restricted to Symbolic Nest Building encounters. It is performed by males when a female lands nearby (13 instances) and, as noted above, is a regular activity of Sky-pointing birds. It also appears in agonistic encounters. Males mandibulated items between headshaking or jabbing bouts on 35 occasions and females did so as well (four times) when their mates defended the territory. Thus, this primarily epigamic activity may have aggressive valence as well.

COPULATION

Copulation in Blue-faced Boobies is a fleeting event requiring about 10 to 20 seconds. It accompanies Symbolic Nest Building and is so closely allied to it that the precursors to mounting are very easily overlooked. Both Dorward and Nelson have found this as well and conclude that copulation is not solicited by any specific behavior patterns. There is, however, certain behavior which, alone or in combination, preceded most of the 23 copulations or copulation attempts that I observed. The females normally manipulate materials in front of themselves, often stretching their heads and necks far forward and lowering their foreparts. This appeared exaggerated in several of the copulations, and may have been solicitation, differing from normal mandibulation in the distance stretched forward and the duration of the maneuver. Males were occasionally noted putting their bills on top of the heads of their mates and pushing down firmly. Males prior to mounting always faced the flanks of the female. This occurs often during Symbolic Nest Building. However, before copulation males were noted to have a strange appearance, resulting from an Alert Gaze at the female, with the head stretched up and forward as they walked forward with exaggerated high

steps. This Alert Walk was very conspicuous because gazing in Blue-faced Boobies is normally given from a stationary position. The combination of a walking gaze with high steps was never seen in other contexts and always signalled an attempt by the male to mount.

Males approaching females still mandibulating materials will mount, but they will not do so if the females look up. On one occasion a female raised the feathers of her head as the male approached her flank and the male did not mount. Males will mount females that are sitting down.

Mounting is accomplished by merely stepping up on the female's back. During copulation the male's wings are held in place and his head is stretched forward and down on, or beside, that of the female. He does not bite or grip her in any way. His tail may be wiggled back and forth as he treads alternately with his feet. The tail is fanned as it is thrust down and under that of the female to effect cloacal contact. The female's wings are held loosely from the body and may (one time) scrape the ground. Her bill is opened slightly, her head is forward and down, and her tail is elevated. A non-receptive female may turn toward the male and mutually jab with him; this always breaks up a copulation attempt.

Following copulation the male normally walks, with head strongly averted, one to two meters from the female. She continues to mandibulate materials on the platform. The male then may stare at his mate and his gaze is often met by hers. The male then normally returns directly to his mate and the pair continues to manipulate items together, remaining very close together at this time. The entire copulatory activity, from the Alert Walk to post-copulatory walking, gazing, and Symbolic Nest Building, ordinarily takes less than one minute.

SUMMARY

1. From January 1964 through August 1965 the breeding biology of the Blue-faced Booby (*Sula dactylatra personata*) was studied on Green Island, Kure Atoll, as part of the Smithsonian Institution's Pacific Ocean Biological Survey Program. My work commenced on 25 October 1964 and ended on 28 February 1965, during which time all the behavioral observations presented in this paper were made. Ecological studies initiated during this period were continued after I left the island.

2. Green Island, 2.3 km long by 0.6 km wide, lies in the southeast corner of the atoll, and is located at 28°25' N. latitude, 178°10' W. longitude. A six hectare flat central plain, covered with a mat of low-lying plants and surrounded by *Scaevola taccada*, occupies the center of the island. Blue-faced Boobies nest exclusively on the plain.

3. *S. d. personata* has an extensive range in the Pacific Ocean, breeding from Kure Atoll south to the Kermadec Islands, and from the Marshalls and New Caledonia east to the Line Islands and the Tuamotu Archipelago.

4. The species is sexually monomorphic in plumage but females are significantly larger than males.

5. The average population from 1963 through 1966 was 140; the population showed a slight decrease each year during this period (Fig. 3.1).

6. There are two discrete sub-colonies with virtually no interchange between them. All birds breed or attempt to do so. There are no "clubs" of non-breeders.

7. Numbers fluctuate regularly throughout the day, with maximum numbers at night and minimum numbers in early morning, from 09:00 to 11:00.

8. Time spent at sea during the day averaged 4.9 hours for males and 5.9 hours for females, before egg-laying began.

9. Boobies occupy only part of the suitable habitat. Each pair uses about 50 m² of land, although four times this amount is available. The territories of mated pairs are larger than those of bachelor males. Unmated females have no territory. The territory shrinks to one-quarter of its original size when the first egg is laid. Airspace above the territory as well as the ground itself is defended.

10. Territories, including areas not used during incubation, are defended against Laysan Albatrosses. The extra space is used as a display ground; excluding the albatrosses may function in increasing the efficiency of courting, as albatrosses disrupt displays.

11. Nest sites, and usually (90% of the time) territories, are not reused from one year to the next, although the birds are permanent residents.

12. Territories on Kure are ten times the size of those reported on Ascension Island. Nest success (56%) on Kure is over five times that on Ascension (9.7%), due in part to decreased interference with courtship, egg-rolling, and other pair-pair interactions disruptive to nesting.

13. The main laying period extends annually from January to May. The 1964 and 1965 seasons differed importantly. The 1965 season began two weeks later, averaged 26 days later for the colony and 4.5 weeks later for known individuals, showed no marked laying peak, lost more early nests, had more renesting, and had a lower overall breeding success. These factors are believed an outcome of adverse environmental conditions and a violent pre-1965 season gale which presumably effectively prevented feeding just prior to laying.

14. Pairs that kept their mates for the two seasons bred sooner in 1965 and had a shorter time interval between 1964 and 1965 nests than those that switched mates. Pair maintenance, with the resultant familiarity of pair members, may increase the courting efficiency, which in turn may help maintain the annual laying cycle.

15. The normal clutch is two; the average interval between first and second eggs is 5.6 days. Mean incubation time is 43 days. Although incubation begins with the first egg, it requires one more day to hatch than the second egg.

16. Incubation bouts average 11 hours for males and eight hours for females, one-third the time reported for other colonies. The time between incubation bouts in seabirds is a good index of food availability. The short incubation bouts on Kure, as well as short feeding times at sea (average less than 6 hours), high survival of young (81% of eggs hatched), and smooth growth curves for the young, suggest that food is more abundant at Kure than it is around islands of tropical populations.

17. Renesting was rare in 1964 and common in 1965, inversely related to the success of early nests in the two seasons. In 1965 second nests were more successful than first and contributed 24% of the 1965 production of young. Renesting is seen as an adaptation offsetting high early nest loss due to adverse environmental conditions.

18. Hatching is asynchronous and only one chick is raised, the second dying soon after hatching. Lack and Nelson have argued that the two-egg clutch is maladaptive at the present time. However, on Kure second eggs gave rise to 22% of the chicks fledged in 1964 and 1965. The second egg effectively buffers against the loss of the first egg or chick and is highly adaptive on Kure.

19. Pairs that retained mates through two seasons were more successful in 1965 than pairs that switched mates. Success in 1965 was not related to success in 1964.

20. Growth is highly allometric. Young exceed their parents in weight at 85 days of age and fly at 120 days when their primaries reach adult length.

21. Agonistic displays are similar in form and function to those described in other colonies. Fighting does not occur. Jabbing appears to help delineate territorial boundaries. Yes/No Headshaking is the most common display, accounting for 86% of the 754 observed agonistic bouts. Males are the predominantly aggressive birds, participating in 99% of all observed encounters. Females are involved in 32% of the encounters. Most of these females defend territories when their mates are on eggs.

22. Redirected aggression is common in high-intensity or prolonged encounters, and takes the form of pulling vegetation, displaying at small birds (e.g. Ruddy Turnstones), or attacking pairs not involved in the encounter.

23. Anti-predator responses are poorly developed. Calling by an alarmed bird at night alerts the entire colony. Boobies can defend themselves against Polynesian rats, which prey heavily on other seabirds on the island.

24. The male advertising display (Sky-pointing) is slightly different in form from that described for other races. Differences in tail and bill position between races may indicate long geographic isolation and behavioral plasticity for these traits. Males Sky-point to birds either walking through or flying over the colony. Males advertise only to females on the ground, but to both sexes flying overhead. Bachelors Sky-point to mated and unmated females with equal frequency, although mated birds advertise only to their mates. Bachelors account for 95% of the advertisement to flying birds.

25. Pairs restrict most activity to an area near one or more cleared platforms ripped from the vegetation. Territorial parading is an important component of courtship utilizing defended territorial space later abandoned. Pelican Posture is a commonly employed ritualized modification of the normal gait. The cocked tail associated with this display differs from the horizontal position found in other races.

26. Symbolic Nest Building, the most common epigamic activity, always occurs on a platform, functioning in pair formation and maintenance, and perhaps helping to synchronize reproductive cycles. No nest is ever built. As in other Pelecaniformes, the males gather and present materials to the female, who arranges them.

27. Copulation is linked with Symbolic Nest Building and is preceded by little overt behavior. The sequence of events leading to and concluding with copulation takes less than one minute.

28. The importance of bill positions during agonistic and epigamic displays have been emphasized. Facing an opponent is aggressive; turning the bill away from mates is common and appears to be appeasing.

APPENDIX

Capturing study birds. Breeding Blue-faced Boobies are relatively fearless of man and generally can be approached to within three meters during daylight hours. Non-breeders are more wary and often will fly before they can be captured. Birds at night are immobilized by dark and can often be picked up without a chase. If birds are chased through a colony in daylight, nearby individuals may panic, resulting in severe disturbance to the colony and, if repeated frequently, may result in an "edgy" colony that is unduly disturbed by any visit. For these reasons, almost all capturing of birds for banding and marking was done at night. We wore battery-powered headlamps in order to have both hands free. Birds are either grabbed directly by hand or are immobilized by holding a stick across the bird's neck. Fleeing birds can be halted in this manner, although care must be exercised to avoid striking them. The animals should be approached downwind, as they try to escape into the wind. They tend to fly up a beam of light, so one should at all times be prepared to duck an airborne bird! Light should be directed away from the colony, as careless shining of the beam may activate the birds, who may wander and become separated from mates or young; this could result in the loss of considerable information if a colony is visited at infrequent intervals. If it is necessary to capture birds during the day, they may be approached closely if they are on eggs or with young.

Handling. Adults should always be gripped tightly just behind the head. Boobies are very strong and will always attempt to bite. The bill is equipped with serrations and is quite capable of inflicting deep wounds. We never pulled away from a bird biting us for this reason. In addition to biting, boobies will scratch, defecate, and regurgitate. After the bird has attempted all these methods of escape, it will usually remain calm.

Both hands are needed to paint, measure, or band the birds. We placed their heads between our calves, holding them tightly with our legs and in this way were free to work with them. It was often necessary to hold two, three, or even more individuals at one time, and in such cases our legs were fine "storage areas." If birds are held for a long time it is necessary to check them regularly to make sure they have enough air.

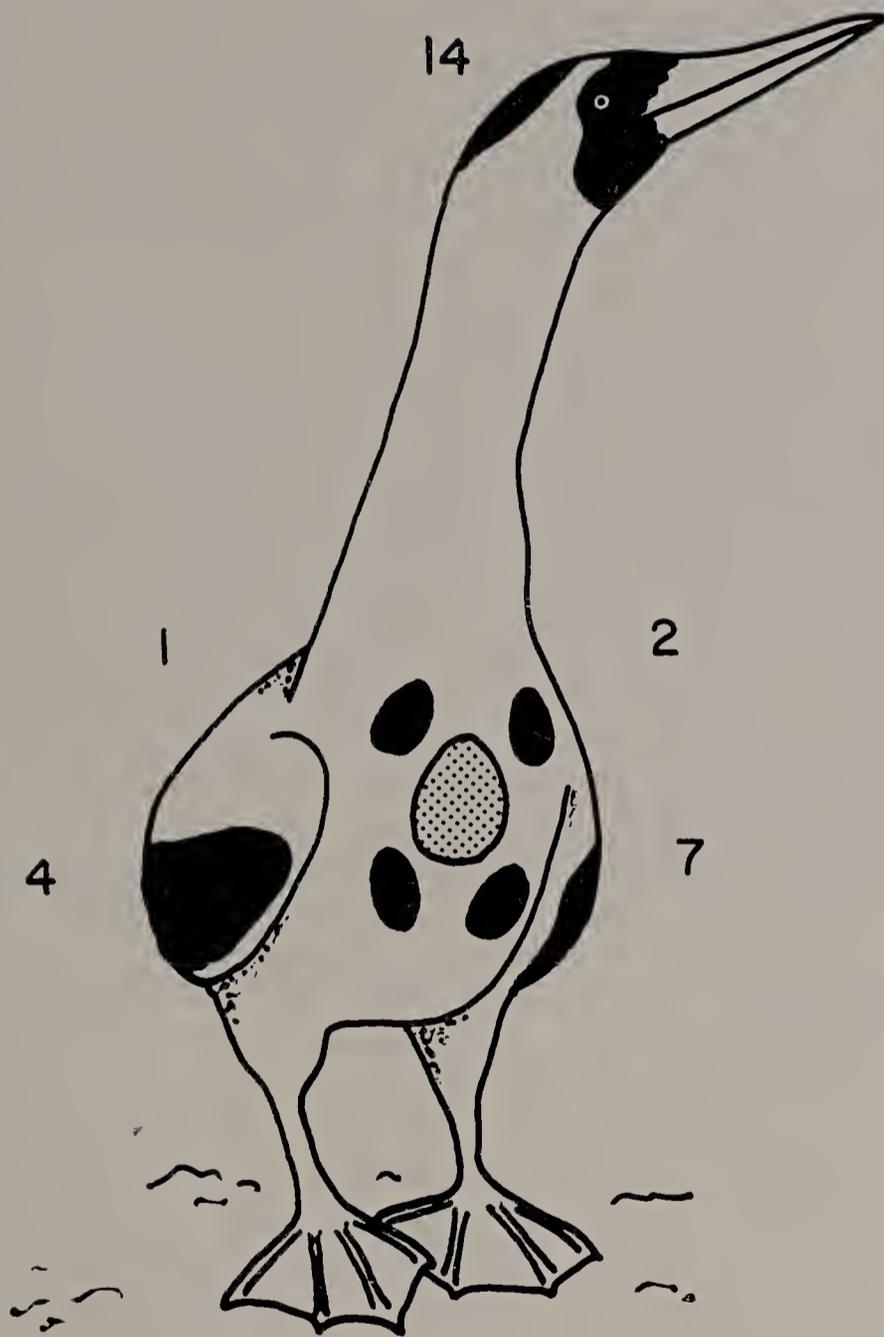
Banding. Blue-faced Boobies were banded with U.S. Fish and Wildlife Service number 7B bands. Smaller sizes are too tight and may injure the foot. Number 8 bands are useful on fledglings whose legs are thicker than those of adults. A bird is easily banded by holding it firmly at the base of the head and holding the band with the same hand. The bird's leg may then be brought up with the other hand, and the band attached. Every Blue-faced Booby on Kure had been banded prior to my arrival, either by POBSP personnel or Fish and Wildlife Service personnel.

Color Marking. Bands are easily seen on the birds. We did not, however, have permission to color band, so we used spray enamel paints to mark birds for individual recognition. Most birds were spray-painted at night. In addition to the other advantages of night work, the birds rarely tried to rub the paint off or fly to sea to wash. One painting normally lasted three to four months; birds are easily recaptured for additional painting if necessary.

On 26 October 1964 all birds then present in the colony were captured and

painted on the breast with a spot approximately eight centimeters in diameter: green for NAF and red for SAF birds. Subsequent checks of the colony revealed movements between the two areas. If unpainted birds were found, they were captured and marked.

It was necessary to recognize individual birds in order to study their behavior. Seventy-four birds were painted distinctively. Areas on the bird were assigned numerical value and, if the area was painted, the bird was assigned the corresponding number. Several areas could be painted and the values summed. Four areas around the breast colony spot were given the values one, two, four, and seven. In order, these areas were (anatomical position on the bird, not "as seen" when looking at it) upper right breast, upper left breast, lower right breast, and lower left breast, respectively. In various combinations these four numbers will sum to any value between one



BLACK 28

FIG. App. 1. Adult "Black 28," illustrating marking system.

and 14. For example, number 10 was marked by painting the one, two, and seven spots. If the top and sides of the head were painted, 14 was added to the total read from the breast. Four colors, one to a given bird, were used: red, orange, black, and blue. As far as I could tell, the resultant harlequin patterns (Fig. App. 1) in no way affected behavior. Dorward (1962a) reports that dyeing his birds also failed to disrupt their normal behavior.

The marking system proved highly successful. The center spot gave immediate information as to the colony, and provided a location guide to the other marks. Birds up to 450 m away could be read with 7 x 50 binoculars, and birds in flight, even at sea, could be read when they banked. The presence of given individuals within the colony could be determined without disturbing them, and birds could be singled out for observation.

Nest marking. In 1964 POBSP personnel drove a numbered red stake within two feet of each nest found. The numbers were in chronological order, beginning with the first nest of the season. Every nest in the NAF colony was marked. In 1965 these stakes were used as reference points for all activity noted in the colony. The locations of all new nests, marked birds, and behaviors were recorded relative to these stakes. I mapped the entire colony, recording from one stake the azimuth and distance to all stakes and new nests within 90 feet. Surveying was then moved to another centrally located nest and the process was continued. In addition, a gridded area of 25,500 square feet was laid out in the northeast section of the colony. Thirty-one stakes were placed on north-south and east-west lines at 33- $\frac{1}{3}$ -foot intervals. This area was used most extensively for behavioral observations: all birds were recorded with reference to either my grid or the nest markers. The nesting locations of known individuals for two years were in this way determined, and territory sizes and locations in 1965 were calculated by plotting every position at which individual birds were seen. All English system units have been converted to the metric system for this publication.

Egg marking. All eggs found were marked with felt-tipped pens and were in all cases accepted by the adults. The volatile ink solvent caused some incubating birds to shake their heads if they returned to the egg within one or two minutes of our marking it.

Chick marking. The nests in the Kure colony are well spaced, so young chicks cannot stray from one nest to another. As the eggs hatch asynchronously, it was not necessary to mark nest-mates in order to tell them apart. Since the second chick usually died, was evicted, or disappeared within a few days of hatching, it was unnecessary to mark them as they grew. U.S. Fish and Wildlife Service bands were applied as soon as the young could wear them. Older young wandered and their bands became encrusted with guano. It was often necessary to scrape this encrustation off before the band could be read. When the young fledged the guano would wash off at sea.

Weighing and measuring. All large birds were weighed in a wire-mesh basket suspended from a spring balance scaled in ounces. Center beam balances scaled in grams were used for newly hatched birds.

The following measurements were taken at three-day intervals on selected growing chicks: culmen, middle toe, tarsus, wing (from carpal joint, against the ruler stop, to tip of longest primary; flattened), and tail (longest rectrix only). A steel 30-centimeter ruler with end stop was used for all measurements. Steel-pronged dividers were used for culmen, middle toe, tarsus, and tail

measurements. The culmen was measured from the base of the anterior feather tract of the head to the tip of the bill. Unfortunately, these growth and development measurements were made by many POBSP personnel and are therefore subject to sampling error, as methods may have differed from one man to the next.

Censusing. Three different censuses have been maintained during this study. Night counts of birds in the colony were conducted by POBSP personnel at biweekly intervals from November 1963 to August 1965, and from April to September 1966. During the breeding season the colony was checked daily and all new nests, eggs, and chicks were recorded. I desired more accurate information about diurnal colony activity, and established, on 1 January 1965, a census every hour on the hour to determine the location of every numbered bird in the colony. This continued once a week through April 1965. The data from the various censuses yielded precise information on annual changes in colony size, precise nesting phenology for the colony and known birds over two breeding seasons, and information on diurnal fluctuation in numbers, sex ratio throughout the day, territory size, time of day pairs are together, and many other important parameters, most of which appear in Chapter 4. Data appearing in Tables 3.1 and 4.7 to 4.11 and in Fig. 4.3 were obtained during the 15 days in which hourly censuses were conducted.

Behavioral observations. All observations were made from a position within or marginal to the NAF colony. No blind was used, as the docility of the birds permitted observation from positions relatively close to them. Behavior was observed with 7 x 50 binoculars, and all observations were dictated into a Minifon tape recorder and later transcribed, thus permitting extended observations uninterrupted by looking down at a writing pad. Birds were viewed at distances ranging from less than three meters to approximately 60 m. These observations were begun on 25 October 1964 and ended on 25 February 1965.

Activity in the colony was most intense at dawn and dusk; observations were concentrated at these times. Well over 90% of my observations were made within one hour of sunset when birds returned from sea, pairs were reunited, and territorial squabbles were most common.

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