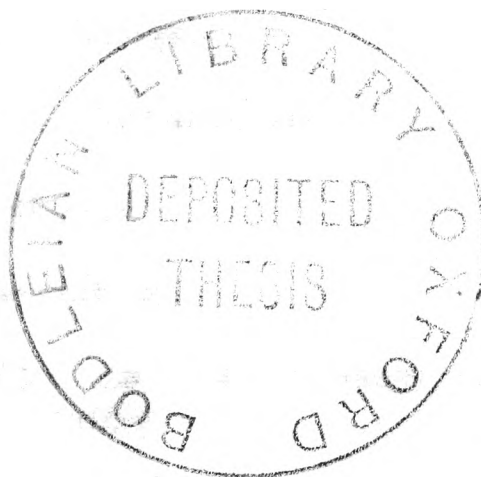


COMPARATIVE BREEDING BIOLOGY  
OF SOME SEABIRDS OF ASCENSION ISLAND  
with special reference to two species of Sula  
and the Fairy Tern.

DOUGLAS F. DORWARD



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Edward Grey Institute,  
Botanic Garden,  
Oxford.

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ABSTRACT

The work of which this study is an account was carried out while the author was Deputy Leader of the British Ornithologists' Union Centenary Expedition to Ascension Island, from November 1957 to April 1959.

The objects of the expedition were to investigate the general breeding biology of the resident tropical seabirds with a view to discovering how the timing of their breeding was controlled. In most temperate birds the controlling factors are changes in day-length, temperature, and availability of food; the particular interest of the eleven species at Ascension was that they were living in an environment with no seasonal change in day-length or climate, and apparently a uniform availability of food.

The author was responsible for studies on three of these species, the White Booby Sula dactylatra, the Brown Booby Sula leucogaster, and the Fairy Tern Gygis alba. A few observations were also made on the ten or so pairs of the Redfooted Booby Sula sula which were present. The bulk of this study is an account of the comparative breeding biology of the White and Brown Boobies. The Fairy Tern is not closely comparable to them, and only those aspects of its biology relevant to the general problem (breeding, food, and moult) are dealt with, in an Appendix.

The study is divided into nine sections, of which four deal with the breeding of the boobies, and three with other observations on the species' biology, viz. moult and food (both of which were found to have an important relation to the breeding biology), and behaviour, which had neither been fully described nor analysed before.

Section I is introductory, the aims, scope, and methods of study being described, together with the habitat. Ascension Island lies roughly in the middle of the South Atlantic (8°S, 14°25'W). It is a peak of the Mid-Atlantic Ridge, triangular in shape, with sides/

sides of about eight miles, and rises from coastal plains to 2,800 ft. in the middle. Its volcanic origin is clearly seen in the numerous extinct craters, ash-fields, and lava-flows, which are little weathered by the uniformly warm and sunny climate and the continuous south-east Trade-winds. Vegetation is confined to the slopes above about 1,000 ft.

As a result of man's introduction of rats and cats, the seabirds are no longer found on the main island and, with the exception of the Wideawake Tern, are now confined to off-shore stacks and islets. The expedition's main work was therefore done on Boatswain-bird Island, a volcanic plug some 300 ft. high and 400 yds. across, about 300 yds. off the south-east corner of Ascension. Only intermittent visits could be paid to this island, and the author spent about 130 days, spaced over 15 months, on it.

Section II deals with the colonies and breeding seasons. There were 1200-1300 pairs of White Boobies breeding on Boatswain-bird Island, and one or two pairs elsewhere. 600-700 pairs of Brown Boobies bred at Ascension, of which about two-thirds were on Boatswain-bird Island and the remainder on small stacks.

In both species there were clearly-marked peaks of laying, with intervening periods when the number of new clutches was very small. In the White Booby breeding appeared to occur annually (only one full season was studied, but deductions were made about the preceding and following ones), in the Brown about every eight months (two full seasons were seen, and again deductions were made about others). In both species the time taken from laying of eggs to fledging of chicks was the same, six to seven months. Individuals of both species conformed to the breeding seasons of the population, and if out of phase for some reason, they had a longer or shorter "rest" period as necessary to bring them into phase again at the next season. These two discoveries at once suggested that external factors were modifying the birds' internal physiological cycles and controlling the/

the time of breeding. What these factors might be is discussed later in the study, in the light of subsequent discoveries about the species' breeding biology.

The two species differed not only in periodicity of sexual cycle but also in the time of year at which laying took place. The periodicity was such, however, that every two years the Brown Boobies would lay at almost the same time as the White. The significance of this, and its possible relation to annual variation in oceanic conditions with their origin in the melting of the Antarctic ice, is discussed, together with published information about the species' breeding seasons in other parts of the world.

Section III deals with clutch-size and incubation. Both species were found to lay two eggs, with very few exceptions, but only one chick was raised. Incubation is described, and the attentive spells at the nest analysed; the attentive spells of both species were found to be variable, those of the White Booby being about 48 hours and those of the Brown about 24 hours. This probably indicated a difference in the birds' feeding range (partly confirmed by a study of their food), important in the consideration of the two species' ecological differences. Some desertions occurred during the study of attention spells, and the circumstances of these strongly indicated that the birds were experiencing difficulty in finding food, this view subsequently being supported by other events.

In Section IV the feeding, care, and growth of the chick are described. Records of growth rates of both normal and abnormal chicks were obtained, and these provided further evidence of the operation of a food shortage. Losses in weight and reductions of growth rate occurred in chicks of varying ages but at roughly the same date, August and September 1958.

The second chick of the clutch hatched about five days after the first and never lived more than two or three days. The curious circumstances of this are described: the smaller chick was apparently expelled from the nest by the larger, and not starved to death as a result/

result of the larger chick's more vigorous demands, as has been shown in some other species of birds. Experiments with twins were carried out to investigate this situation further; the larger chick's ability to establish a supremacy was found to be so strong as to operate even when the difference in size between artificial twins was very small; and some parents were able to raise twin chicks at apparently the normal rate of growth for two weeks or more. Possible reasons for this striking behaviour amongst the chicks and its relevance to clutch size and breeding success are discussed.

In Section V, breeding success is described. Both species had a low breeding success, and big losses of eggs and chicks of the White Booby occurred in August and September 1958, supporting the other evidence concerning shortage of food. In one area of the White Booby colony studied only 4.5% of the eggs laid gave rise to flying young, in another area the figure being 9%. In the Brown Booby 5% of the eggs laid gave rise to flying young in one season, while in the following season the figure was 13%; the difference here was probably due to shortage of food in the first season causing late deaths among chicks.

Section VI deals mainly with moult in the White Booby. Less information was obtained about the Brown Booby but the procedure appeared to be the same as in the White; in view of the Brown Booby's shorter sexual cycle, however, more information than could be obtained would have been interesting. The sequence of primary moult was discovered when examining juvenile White Boobies which had returned to the island after a post-fledging dispersal. The change from juvenile to adult plumage took more than two years, the shedding and regrowth of the primaries, from the innermost outwards, occurring in three spaced concurrent cycles. This remarkable procedure was found to operate in adults as well. There was also a period of pause in the primary moult of some adults, correlated with the time when most birds had chicks, but there were exceptions to this and some/

some birds were moulting their primaries throughout their breeding. The primary moult of some of the other species of Ascension seabirds was examined in the light of these discoveries, and the results indicated a prolonged moult with a period of pause during breeding. This, together with the relation of moult to the availability of food and the breeding seasons in tropical seabirds, is discussed.

Section VII is an analysis of the food of the boobies with some observations on their feeding behaviour. Both species regurgitated freely, the contents of all such food samples being noted and specimens preserved for later identification. Flying-fish were found to be prominent in the diet of both species, but both also took small fish on occasion, sometimes in large numbers, and, particularly in the case of the Brown Booby, to the exclusion of Flying-fish. White Boobies generally concentrated more on large Flying-fish (about 20 cm. long) than Brown Boobies, and the latter took a higher proportion of small fish of more species than the White Booby. When they did take large fish, the Brown Boobies took a slightly greater variety than the White. Only Brown Boobies were seen regularly to fish close inshore. Thus there was an overlap in the two species' food, but they appeared to differ in feeding methods, in the variety of species taken, and in size preference.

Section VIII is a comparative account and interpretation of behaviour patterns observed in the course of other observations on establishment of territories, conduct of mated birds, pairing, territorial behaviour, and permanence of pair-bonds. These patterns and the situations in which they occurred have not been described before and are important for the understanding of the derivation of certain behaviour patterns in other members of the family Sulidae. Some of the behavioural differences between White and Brown Boobies were apparently related to differences in their nesting habits.

Section/

Section IX contains the general conclusions from the above findings and a discussion of their relation to the regulation of seabird numbers and the control of breeding times of birds in a tropical marine environment. Particularly stressed are the importance of studies on the moult cycle and availability of food in relation to the breeding seasons. It is argued that the two boobies may have evolved the observed differences in breeding biology as a means of exploiting, in different ways, cyclical variations -- perhaps small -- in the availability of food, these being a result of variations in oceanic conditions.

## 1 INTRODUCTION, HABITAT, METHODS.

### 1. Introduction.

This study was undertaken as part of the programme of the British Ornithologists' Union Centenary Expedition to Ascension Island. The aims of the expedition were to investigate the phenomena of breeding seasons in the seabirds of an area with no appreciable variation in climate or day-length throughout the year. The expedition was on Ascension from November 1957 until April 1959.

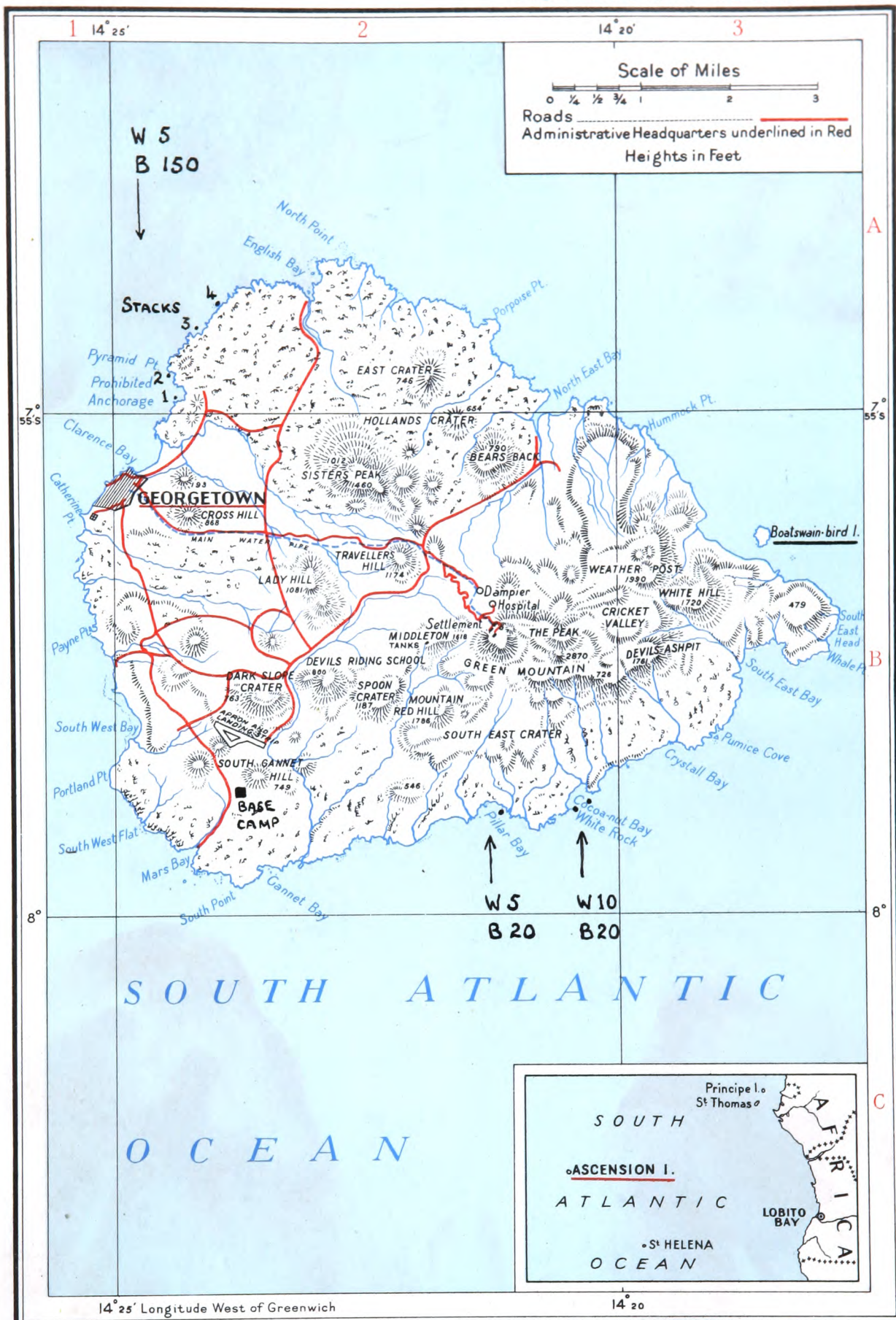
Eleven species of pan-tropical seabirds breed at Ascension, and of these I studied the Boobies Sula spp. and Fairy Tern Gygis alba. Most of the information here presented was obtained from studies of the White Booby<sup>1</sup> S. dactylatra and Brown Booby S. leucogaster. About ten pairs of Redfooted Boobies S. sula were also present, but only one nest was accessible and the others (I was not certain how many of them did nest) could not be observed except from the sea. Hence the White and Brown Boobies are the main subject. A short account of the Fairy Tern has been included as an appendix, with special reference to aspects of its biology relevant to the study of the Boobies.

The scope of the study was determined by several factors. Firstly, I did not have 18 months' continuous residence with the birds. The colonies were difficult to get at and only/intermittent

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<sup>1</sup>S. dactylatra is known as the White, Blue-faced, and Masked Booby. Its face is not strictly blue, certainly not so blue as that of the Redfooted, while the male Brown Booby in non-breeding dress also has blue about the face. Furthermore, all the boobies have conspicuous face patterns and in that sense are "masked". I therefore propose to use the term White Booby, which emphasises the contrast with the Brown; the Redfooted is also usually white, but its red feet are always conspicuous and its name is already universally employed.

ASCENSION ISLAND 27



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**Fig. 1. Map of Ascension, showing off-shore stacks with approximate number of nesting pairs of White (W) and Brown (B) Boobies.**

intermittent visits could be paid to them; this meant many problems in the recording of events. Secondly, the study was restricted to the birds while at the breeding colonies; their range and behaviour at sea, for instance, could not be investigated. Thirdly, there was no way of assessing the marine life and its availability as food to the birds, except through what they brought back to the colonies. Finally, the scope was limited by the length of the expedition's stay. It was planned that we should see two laying seasons, or at least one complete breeding cycle. It was not desirable that a pioneer study of this nature should be longer; practically nothing was known of the breeding of the Ascension seabirds, with the exception of the Wideawake tern, which was known to lay at roughly 9½-month intervals (Chapin, 1954). It happened that I saw one complete breeding season of the White Booby, one and most of a second of the Brown Booby, and almost two complete ones of the Fairy Tern.

How far were these particular seasons representative of the birds' normal way of life? And how normal were the lengths of sexual cycle that were indicated? In this thesis I present the findings and draw conclusions where possible, and relate these to the wider problem of the breeding of tropical seabirds. It will be seen that many more problems have been raised than have been answered.

## 2. Habitat.

Ascension Island (Fig.1) lies between latitudes 7 and 8°S, and at 14°20'W, in the Atlantic Ocean, approximately midway between West Africa and South America, about 1600 miles west of the former and 1500 east of the latter, and 1000 south of Sierra Leone. The nearest land is the island of St. Helena, 700 miles to the south-east. Ascension is a peak of the mid-Atlantic Ridge. It lies in the middle of the belt of south-east trade winds.

The/

The climate is uniformly warm and sunny, and there are rarely extremes of wind or temperature. The rainfall on the central peak, Green Mountain (at about 2,500 ft.) is roughly 25 inches annually, but on the coast is an irregular five inches, in some years negligible. The day-time maximum temperatures are about 85°F, occasionally rising to 95; at night the minimum is about 78. Exceptional periods of rainfall have been known, for example in 1924 and 1959, and the existence of dry watercourses about the island testifies to such events. Once the nesting colony of Wideawake Terns Sterna fuscata was reported to have been washed away (Huckle, 1924). Immediately after the expedition left, in April 1959, a period of rain began and lasted until July; R.G.Allan, one of the expedition members who stayed behind, visited the booby colonies then and reported that rivulets had formed in the thick guano layer and many eggs had been washed away. After weather of this sort, much of the island becomes covered by grass and other plants, but in normal times it is very barren, except for the upper 1000 ft. of Green Mountain. Numerous craters, lava fields, clinker and ash are the features of the landscape. There are no birds on most of the main island except at the "Wideawake Fairs", and none even there when the Wideawakes are not breeding. Later I estimated the Ascension population of White Boobies to be about 9,000 birds and that of the Brown Boobies to be a minimum of 1400, but none of these birds was breeding on the main island. Most of them were on a large off-shore stack called Boatswain-bird Island.

However, we found evidence that there must once have been very large colonies of seabirds on the main island, although we could not guess the actual numbers. Two areas in particular were important: that stretching from South Gannet Hill (the name is significant) to the southernmost point of the island, embracing Mars Bay to Gannet Bay, this area being a very rough lava field; and that at the north corner of the island, from Sisters Peak to Pyramid Point and east as far as Porpoise Point, again mostly rough lava. In these areas the rocks were encrusted with a white substance identified later as phosphatic guano derivatives. In the hollows and crevices was much dust/

dust, again of a phosphatic nature, some of it occasionally being recognisable as guano, and amongst the dust were fragments of feathers (some clearly those of boobies from their size and shape but not assignable to species), bones, and egg-shells. Some bones were later identified as those of White and Redfooted Boobies, but the relative numbers could not be established, and bones of Brown Boobies, difficult to distinguish from those of White Boobies, were not certainly found.

Near the foot of Sisters Peak was a fumarole. It had a narrow vertical shaft, opening at the top of what looked like a gigantic mole-hill, while at the bottom, some 20 feet down, was a chamber. The floor of this natural trap was littered with bones which proved to be mostly those of Wideawakes and White Boobies. Two further pieces of evidence confirmed that there had once been a booby colony there: A panorama of the island, painted from a sketch made in 1819 by Admiral Sir Jahleel Brenton<sup>1</sup>, shows birds in flight and on the ground in this area, some of them being unmistakably White Boobies. Also, a map of the island made in 1838 designated this same area as "North Gannet Fair"; White Boobies are still called Gannets on the island, and "Fair" is the term still applied to the Wideawake breeding colonies. The same map also marked a South Gannet Fair near the present South Gannet Hill. This colony must have been on the lava field that stretches from this hill to the southernmost corner of the island, where there is much phosphatic dust and again fragments of feathers. Further evidence of this colony was given by Darwin (1845), who wrote of his visit to Ascension in 1836, "One of my excursions took me towards the S.W. extremity of the island. ... Whilst passing this end of the island at sea, I could not imagine what the white patches were with which the whole plain was mottled; I now found

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<sup>1</sup> The painting now hangs in the Africana Museum, Johannesburg.

We were shown a photograph of it.

that they were sea-fowl, sleeping in such full confidence, that even in mid-day a man could walk up and seize hold of them." He did not say what the birds were, and they might have been Wideawakes, which are still found there; but it is not the habit of Wideawakes to remain asleep "in full confidence" while you walk amongst them. This is true of boobies, however, and I could often seize hold of a sleeping bird. I believe that Darwin saw White Boobies there, where now there are none.

The reason that they, and the other species as well, have gone is probably predation by cats or rats, both of course introduced by man. The history of this has been dealt with by Stonehouse (1960). We found no evidence that the rats were affecting the birds at the present time, and they could certainly not be described as a plague. If they had been a serious menace to the Wideawakes, we would have seen some evidence of it. They may, however, have been important predators at one time. It is generally assumed that the introduction of rats to a colony of ground-nesting birds inevitably results in the eventual demise of the birds, as happened for example to the Puffins Fratercula arctica on Ailsa Craig (Fisher & Lockley, 1954). On the other hand, Vogt (1942), in his study of the Piquero Sula variegata and other guano birds on the island of Lobos de Tierra off Peru, advocates the destruction of rats in the colonies not because they are harmful to the birds or eggs or chicks, but because they prey upon the lizards which eat the birds' ectoparasites. It is therefore difficult to assess how important the rats on Ascension have been in reducing the numbers of birds. About the cats there is more information. Darwin (loc. cit.) described them as being a plague (1836); like the rats, they are not a plague now, but their numbers are probably kept in check by food shortage during the absence of the Wideawakes. Probably this is also why the Wideawakes survive; boobies are resident more or less all the year round on their breeding colonies, and would provide a continuous source of food for cats as long as they survived. I imagined, after being painfully/

painfully attacked myself by boobies, that the adults would be able to defend themselves and chicks from cats, but I was proved wrong when watching a small stack at Coconut Bay, separated from the mainland only by a deep chasm some twenty feet across. A few Brown and White Boobies were nesting on the stack, and occasionally a bird landed on the mainland side of the chasm. I found a freshly-killed adult male White Booby there, its head torn off, and at the same time saw a cat disappear among the rocks; there were heaps of bones and feathers from other boobies that had previously presumably died the same way.

Thus all the Ascension seabirds, with the exception of the Wideawakes, are confined to off-shore stacks and cliffs where they are safe from ground predators. The positions of the various colonies and their approximate numbers of breeding pairs are marked on the map (Fig. 1). There may have been a few pairs on some inaccessible parts of the south coast that I did not see.

My work on the boobies was done in two places: i) four stacks between Pyramid Point and English Bay, which could be reached by rowing-boat from Georgetown (see Fig. 1, Stacks 1-4), and where only Brown Boobies nested, and ii) Boatswain-bird Island.

Boatswain-bird Island is a volcanic plug, separated from the south-east corner of the main island by a channel about 300 yards wide (Plate 1). It is 300 feet high and almost sheer all round; the top is an undulating plain of some seven acres, and this is where the White Booby colonies are. The Brown Boobies occupy the edges of the plateau, the gullies, and steep slopes above the sheer cliffs. The guano layer on top was about two feet thick in the valleys, and the whole island was whitened by encrustations of it. The softness of the underlying rock (trachyte) and the crust of guano made the island a treacherous place to work on.

The guano deposits were last exploited in the early 1930's, and the island has been undisturbed since then. The guano workers built/

built a small landing stage at the southernmost tip of the island, where the drop to the sea is least steep, and from there a precarious path has been cut to the top. In spite of this assistance, we found that operation of the landing was never easy, and hazardous when high seas were running.

The expedition Base Camp was situated at the foot of South Gannet Hill, in the south-west corner of the main island, from where we visited the stacks and Boatswain-bird Island at regular intervals. Three or four days at a time, occasionally six, were spent at Boatswain-bird Island, where we built a hut and put down a mooring buoy for the boat; all stores and fresh water had to be ferried out. The nearest possible permanent mooring for the boat was in North East Bay, which was a three-mile run from the island. The sea conditions were rarely so rough as to prevent us making this run, but sometimes heavy rollers prevented us getting to the boat at its mooring. These rollers, a feature of oceanic islands, usually lasted three or four days; their origin is uncertain (Murphy, 1936). They sometimes prevented us from visiting the stacks from Georgetown.

A general account of Ascension, its history, and the work of the Expedition has been given by Stonehouse (1960).

### 3. Methods.

In our 15 months in the field I spent about 130 days on Boatswain-bird Island and visited the stacks 23 times, at roughly monthly intervals.

Most observations were made during daytime, a few at night. Behaviour studies were most fruitful in the early part of the day, and generally the birds were least active during the hottest time, about mid-day and afternoon. Observations after dark were confined to times when moonlight made it possible to climb about on Boatswain-bird Island, which was perilous in complete darkness. Mostly such excursions were for the purpose of checking the presence of/

of known birds, or for estimating total numbers, since more birds were always present at night. Some checks on incubation spells necessitated night work.

Brown Boobies were less convenient to study than White, as they were more timid and took flight more readily if alarmed. Binoculars were rarely necessary, and if one kept still or moved only carefully most birds were undisturbed by the presence of an observer, even within a few feet.

Ringings: Both species of booby were marked with numbered aluminium rings. The first series was supplied by the National Institute for Oceanography, and the size used was No. 6 (with clip), but as this was just too large for both species every ring had to be adjusted to a small<sup>er</sup> internal diameter before using. Later we received rings from the British Trust for Ornithology; their size No. 4 (with clip) fitted the Brown Booby but was too small for the White. Some of the new Monel rings were used (overlapped) on the White Boobies, but the hardness of the metal made this a complex operation and the White Boobies were difficult to deal with single-handed anyway.

Rings were easy to see on standing birds, and sometimes one could crawl close enough to read the number without catching the bird, but this was dangerous if within striking distance of the beak.

Coloured celluloid rings of the "flatband" poultry type were tried at first. Even when sealed with acetone, however, they could still be removed by the birds, either completely, or so that they became jammed over the webs of the feet. This practice was therefore discontinued. The aluminium rings could be coloured with cellulose lacquer or paint, which remained recognisable for about two months, or longer if seen at close quarters. Lacquer had to be applied after the ring was put on, otherwise it flaked off when the pliers were used; in most cases the process was not worth the trouble. I used these painted rings to identify immature birds whose plumage was not distinguishable from that of the adults, and also for some

of the individuals that were being closely observed in a behaviour study. Adults whose breeding histories I wished to follow were ringed on the left leg, those that were being observed for daily habits on the right; chicks were ringed on the left leg and immature birds of unknown age on the right, their subsequent plumage changes helping to keep the categories distinct. A system of this sort was quite easy to devise and made the lack of colour-rings but little drawback. The chief aid to the identification of ringed birds, however, was locality. Each bird, when it was on the colony at all, could nearly always be found in the same place. Hence a ringed bird found in the colony where no adult had previously been ringed was almost certainly an immature bird just visiting.

374 White Boobies and 244 Brown Boobies were ringed. Nearly three-quarters of these were chicks ringed towards the end of our stay, in the hope of recoveries away from the colony. (This has proved an empty hope, to date.) My policy was to ring few birds and to concentrate on those likely to provide information over the succeeding months; too many ringed birds would have resulted in much wasteful catching of birds and the checking of numbers. 106 adult White Boobies and 64 chicks, and 33 adult Brown Boobies and 33 chicks, were ringed with this policy in view. This selective ringing was justified, I think, because of the White Boobies only 11 out of 106 were never seen again; a remarkably small figure, considering mortality and the possible loss of rings. None of the adult Brown Boobies was never seen again, I think, but some could not be caught again and I cannot quote definite figures.

Dyeing: Dyes were useful for short-term work, since they were easily applied and showed up well on the White Boobies' plumage. But after handling the birds usually went and bathed, thus immediately diluting the colour. Methasol Fast dyes, soluble in alcohol, were supplied by Imperial Chemical Industries Ltd. /

Ltd. Paint lasted longer than dye, and also showed up well, but it tended to become patchy as the bird's body-moult proceeded, and sometimes also picked up dust before it dried. Neither ringing nor dyeing nor painting appeared to have any permanent effect on the birds' behaviour.

Nest-marking: Marking of individual nests was a problem. Numbered pegs stuck into the ground or placed near a nest were either quickly pulled up and used for courtship and nestbuilding, or soon became obscured under a crust of squirted excrement. Eventually I used numbered pieces of plywood placed face-downwards under a heavy stone, but checking the number thus became an unwieldy operation, especially if the owner of the nest was aggressive. Some of the Brown Booby nests were near a rock-face on which a number could be painted above the line of guano-spray. The methods used for marking nests or recording numbers of nests in the various study areas are described later when dealing with the laying season of the White Booby; all the Brown Booby nests on Boatswain-bird Island were individually marked, but those on the stacks were not.

Egg-marking: Eggs disappeared from some nests and appeared in others. All eggs were therefore marked with pencil as soon after laying as possible, and this turned out to be a very necessary help to the understanding of what was happening, and the establishment of incubation periods. The eggs' surface layer of chalk was soft when laid, and marks made then never became obscured, even though the egg subsequently became dirty. Often the discolouration of an egg was a good indication of its age.

Chick-marking: This was not easy because the chicks were naked at hatching and the growing white down quickly lost any paint or dye applied. However, it was not necessary to mark very young chicks; there was never more than one in a nest for more than two or three days, the two differing in size anyway, and until the chick was old enough to be marked by ringing it never strayed from the nest or from the company of its parents, one or other  
of/

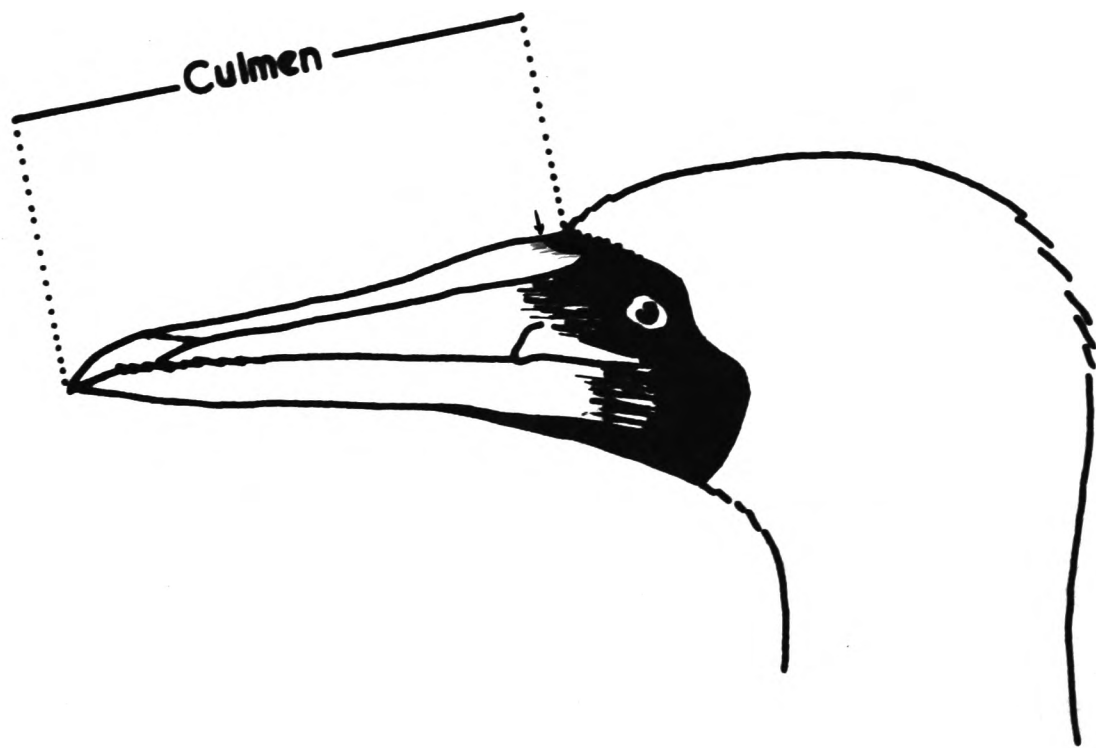
of whom was already ringed. Chicks' ring-numbers were soon obscured by a crust of guano, and for checking this had to be scraped away. This crust disappeared as soon as the chick paid its first visit to the sea, and the condition of the ring was a very good indication of whether the chick had done this or not. Chicks had to be marked for the experiments with twins, and this was done by tying a piece of soft thread round the tarsus and changing it as the growth of the leg made necessary.

Handling: The technique of catching and handling boobies deserves mention. White Boobies on the breeding colony usually stood their ground and were easy to approach and catch with a short hand-net. But in the "clubs" or resting groups (see later) they panicked into flight. Brown Boobies frequented places from which they could easily take flight and were more timid. However, a cautious approach followed by a sudden dive with the hand-net was usually effective for catching both species. For birds on places where a sudden dive was out of the question, or for more timid individuals, a long-handled net with a frame of about 2 ft. diameter was used.

A booby in a net had to be handled with care and skill; until the latter was achieved I suffered numerous minor injuries from the strike of the beak and the strong grip of the mandibles. A firm grip of the head, with the fingers kept clear of the gape, was necessary from the moment of capture until the bird was finally released. This meant sitting on the ground and clasping the bird's wings and body with knees and right elbow, leaving the right hand partly free to operate. Thumb and index finger of the left hand could be used by bringing the bird's head round as required, but retaining the grip with the other fingers. Leather gloves proved useless.

Long chases of birds were avoided when possible, partly because of the pursuer's fear for his bare toes, and partly because the pursued birds became very alarmed and were therefore more difficult to catch subsequently.

Weighing: /



**Fig. 2. Culmen measurement. Arrow shows point of transition between bill and facial skin.**

Weighing: Adults and large chicks were weighed in a hessian bag, small chicks in a cloth bag; the weights of these were checked regularly because there was some variation due to the birds regurgitating into them while being weighed.

Spring balances, measuring up to 200g x 2g, 500g x 5g, 1Kg x 10g, and 5Kg x 100g were used (according to the size of the chick) and were checked periodically. They remained extremely accurate in spite of hard usage and rough treatment in dusty conditions. The chief difficulty about weighing was the continuous wind everywhere on the island. Nearly always the birds had to be taken to a relatively sheltered spot and several readings made.

Weights recorded were accurate to half of each division on the balance, i.e. to 1g up to 200g, to 2g up to 500g, to 5g up to 1Kg, and to 50g up to 5Kg.

Measuring: Measurements were made with a stainless-steel 30cm rule mounted on a wooden block with an end-stop. Culmens were measured with dividers, and wings longer than 300 mm with a flexible steel rule.

As the transition point between beak and facial skin was not always clear, the culmen length was taken to be the distance between the tip of the beak and the bases of the anterior feather tracts of the forehead (Fig. 2). This measurement could also be made on small chicks because the feather-tracts were quite distinct from the smooth skin immediately behind the beak.

Wings were measured from the carpal joint, held against the stop, to the tip of the longest primary, the wing being flattened and straightened on the rule. Until the primaries had erupted, the measurement was made to the tip of the wing stump excluding down. In older chicks and adults the accuracy of the wing measurement was more in doubt, but a series of measurements taken over a period of four weeks on chicks whose feathers had finished growing showed a good consistency, with accuracy to the nearest 5 mm. The end of the flexible rule was held against the carpal joint, the/

the wing folded, and the free hand was drawn along the outermost primary. This measurement is close to the "standard wing" measurement of skins, i.e. the wing was flattened and straightened, not measured as an arc.

These two measurements, culmen and right wing, proved to be good indices of growth rate. Growth curves of both were plotted against age, and were used to estimate ages of other chicks from their measurements. Other measurements were found to be inconvenient; the gape, for instance, varied with the pressure put on the buccal skin, the foot length with the bird's effort to curl its toes; and on the tarsus (which was a relatively short measurement and therefore subject to greater proportional error) it was difficult to establish fixed points, especially when the chick was small and its legs chubby. The tarsus and longest toe measured together were also subject to the same difficulty.

Photographs were taken with a 35 mm Leica camera. Extremely bright light and excessive contrast necessitated care with exposure and development, in the case of monochrome; colour generally gave good results. The film used was Panatomic X and Kodachrome. All monochrome film was processed and printed at Base Camp. A Bell & Howell 16 mm ciné camera was used to take shots of behaviour sequences.

A BBC tape-recorder was used to obtain a complete repertoire of the calls of both species of booby at the breeding colony. This is now in the Natural History Sound Library of the BBC.

Differences between the sexes: In the adults of both species the sexes differed in three respects, which made their distinction easy and aided in the recognition of ringed pairs.

1. **Voice.** The male's voice was a high-pitched asthmatic whistle, while the female's was louder and a strident goose-like honking. In the Brown Booby the timbre in both sexes was weaker and less musical, but the description is generally true for both species. One or two of the females' voices lacked the normal sonority/,

sonority, their call being a hoarse rattle, but even these could not be mistaken for males. Murphy (1936) established that in the White Booby and the Blue-footed Booby *S. nebourii* this voice difference was due to an anatomical difference at the junction of the trachea and bronchial tubes: the female had a thin membrane whereas the homologous structure in the male was a hard egg-shaped protuberance. By dissection of an adult male and female found soon after death I confirmed this for the Ascension White Booby. Murphy also said that the tracheae of young males and females showed the same structure as those of adult females, indicating that the voice of the adult male is a secondary sexual development. I did not dissect any immature birds and cannot say at what age the change took place, but in handling them I noted where possible the voice of each. Of 47 immature birds handled, 26 had the female or juvenile voice and 21 were not heard to call; none had a male voice. They ranged in age from 7 to 27 months, but were mostly about 14 months. No bird with traces of brown feathers in the rump (the last sign of immaturity to remain) had a male voice. I therefore conclude that the male voice is not attained until birds are in adult plumage, and perhaps not until they are ready to attempt breeding.

2. Colour of soft parts. In both species the soft parts of the male were more brightly coloured than those of the female, less so in the White than the Brown Booby.

In the White Booby, the beak of both sexes was straw-coloured and the legs a dull orange. Some females had dull olive legs without any orange tinge at all. Some males had rich orange legs, and beaks a bright straw colour. I could not definitely establish that the assumption of brightly-coloured soft parts was associated with courtship or breeding; this was so in some cases but not in others. The main difference between the sexes was that the female never attained the rich orange legs that the male sometimes did; a few females had beaks nearly as bright as the/

the male colour.

Colour-differences were always more distinct in the Brown Booby. Except when in nuptial dress, the male's legs were olive-green and the beak tip a pale flesh, the eye-rim blue, and the facial skin, gulars, and base of beak greenish yellow. During courtship and before egg-laying, however, the legs and gulars turned bright chrome-yellow, and the blue eye-rims became more noticeable. The return to the non-breeding condition began soon after egg-laying; the yellow was lost gradually and remained longest on the gulars. In the female there was also a change correlated with breeding activity, but it was less striking. The facial skin, legs and feet were always pale yellow, but the yellow became stronger during the nuptial period. Females were easily distinguished also by their conspicuous inky patch immediately in front of each eye. The males had a smudge in front of the eye too, but it was a paler blue and not a clear-cut patch.

3. Size. In both species the female was larger than the male. This was less obvious in the White Booby than the Brown, but the members of a pair could usually be distinguished by this means when together. Too few White Boobies were measured to be able to establish whether differences between the means of wing-length, culmen-length and weight in males and females were statistically significant. By considering first voice, then colouration and size, it was always easy to distinguish the male from the female in a pair.

In the Brown Booby the size difference was more noticeable. 14 males and 26 females were weighed and their wings and culmens measured (Appendix B). The differences between the means were significant for all three measurements ( $P < 0.001$  in each case, variance taken into account). Fig.3 shows culmen and wing, and weight and wing, plotted against each other. There is a slight overlap in the weight-wing; weight being the most variable of the three measurements, this might be expected. The sex of juveniles/

juveniles could thus not be reliably determined from measurement alone; in adults the difficulty would not arise because they could be sexed on the basis of other characters.

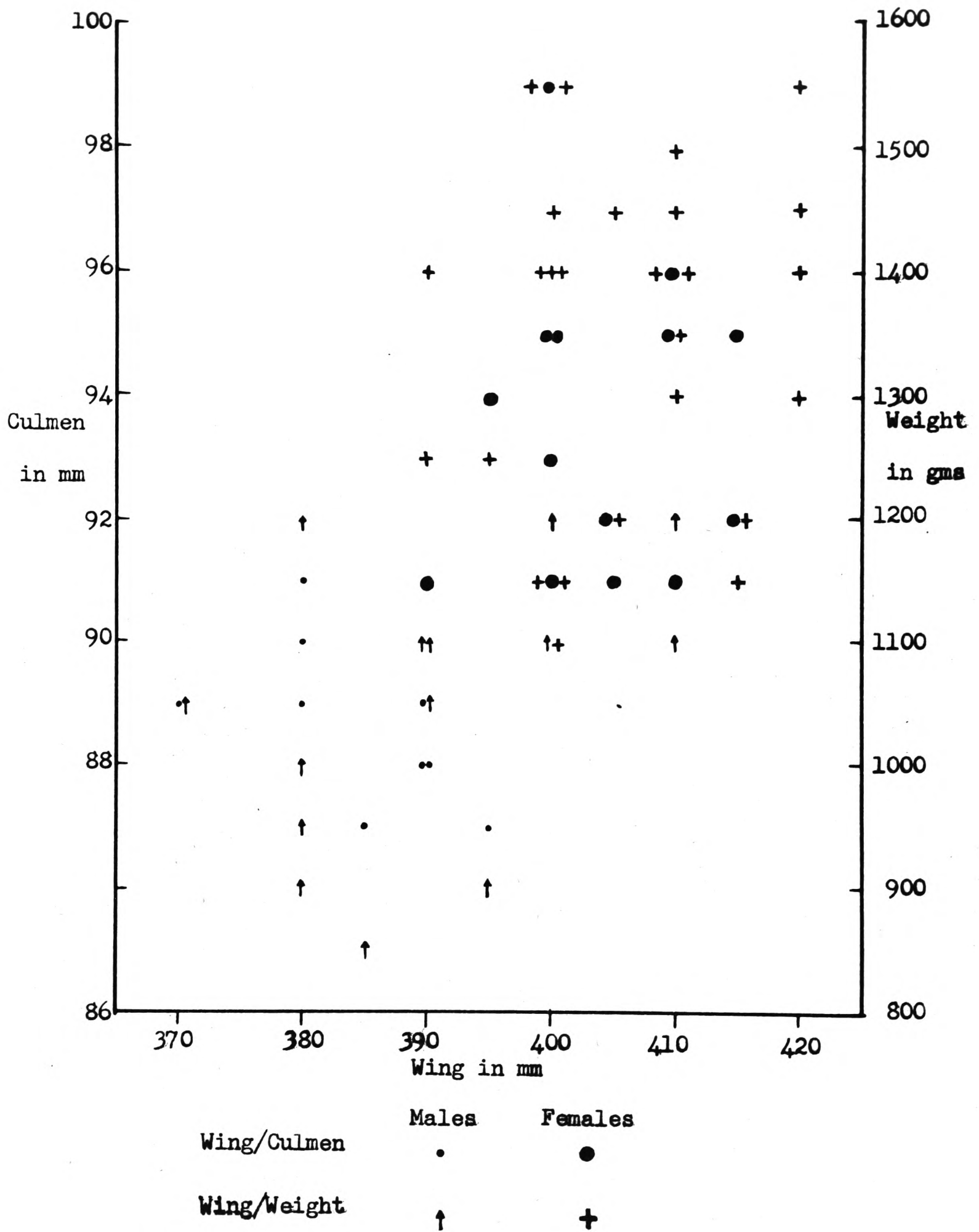


Fig. 3. Difference in wing-length, culmen-length, and weight between male and female Brown Boobies. 14 males, 26 females.

## II BREEDING, PART I: Population, the colonies, breeding seasons.

### White Booby.

#### 1. Population.

I estimated that there were 1200-1300 breeding pairs on Boatswain-bird Island. On a night-time census in March 1959 I found more birds than on any other occasion, and the following figures are based on this. There were about 6,500 non-breeding birds in the "clubs" (see below). In the dark it was not possible to distinguish birds in late immature plumage from adults, but from estimations made during daylight I calculated that about half of these 6,500 would be immature birds. The total number would therefore be about 9,000 birds, made up of 2-3000 breeding adults, 3-4000 "unemployed" adults or young adults about to attempt breeding for the first time, and 3-4000 immature and juveniles (not chicks). It seemed at that time that Boatswain-bird Island could hardly have carried any more White Boobies.

A few pairs bred in other places (see Fig. 1) but not in sufficient numbers to affect the general population figure.

#### 2. The colonies.

The White Booby colonies occupied most of the top of Boatswain-bird Island (Plate 1). A few nests were lower down on level parts such as the path. The nests were most dense on level or slightly sloping parts of the plateau, the steeper parts being occupied by Frigate Birds. The colonies were always occupied by adult birds, their density varying with the time of day and stage of the breeding season. From noon until evening most adults were away from the colonies unless they had eggs or chicks; they began to return at sundown or before, and during the night, at least prior to laying, both members of the pair were present in nearly every territory. When a pair had eggs or a chick, the parent not on incubation duty usually stayed away from the territory/

territory at night. Apart from adults, the only birds in the colonies were chicks of varying ages or recently-fledged juveniles. Once a juvenile had finally left the breeding colony, however, it apparently did not return there until in adult plumage. Even though present on the island, immature birds were never seen on the breeding colonies. Some of the birds on the colonies were unmated, and probably young adults, but they could not be distinguished from the established pairs except by their behaviour (see Section VIII). Territories were strictly defended even outside the breeding season, and as will be seen later, these and the pair-bonds were permanent.

Away from the colonies, in what were obviously traditional places round the edge of the plateau and on the steep edges, there were always congregations of White Boobies which we called "clubs". The birds in them were roughly classified as follows: "near-adults" were birds with only a few brown flecks on back and rump (the sequence of the change from the brown juvenile to the white adult plumage is fully described in Section VI, Molt); "juveniles" were dark brown on back, rump, and head; "immatures" were stages between the two. There were six such clubs. One consisted usually of adults and/or near-adults, one of immatures and adults (usually segregated), one mostly of adults and near-adults but with a few immatures, another mostly of juveniles, and the remaining two exclusively of juveniles and immatures. The numbers in these clubs varied greatly and were highest at night. (This, together with the fact that established pairs tended to return to the colony at night, suggested that the Ascension White Boobies were relatively sedentary and did not spend very long periods away from the island; as will be seen later, this may be important when considering the degree to which the populations of Ascension birds may be isolated from others.) From their different types of plumage it was clear that the juveniles in the clubs were of a variety of ages. Breeding adults also used the clubs, as was shown by marking  
with/

with dyes; adults marked when incubating were later seen in the clubs when the other partner was incubating, and adults dyed while in the clubs were later seen on the breeding colonies in a territory. Ringed unmated adults that I was watching in connection with pair-formation were also seen in the clubs. The activities carried on in them were mostly preening, resting, and sunning. Individual distances were less in the clubs than in the breeding territories, and there was some mutual preening between adjoining adults (irrespective of sex or whether they had a mate elsewhere), between adults and immatures, and between juveniles; but self-preening was most frequent.

### 3. The breeding seasons.

#### a) General.

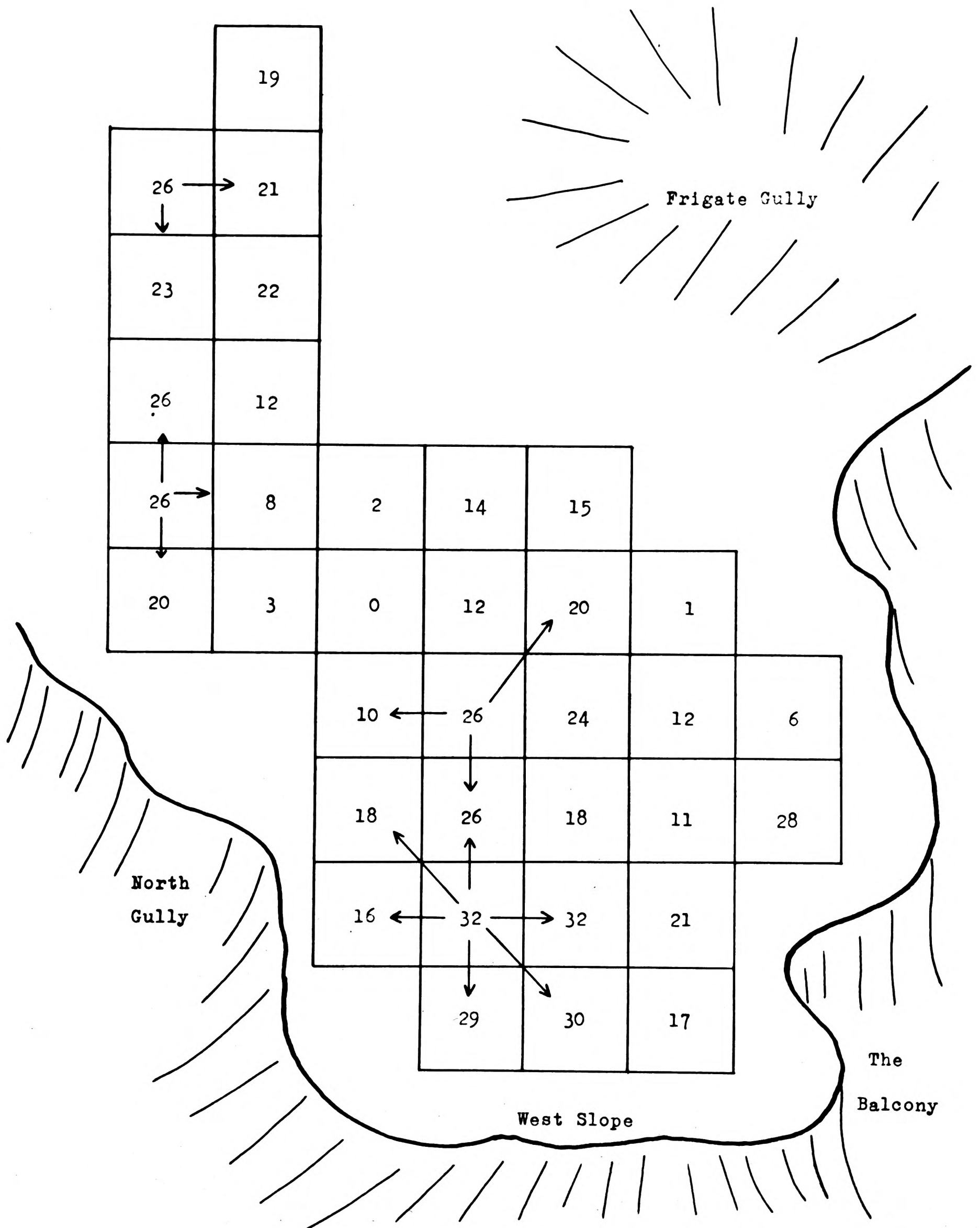
Our first visit to the colony was in November 1957. I found 98 nests with eggs (less than one-twelfth of the total breeding population), and chicks in all stages from newly-hatched to recently fledged, but the majority were at the fully-feathered stage, not yet flying, i.e. about  $3\frac{1}{2}$  months old. On that visit the number of young birds indicated that a breeding season was almost over. Subsequently two areas were selected for special study; one, "Far Area" (Fig. 4), containing about 600 pairs, was marked out as a grid of squares 10 yards x 10 yards, and the contents of each square was checked once a month. In the other, "Hut Area", where there were 70 pairs, each nest was marked and its progress followed more closely.

The date of laying of the first egg was taken as the "fixed point" of the breeding season for each pair. All new eggs were marked with a code indicating their approximate time of laying. All deserted or abandoned eggs, or eggs found out of the nest, and dead chicks, were removed at each visit so that they should not be counted a second time.

The/

Fig. 4. White Booby colony. Far Area.

Number of clutches per 10-yard square, Season II.



Note: Arrows radiate from centres of first laying to areas of later laying.

The numbers of clutches started in each month from December 1957 to April 1959 are shown in Table 1. It can be seen that there was a definite peak of laying, and that laying in Far Area and Hut Area, about a hundred yards apart, was at approximately the same rate throughout the season.

The numbers of clutches laid each month give a clear enough picture of the progress of the breeding season for the months during which I was actually counting eggs. <sup>(Fig 5).</sup> But my deductions about the previous breeding season and the subsequent one require more detailed explanation. For the purpose of discussion I shall refer to the seasons as I (1957, before my arrival), II (as observed), and III (after our departure).

Season I: Observations in Far Area began in January 1958, when there were 23 pairs incubating eggs. As part of an attempt to find out about replacement of lost clutches, all these eggs were removed, the age of the embryos estimated, and the date of laying calculated. From the number of young of various ages, I also deduced that 50 clutches were laid before the beginning of November and an additional 34 in December. These numbers are probably too low because chick mortality was not taken into account. The number of newly-fledged juveniles on the colony could not be taken to correspond to the number of clutches at any particular date because they were not all on the colony at the same time, and also their ages were impossible to estimate. The ages of the downy chicks were only roughly assessed, and dates of laying of the eggs from which they hatched were approximate. However, by comparing later with the situation at the end of Season II, it was clear that the peak of laying in Season I certainly occurred before October, and probably about August 1957.

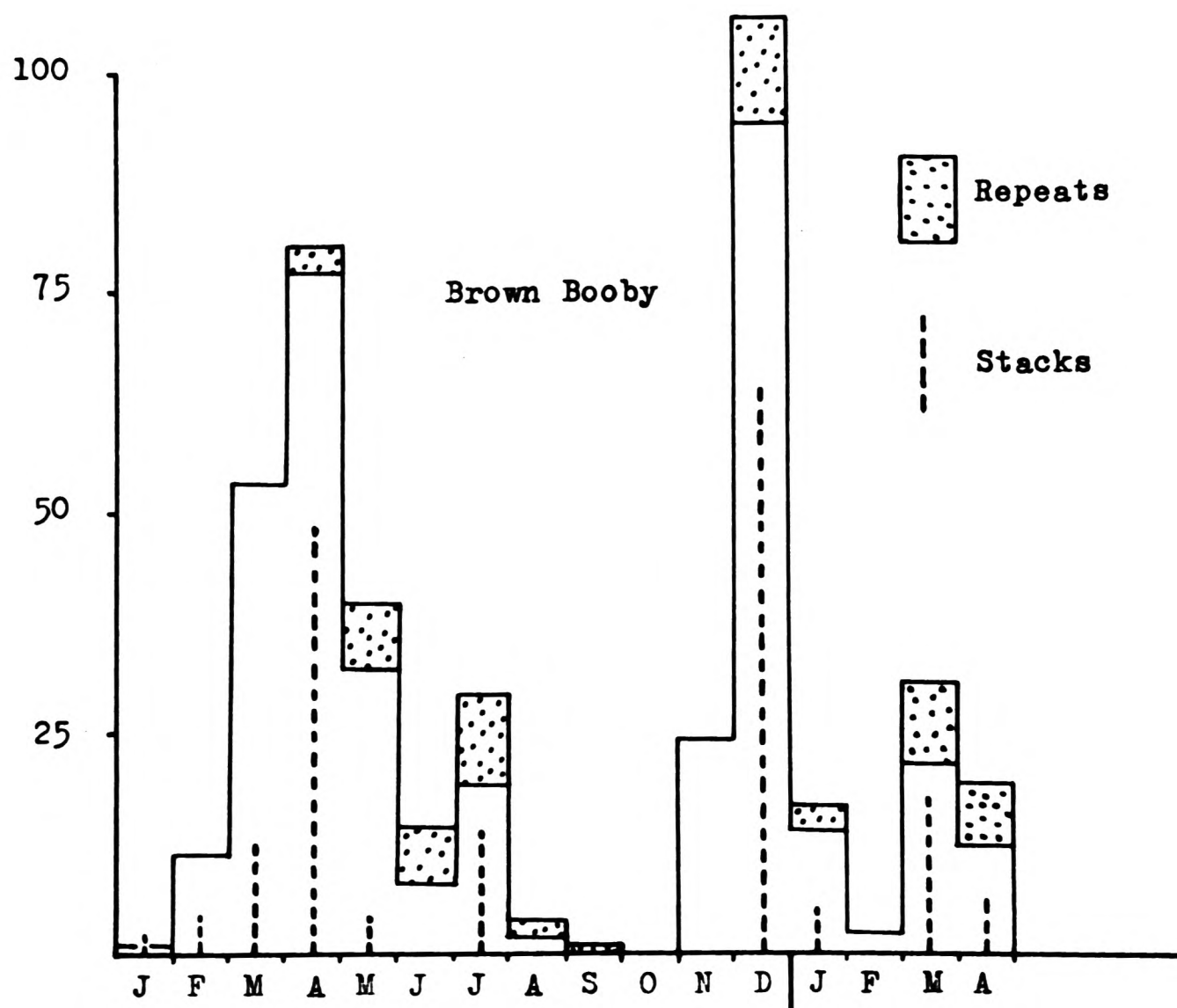
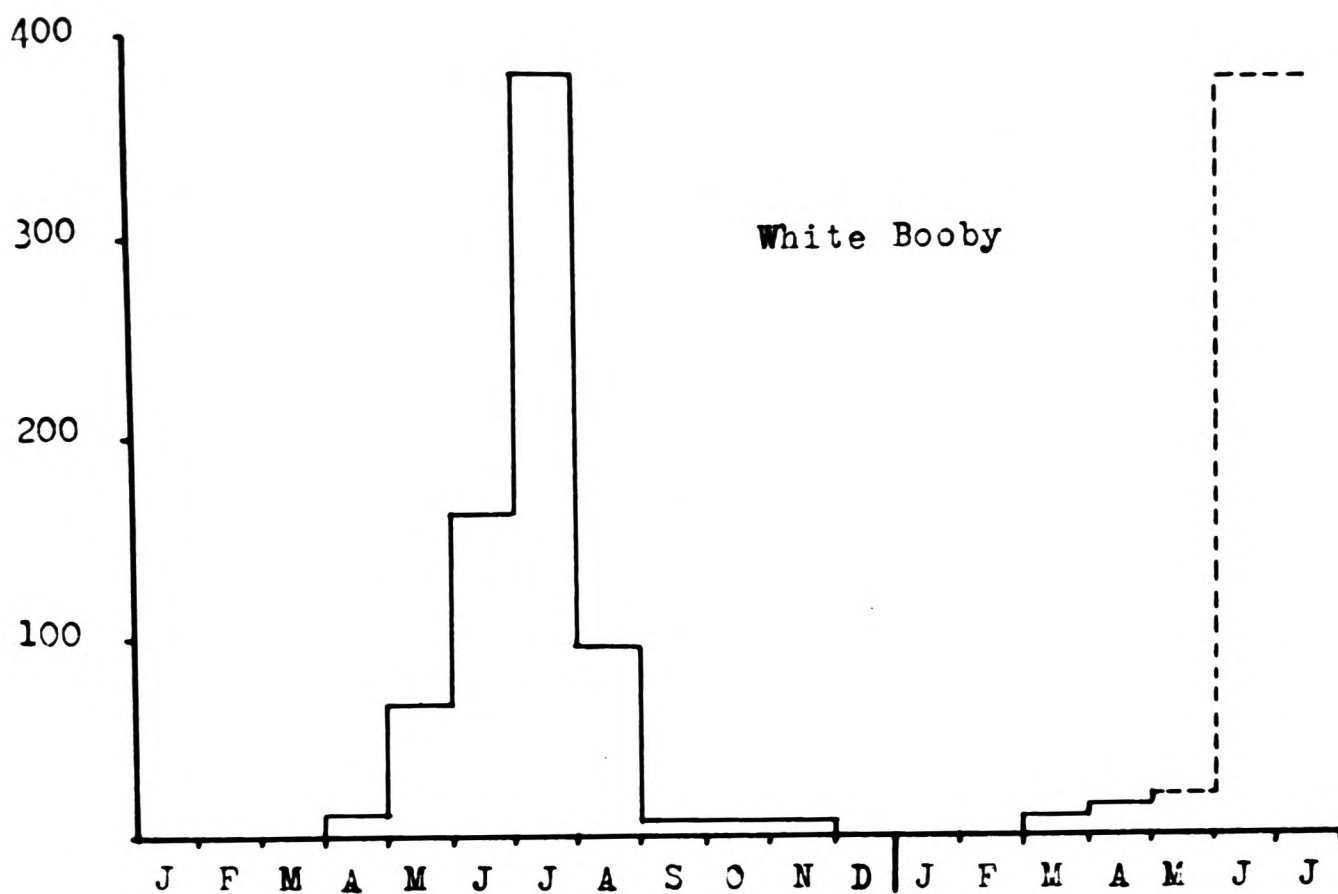
Season II: As mentioned above, Season II clearly had its peak in July 1958, starting in May and ending in August. After that, laying was sporadic until early April 1959, when the number of fresh clutches began to increase, indicating the start of Season III. My last visit to the colonies was on April 5, 1959.

Season/

Table 1. Number of clutches started in each month, White and Brown Boobies.

	1958												1959				
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	
<u>White Booby</u>																	
(Far Area)	4	0	0	5	50	123	358	96	2	2	5	4	1	0	5	9	
(Hut Area)	0	0	0	5	15	24	22	6	1	0	1	1	0	0	2	2	
<u>Brown Booby</u>																	
(Boatswain-bird Island)	1	6	53	80	42	14	29	4	1	0	22	102	17	1	30	19	
(Georgetown Stacks)	3	2	12	48	5	0	14	0	0	0	0	63	5	1	17	7	

Fig. 5. Number of clutches started each month.



Season III. The main evidence for Season III was however obtained by R.G.Allan during his visit to the colonies in July 1959. In Far Area he selected three of the most dense squares and made a count of their contents, describing the chicks so that I could make a rough estimate of their ages. His figures compared closely with mine for the previous season: in the first square he found six clutches, one chick, and 28 abandoned eggs. The latter had been washed out of nests by the prolonged rain mentioned earlier, and I have assumed that these represent 14 clutches. The number of clutches in that square in Season III was thus two-thirds of what it was in Season II. Probably the figures would correspond more closely if, as I think likely, the 28 eggs represented more than 14 clutches, some other eggs having rolled or been washed well away from the square in question. In the second square, Allan found 15 clutches, one naked chick, and three older chicks. Except for the three chicks, this is the same as my figure for Season II. In the third square, Allan's figure of 20 clutches was exactly the same as mine for Season II.

These figures show such a close correspondence that I conclude that there was a peak of egg-laying, in June or early July 1959, which was of roughly the same magnitude as the one that occurred in June/July 1958; I have represented this on Fig.5 as being 350 clutches.

The figures for Hut Area also agreed very closely. Here Season II showed a flatter peak of laying than in Far Area, but it came at the same time; no clutches were laid between August 1958 and the following April. Allan made a complete census of this area in July 1959, and from his descriptions of chicks I was able to calculate that the build-up to the peak of egg-laying was approximately the same as in the previous season. The remarkably close correspondence between his figures and mine is shown in Table 2. He found more chicks at a more advanced stage than I did at the nearest corresponding time in Season II, but his visit was 10 days later/

**Table 2.** White Booby: comparison of a census taken on July 5, 1958 with one taken on July 15, 1959 by R.G. Allan. Hut Area.

Category	No. of examples of each category:	
	<u>Season II (1958)</u>	<u>Season III (1959)</u>
Eggs: 1	12	11
2	22	12
3 or more	1	3 (one 6 and two 3's)
Chicks: Naked	4	1
Downing	0	7
$\frac{1}{2}$ -downed	4	4
Full-downed	3	6
$\frac{1}{2}$ -feathered	0	4
$\frac{3}{4}$ -feathered	1	0
<u>Totals</u>	<u>47</u>	<u>48</u>

**Note:** The later date of Allan's visit explains some of the differences between the two censuses. e.g. 10 days is about the time that elapses between the newly-hatched or naked stage and the "downing" stage.

later in the year than mine. 10 days was about the time that the chick took to pass from the naked stage to being covered with down and from the fully-downed to the half-feathered stage. Hence the two censuses correspond even more closely than it at first seemed.

The general conclusion, then, in spite of rather little information about Season I, was that the White Boobies' breeding seasons occurred at approximately annual intervals.

b) Individuals.

So far, the findings were straight-forward. I also wanted to know how individual birds or pairs behaved in this routine, and what was the length of their sexual cycles. As might be expected, the results of this were less clear, presumably because of the great variability in breeding success, and the spread of laying.

First it should be mentioned that the time taken from the laying of the first egg to the fledging of the chick was about 165 days ( $5\frac{1}{2}$  months). Even after fledging, the chicks returned to the nest site and were fed (or at least begged to be fed) for three or four weeks, and so the length of a successful breeding season is probably close to six months, perhaps a little more.

In order to find out the intervals between successive layings (not replacements) of individuals, 116 adults of 75 pairs were ringed. Since the pairs were permanent I have taken the information from one ringed bird to be true also of the pair, although the mate was not ringed. My observations began so late in Season I that some of the 75 pairs had to be selected from outside the two study areas. Furthermore, I believed that birds with eggs or small chicks in January might be exceptional cases (as later proved true) and so I also selected birds which had well-grown or flying young. The laying dates of these ( $\pm$  one week) were calculated from the measurements of the chicks; in the cases of flying young, as explained above, such estimations could not be closer than  $\pm$  two weeks. As well as these chicks' parents (i.e. the successful breeders/

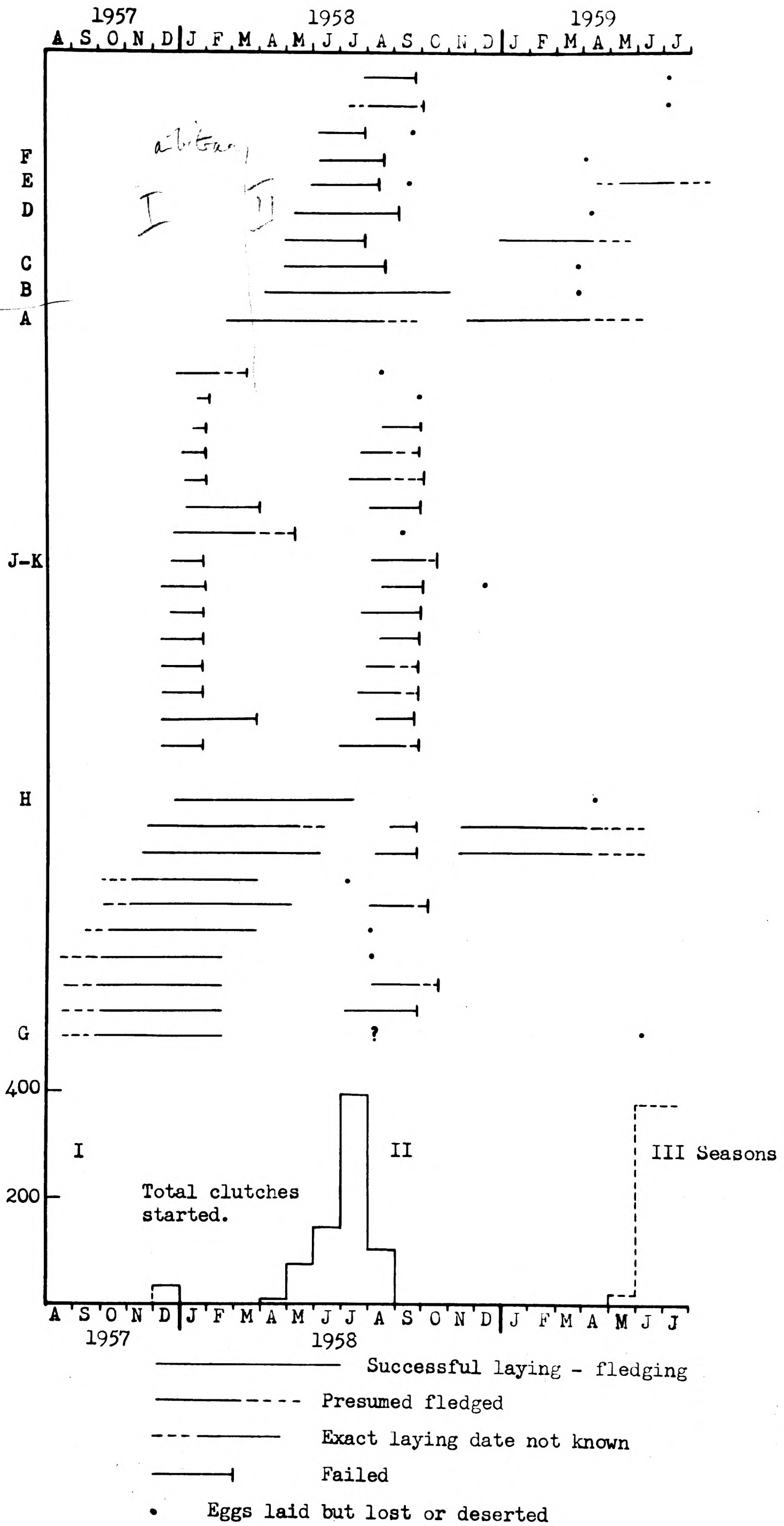
breeders of Season I), I have included the birds whose eggs I removed in January<sup>1</sup>; since many of these would probably have been unsuccessful anyway, (by analogy with late clutches in Season II), I think this does not seriously bias the results. I also ringed adults which laid late in Season I and whose chicks died before fledging. Summing up, the 75 pairs in this study were made up as follows: successful and unsuccessful breeders which laid near the peak of Season I, and successful and unsuccessful breeders which laid late in Season I. I also used birds not known in Season I but which laid near the peak of Season II, were unsuccessful, and laid at a known date in Season III.

Results: Of the 66 pairs that bred in Season I (successfully or not) only 26<sup>5</sup> were found breeding again the following season. <sup>(are doubtful)</sup> The other 40 were all seen at some time during Season II, some more than once, but so far as was known, did not breed. These 40 pairs emphasised the misfortune of not being able to keep continuous records; some of them may have laid eggs and lost them again between my visits, so that although I saw the birds at the peak of Season II I had no means of telling whether they had bred or not (except by dissection, which would have destroyed the chance of later information). The birds' behaviour like-wise did not help, since some pairs were seen intermittently courting, nest building, and even copulating without necessarily laying eggs subsequently. Of these 40 pairs, therefore, it can only be said that none bred successfully in Season II; and if any did lay eggs they lost them again very quickly. The problem was further complicated by the fact that in Season II there were many unsuccessful breeders anyway, the reason for which is discussed later. A few, however, may not have bred in Season II because they had started late in Season I and therefore were not rid of their chicks in time to lay again early in Season II; as I did not follow all such chicks to fledging (or to their death) I do not have full details about this. If such pairs had been going to breed late in Season II, i.e. a year after their previous attempt, they might have been prevented/

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1 Pairs J-K, Fig 6.

Fig. 6. Breeding intervals of individual White Boobies.



prevented from doing so by the same factors as caused so many other birds to be unsuccessful.

The information from the 35 pairs which did breed again is set out in Appendix C and shown in Fig. 6. The cases have been arranged in chronological order showing clearly the birds that laid late in 1957. This slant towards the right, however, is not reflected in Season II, although in one case, A, a pair which bred late in Season I and was successful bred again late in Season II. Five pairs (B - F) which were very early in Season II were equally early in Season III, all thus remaining out of phase with the rest of the population. A successful pair, G, which laid in the middle of Season I, appeared to miss Season II altogether and laid again at the peak of Season III, but they may have laid and lost eggs in Season II without my knowing. The same may have been true of a pair, H, which laid late in Season I, raised their chick successfully, and apparently did not lay in Season II although they were similar in timing to two other pairs which did. Fifteen pairs (J - K) were seen late in Season I to have eggs, lost them, and laid again at the peak of Season II. These eggs late in Season I may have been second attempts after earlier failures.

Brown Booby.

#### 1. Population.

The numbers were more difficult to estimate than in the case of the White Booby, largely because the birds were less sedentary and many nested in inaccessible places. I estimated that there were 600-700 breeding pairs on Ascension, of which two-thirds were on Boatswain-bird Island. I could not estimate the number of immature or non-breeding birds, and furthermore, some adults may have been omitted from the count of breeding pairs because they had lost their eggs. The total population, then, was likely to have been greater than 700 pairs, but how much greater could not be assessed; my guess is/

is that it was not much more than double that figure.

## 2. The colonies.

Brown Boobies nested on the steep higher slopes of Boatswain-bird Island and the broader ledges lower down. A few pairs encroached on to the edges of the plateau occupied by the White Boobies, but generally the two species kept apart. This might have been by preference of habitat, and interspecific fighting over territories was extremely rare, but the general impression gained was that the Brown Boobies nested where they were not pushed off by the White. There were, however, what seemed to be possible nesting places unoccupied by either species.

There were also small colonies of Brown Boobies on each of the Georgetown stacks numbering from less than 10 pairs to about 40 (Fig. 1). All four stacks were treated together when counting the number of clutches, and there was no difference amongst them in the timing of laying. The work done on the stacks was on numbers of fresh clutches, survival of young, and ringing of some adults. Individual nests were not marked.

On Boatswain-bird Island the density of nests in different areas depended on the topography, although even where this was favourable it seemed that the density was less than that in the White Booby. Outside the breeding season, the Brown Boobies were usually absent, and as the breeding season approached, they spent more and more time at their nest sites, coming in at night or early morning before first light and leaving again soon after sunrise. There were no clubs formed by Brown Boobies. Immature birds were rarely seen, and then never more than one or two at a time; six birds, ringed as chicks, returned to the island at 12-15 months old, and stayed near their respective birth places. There may have been places on the inaccessible cliffs of the main island where unemployed adults or immatures roosted in clubs, but I could see no reason why they should do that in preference to staying on Boatswain-bird Island/

Island itself like the White Boobies. The change from juvenile to adult plumage was similar to that in the White Booby (see section on moult) as far as I was able to follow it, and therefore probably continued similarly as far as the adult form; yet no Brown Boobies between the age of about a year and full maturity were seen on the island. One or two birds which had a few brown flecks on the upper part of the white breast (suggesting they were not quite mature) were the nearest approach to a sub-adult condition ever seen. The length of the intervening period was unknown, but by analogy with the White Booby it may have been as long as two or three years; where the immature birds went in this period, I do not know. They may have remained at sea. Certainly the absence of immature birds, which were a feature of the White Booby colonies, was striking.

Summing up, the Brown Booby colonies differed from those of the White Booby in that they appeared to consist entirely of established pairs (but see section on behaviour for some exceptions), with an occasional juvenile which had returned to its birthplace for a short period.

### 3. The breeding seasons.

#### a) General.

Most of the accessible nests on Boatswain-bird Island were marked. Dates of laying and the progress of each nest were checked regularly. Monthly visits were made to the Georgetown stacks, and the number of new clutches recorded each time, all eggs being marked as they appeared. A total of 598 clutches was recorded in the two places of study, and the months in which they were laid are shown in Table 1 and Fig. 5. The results for Boatswain-bird Island and the stacks are given separately, and it is clear that the same course was followed in both, despite their being about eight sea-miles apart.

In December 1957 a few pairs had eggs, but there were also chicks of/

of all ages in the colony. The approximate number of clutches laid between October and December could therefore be calculated, although this must be smaller than the actual number because losses of eggs and chicks could not be taken into account. From January 1958 onwards the pattern of laying was clearer: there were two marked peaks, the first in April and the second in December. There was considerable spread around these two peaks; the laying quickly built up to the peak but fell off slowly. The number of clutches which were second attempts after early losses is shown in Fig. 5; these formed only a small proportion of the totals. Thus the clutches laid in the period following the peak were not only replacements. Judging by later experience of the pattern of laying that followed a peak, and by the ages of the chicks in the colony at such a time in the season, I concluded from what I saw in December 1957 that a peak of laying occurred about the previous August. In the next section I shall show the relation of individual nests to these peaks, and shall refer to the seasons as A (deduced as August 1957, B (April 1958), and C (December 1958). This avoids possible confusion with the Seasons I-III of the White Booby, which were at different times of year. The intervals between the Brown Booby laying seasons were thus approximately eight months.

Four further pieces of evidence in connection with this eight-months periodicity came to light after I had left. Firstly, in July 1959, i.e. seven months after the previous peak of laying, Allan visited the colony and found no eggs and only a very few half-grown chicks in my study area; these few chicks could have been the last stragglers from the December 1958 laying season, i.e. hatched from clutches laid as late as April. The Brown Boobies' nests would of course be particularly susceptible to the effects of the heavy rains, and a breeding-season might have been washed out. Nevertheless, had the birds been present in numbers, Allan would undoubtedly have seen them.

Secondly, on a visit to a small part of the same colony on 9 November 1959, P. Critchley, the Cable & Wireless Farm Manager, caught/

caught nine of my ringed birds. (If a breeding season had not been in progress he would probably not have been able to catch any). Two of them were on eggs and five with chicks, three of the five chicks being large. This means that the season after the December 1958 one must have started later than Allan's July 1959 visit but before October (to allow some of the chicks to become "large"). That peak, around August-September, would be eight-nine months after the previous one.

Thirdly, one of the Cable & Wireless boatmen visited the Georgetown stacks on 16 February 1960 in order to collect Brown Booby eggs required for albumen samples, at my request. He could not obtain any eggs and reported that the birds had not yet started to lay. On 8 March following he again visited the stacks and returned with 10 fresh eggs (containing undeveloped embryos) selected from nests containing a single egg (A.R. Harrison, Cable & Wireless Manager, Ascension, in litt.). In my experience, the chance of finding ten nests on the stacks with fresh eggs was very small, except at the start of a breeding season. I have already shown that in both the breeding seasons I observed, the pattern of laying on the stacks was very similar to that of the Boatswain-bird Island colony, and I therefore conclude that a laying peak occurred about March/April 1960.

Fourthly, H. Hirth of the University of Florida, who was studying the Ascension turtles, visited Boatswain-bird Island at our request on 28 April 1960. He caught 10 ringed Brown Boobies, eight with eggs and two with chicks. This undoubtedly shows that there was a considerable amount of breeding activity at that time, and supports my conclusion that there was a laying peak at Ascension in March-April 1960.

The approximate dates of the five laying peaks between August 1957 and April 1960, and the intervals between them, are set out in Table 3. I conclude that at Ascension the Brown Booby has a sexual/

**Table 3.** Brown Booby laying peaks and intervals between them.

Date of peak	No. of months interval
c. Aug 1957	-
Apr 1958	c.8
Dec 1958	8
Aug-Sep 1959	8-9
Mar-Apr 1960	6-8

sexual cycle of about eight months; that is to say, a breeding season occurs three times in every two years.

b) Individuals.

The time from egg-laying to fledging of the chick was approximately the same as in the White Booby, i.e. about six months. Young Brown Boobies were seen intermittently at the nest-site up to four weeks after first fledging, and begged for food, but their parents were obviously intolerant of this and I do not think the chicks could be described as wholly dependent on their parents for food at that age. Thus although the Brown and White Boobies took the same length of time to raise a chick, the former started to breed again after a much shorter interval.

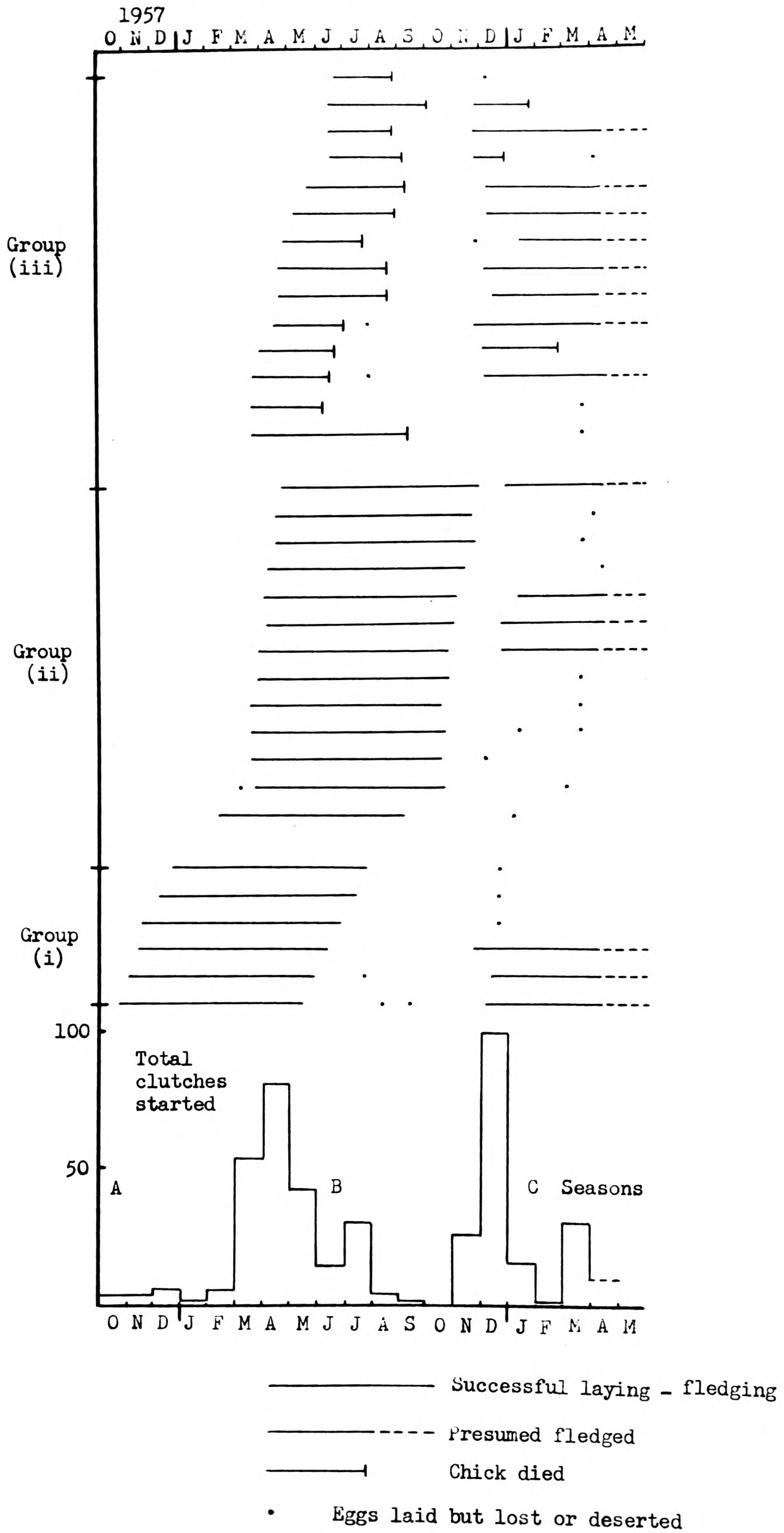
Because Brown Boobies were more difficult to catch than Whites, different methods were used to discover the intervals between successive layings of individuals. 32 ringed birds nested a second time in exactly the same spot as the first, and there were no exceptions; consequently I assumed that wherever this happened the same birds were involved. If there was any doubt about the site of a nest being the same as in the previous season, it was excluded from this study. Thus 112 pairs were used to determine breeding intervals. The results are shown in Fig. 7.

The pairs fall into five categories:

i) Six which laid in the latter part of Season A, and raised a chick. All missed the peak of Season B (the chicks were dependent until then), and four of them missed Season B altogether. The other two attempted to breed late in Season B, one of them making a second attempt after losing the first clutch. All six laid again at the peak of Season C.

ii) Thirteen pairs which laid at the peak of Season B (one rather early) and raised a chick. Seven of them laid again at the peak of Season C, while the other six missed the peak but laid later, at the "secondary" peak. The latter six may have laid also at the peak/

Fig. 7. Breeding intervals of individual Brown Boobies.



peak and lost their eggs without my knowledge, in which case their observed clutches would be replacements.

iii) Thirteen pairs which laid about the peak of Season B and hatched chicks, but all the chicks died at varying ages. All but two of the thirteen laid again at the peak of Season C, but these two, as mentioned in ii), may have laid and lost their eggs without my knowledge. All eleven laid their first egg of Season C earlier than those Season B birds which raised a chick (group ii), with one exception.

iv) 79 pairs not shown in Fig. 7 whose laying dates were spread over the whole of Season B and whose eggs were lost before hatching. In spite of this spread in Season B 70 of them laid again all close to the peak of Season C. The other nine were not known to lay at the peak, but did so at the secondary peak; again these may have been second attempts, the first perhaps being unnoticed.

Summing up, pairs which were successful tended to lay again after about eight months; unsuccessful pairs or those out of phase with the majority tended to shorten or lengthen their interval to the next laying so as to come into phase again. Because there was a big spread of laying, and great variability in breeding success, an average of all the intervals between successive layings does not come to eight months. The behaviour of individual pairs therefore should be viewed in the light of the seasons for the population as a whole.

#### Conclusions.

In both species there were clearly-marked peaks of laying, with intervening periods when the number of new clutches was very small. In the White Booby breeding appeared to be annual, in the Brown, about every eight months. But in both species the time taken to complete breeding, from laying to the fledging of the chicks was the same, viz. six to seven months.

In the White Booby, successful pairs, whether they laid at the peak/

peak or late in the season, came into phase again in the following season; the "rest" period was thus shorter in some birds than in others. Pairs that laid late in the season and were unsuccessful also tended to come into phase in the following season; their "rest" period was thus longer, and they did not attempt to breed again out of phase. Pairs that laid late in the season and were successful either laid late in the following one (because they were not free of their chick in time) or missed it altogether. Again they could have bred out of phase, but did not, and instead the "rest" period was extended until the next season. The general tendency, then, was for individual pairs to conform to the breeding season of the population as a whole, but there were some exceptions.

In the Brown Booby, pairs which laid at the peak of a season and were successful were ready to lay again, and did, near the peak of the following one. Their "rest" period was therefore short. Pairs which laid late in a season and raised a chick were not ready to lay at the peak of the following one and either laid late in it or missed it altogether and laid at the peak of the next season. Some pairs laid at various times throughout the season and lost their chick before fledging; they thus became free, theoretically, to lay again at an even greater variety of times, but instead of doing this they became synchronised once more by laying at the peak of the following season. The same was true of the many pairs that laid at varying times throughout the season and lost their eggs; instead of repeatedly attempting to breed again, they waited until the following season. Thus those that laid late in the season had a shorter "rest" before the next attempt than did those that laid early. This is shown in Fig. 7, where the slope to the right in Season B is not reflected in Season C.

During my study, the two species differed not only in the periodicity of their sexual cycle, but also in the time of year at which they laid. It should be stressed that the periodicity was such that every two years, if the same periodicity was maintained by both species/

species, the Brown Boobies would lay at almost the same time as the White Boobies, viz. in August or September. The importance of this is discussed later.

The significance of the intervals between laying of individual pairs lies in their variation, showing that some external stimulus must have been modifying the internal physiological cycle. The interval was long or short, such that the breeding season conformed with that of the majority, i. e. some pressure was tending to make most birds breed at the same time. In the Brown Booby this pressure apparently acted in the same way on two colonies as far apart as Boatswain-bird Island and the Georgetown stacks. This suggested that the external stimulus or stimuli involved were environmental and not purely social, and is discussed further later.

#### Non-breeding.

Hitherto I have been concerned only with the positive evidence about breeding in both species. Some negative evidence should now be mentioned. I have already stated that of 75 pairs of White Boobies marked while breeding, only 35 were known to breed again the following season. The Brown Boobies were similar: 17 pairs were successful in Season B and bred again the next season, (group (i)), but another 17 such pairs were not known to breed again; 13 pairs were partly successful but lost a chick before fledging (group (iii)) and bred again, while nine similar pairs were not known to breed again; and though 79 pairs that lost their eggs (group (iv)) did lay again next season, another 51 apparently did not. Less was known about individual pairs here than in the case of the White Booby, where (as mentioned earlier) most of the pairs in question were known to be present on the colony and either laid without my knowing or did not lay for some other reason. Fewer Brown Boobies were ringed -- 13 pairs out of the 77 in question -- and therefore it was difficult to obtain information about them.

The possibilities were as follows: Firstly, the birds that were not/

not known to breed in the next season might have died. This seemed unlikely because of the large numbers involved; and of 17 ringed birds, four were seen again at their old nests, showing that at least some did not die. Secondly, some may have moved to different nest-sites in the next season, perhaps because of a slight change in topography due to a land-slide; none of 32 known pairs did this, so probably it is unimportant. Thirdly, nest-markers may have been lost or displaced. I know this happened in about 10 cases because I found the markers later. If a marker had gone, or been covered up, I had to regard a nest as a new one and discount it from the study of breeding intervals. To search the whole study area for concealed markers was impossible. Thus in perhaps ten cases birds may have bred in the same place and yet been recorded as new nests. Probably all three factors were concerned to some extent. In addition, of the 17 successful pairs from Season B, I know that three could probably not have bred again in Season C because they were not free of their chicks in time.

There were 189 clutches in the five months of Season B (second attempts excluded), while for Season C (same period of time, same area, and including new nests) the total was 156. This suggests that even considering the above three factors, there were still fewer birds breeding in Season C, and that the difference in numbers between the two seasons was not wholly due to inaccuracies of recording. Probably, therefore, in both species at least some of the pairs not known to breed a second time really did not do so. This requires some examination.

It should be noted first that it was not the habit of any particular category of birds to miss a season, because the non-breeding pairs in both species came from all the categories of the previous seasons: successful and unsuccessful, late and early.

I think that non-breeding was a result of lack of food.

Evidence that a food shortage occurred at Ascension was found during September and October 1958, when chicks of both species lost weight/

weight or died of starvation, and eggs were deserted. This is fully documented later. Adult Black Noddies *Anous minutus* were seen attempting to feed starving chicks but were unable to regurgitate any food (N.P.Ashmole, personal communication), and many of the chicks died. Although neither of the Boobies was laying in numbers at this time, (the peak for the White Boobies being in the previous July and for the Brown in the previous April and again not until the following December), the food shortage could have extended outside the period in which it was observed, and might therefore have prevented breeding in a proportion of the population. It has been recorded (Murphy, 1936, and Hutchinson, 1950) that on the guano islands off Peru and South West Africa, during times of disturbance of the cold current and consequent shortage of fish, the guano birds deserted eggs and chicks, or left the breeding colonies without attempting to nest.

Food shortage, then, was a possible explanation of the non-breeding on Ascension. How it may have operated is discussed in more detail later.

Breeding seasons in other parts of the world.

#### 1. The races of the White and Brown Boobies.

A taxonomic analysis of the two species is not one of the objects of this paper, but before discussing breeding seasons in other parts of their ranges, it is as well to consider the relationships between the races. Both species, broadly speaking, are distributed all over the tropical oceans, except that there are very few records of the White Booby breeding in the west Atlantic and Caribbean, and the Brown apparently does not breed in the west of the Indian Ocean or in the Galapagos Islands (see Appendix D).

The White Booby is regarded as one species throughout its range (Peters, 1931). Rothschild (1915) gave subspecific rank to races from the Atlantic, Indian Ocean, West Pacific, California and South/

South American coasts, and the Galapagos, all on the basis of the colouration of soft parts. The colouration of soft parts varied considerably in the Ascension birds, even in the same individual at different times of year, and I therefore doubt if true differences can be established on this basis. There are too few skins in the British Museum (Nat.Hist.) for a comparison of the races to be made on the basis of size, but there appears to be some variation; the race from the West Pacific and Australasia (subspecies personata) in particular is larger and more heavily built than any of the others. Murphy (1936) found that birds from the Pacific were larger than those from the Atlantic.

The Brown Booby, likewise regarded as one species and likewise represented in the British Museum by too few specimens for a full study, also shows size differences between the races. Robinson & Kinnear (1928) measured skins from the Atlantic, Pacific, and Indian Oceans, and found no difference between the three means of wing-length<sup>and</sup>/culmen. I believe, however, that it is misleading to consider all the birds from as large an area as an ocean to belong to a single race. I found, for instance, that the mean culmen-length of Ascension birds was less than the mean of all other races considered together, although there was no difference in wing-length (Table 4).<sup>1</sup> A greater difference, however, was found if the Ascension birds were compared not with all the other races, but only with birds from the C. Verde Islands: five females from there had a mean wing-length of 425 mm and a mean culmen-length of 100 m.m. These figures are respectively 19 mm and 6.5 mm greater than the figures for Ascension. I therefore believe that one cannot consider all the Atlantic

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<sup>1</sup> This might conceivably have been due to the facial skin of dried specimens having contracted away from the beak, thus giving a longer culmen measurement.

**Table 4.** Mean wing and culmen measurements of Brown Boobies; Ascension population compared with others.

	Males:			Females:		
	No. of birds	Wing	Culmen	No. of birds	Wing	Culmen
Ascension	9	390	89	14	406	93.5
Rest of world	10	387	95	15	409	99

**Note:** All measurements in mm.

populations as a single race, and a full study might reveal the existence of a cline. Chasen (quoted in van Bemmelen & Hoogerwerf, 1940), referring to the races of Brown Boobies in the Indian Ocean, said, "Almost every breeding colony could be separated on some difference or other ...". This may well be true of other areas besides the Atlantic and Indian Oceans.

If most of the breeding populations are at least partly isolated, as the above evidence suggests, it is possible that a variety of different breeding rhythms has been evolved, depending upon local factors, and this must be remembered when considering breeding seasons throughout the Boobies' range; it should also be remembered that my findings about the Ascension population may not necessarily be true of what ~~it~~ is at present considered to be the same species elsewhere.

## 2. The published records.

Many records of breeding of White and Brown Boobies have been published. Some of these may not indicate the true breeding season. For instance, there were many months when I could have said of the Ascension birds that there were eggs and young of all ages, and on a single visit at any of these times I could have believed them to be in process of breeding; but there were very few months in which there were no eggs at all. This could explain why nearly all the published records give positive evidence of breeding. This information is set out in Appendix D.<sup>1</sup> Vague records of birds "breeding" or "nesting" have been excluded in the light of my experience on Ascension, and only those in which it was actually stated that eggs or chicks were seen are included. Even so, the above qualification holds. Few conclusions can therefore be drawn, except that more long-term study is needed.

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<sup>1</sup> All authors are cited in the Appendix and are therefore excluded from the text here.

a) **White Booby:** In the Indian Ocean the White Booby appears to breed annually on Latham Is. and the Seychelles, and also, but at a different time of year, on the more easterly islands of Cocos Keeling and Goenoeng Api. It is said to do the same on Willis Is. near Australia, on Canton Is. in the central Pacific, and in the Hawaiian group. In the Galapagos, except for one record, breeding has been reported only in the late and early months of the year. No author has suggested that the bird anywhere breeds at intervals that are not annual, although several have noted that it might have a long season.

Past records from Ascension itself are few. Sir David Gill (in Penrose, 1879) reported breeding in January 1878, but his impression might have been gained from the mere presence of the birds, and this need not mean that they were breeding. Simmons (1927) showed a photograph, taken in December 1925, of part of the Boatswain-bird Island colony which I knew well, and it can be seen that although an average number of adults were present, none of them was incubating and there were no chicks. This is particularly interesting because it is exactly what I would expect if the previous breeding season had been in July.

b) **Brown Booby.** It is noticeable that all the Caribbean records of Brown Boobies breeding are in January or February, and all are from different years. Phelps & Phelps (1959), however, indicated that breeding continued well after that, even until October. Both records from St. Paul's Rocks (1902 and 1921) indicate breeding in November and December. The three records from the Indian Ocean, again all in different years, suggest that breeding is in the early months of the year.

Looking at all the records together, it can be seen that nearly every month of the year is represented; an uncritical interpretation of this would be that the Boobies bred all the year round./

round. But it should be remembered that where any bird has a sexual cycle that is not annual, records from different years will inevitably suggest that it lays eggs throughout the year; and statements of this sort have indeed been made.

#### Discussion of breeding seasons.

That breeding appears to occur at different times of year all round the world may be attributed to variation in latitude and climate, for some of the localities are subject to definite periods of rain and wind. The factors controlling breeding in the Ascension boobies cannot be suggested with full certainty since the seasons witnessed might not have been truly representative. It might be argued, for instance, that since the Brown Boobies' Season B was largely unsuccessful, the following one may have begun as soon as possible, perhaps as soon as the shortage of food was relieved. However, successful pairs bred again just as did unsuccessful ones, whereas if the intrinsic cycle were annual, this would not have been the case. Furthermore, the evidence about the breeding seasons subsequent to the period of study suggests that my conclusions are correct, and I shall therefore discuss the breeding seasons as if what I observed was normal at least in rhythm if not in success.

It has been shown by many workers (and reviewed, e.g. Lehrman, 1959) that in birds the timing of the breeding season, and indeed whether breeding takes place at all, is controlled by seasonal variation in such factors as day-length, temperature, food-supply, and availability of nest-sites, these environmental variables acting as the internal physiological cycle allows. I do not know the length of this cycle in boobies, but it must be less than 35 weeks in the Brown: the time between successive layings, a chick being successfully raised from the first, was known in six cases and the mean of these was 35 weeks. The White Booby took roughly the same time over its breeding season as the Brown, and one might therefore assume that their/

their sexual cycles should be the same length. This was not the case. It would therefore seem that the White Booby at Ascension was not breeding as fast, so to speak, as it might have done.

It has been said (Marshall, 1959) that birds emerge rhythmically from their regeneration phase (of the gonads — see Marshall, 1954, for histological details of gonad cycles) at periods characteristic of the species, from which "it follows that the length of the period may be a powerful factor in the regulation of their reproductive date". Nevertheless, such characteristic internal periodicities must have been arrived at by a process of natural selection; and, further, presumably these periodicities would not be maintained unless the selective factor or factors — which must be environmental — continued to operate. An effect of this sort has been postulated by Miller (1959) in Zonotrichia; birds from an equatorial region, where breeding is six-monthly, had a much shorter post-juvenile "refractory period" than relatives from higher latitudes where breeding was annual. Thus although the White and Brown Boobies may now have internal cycles of different length, it should still be possible to discover the factor or factors regulating these. If there were no regulating factor, some boobies would presumably breed at all times of the year, each individual maintaining the periodicity characteristic of the species, but breeding independently. Far from this being the case, the breeding seasons of both species were well-marked, only a small proportion of birds breeding differently from the main body.

The commoner factors controlling the timing of breeding in most bird species have been mentioned above. Marshall & Roberts (1959) hoped to uncover the factors responsible in a species not subject to these obvious influences by investigating a colony of Cormorants Phalacrocorax carbo and P. africanus on Lake Victoria (Lat. 0° 20' N) where climate and day-length were not expected to show seasonal/

seasonal variation and food was abundant throughout the year. They found, however, that breeding was influenced by scarcity of nesting sites and an annually occurring period of bad weather which prevented the reproductive cycles being synchronised in all the individuals of the colony. They suggested that nevertheless the Cormorants probably possessed a sexual rhythm comparable to that of the Ascension Wideawakes, in which the breeding seasons are synchronised and occur regularly at intervals of about  $9\frac{1}{2}$  months. By analogy with the Wideawakes, the boobies' seasons should have been synchronised and regular, since there was no variation in climate or availability of nest-sites throughout the year. This appeared to be the case, with the notable difference that the cycle in the two species was not the same.

Some regulating factor other than availability of nest-sites or climate must therefore have been operating. Apparently the only two remaining possibilities are social stimulation and the food supply.

Whether social stimulation was important or not is difficult to establish. Even if it were, it could presumably act only by compressing the breeding season, and the question of why the White Booby should have an annual cycle and differ from the Brown would still not be answered. In the White Booby, laying did not begin uniformly all over the colony. For instance, in Far Area there were three centres where the first clutches were laid; in Fig.4, arrows from these centres show that laying spread from there to neighbouring squares, and the figures for the number of clutches in each square show that laying began first in the most densely populated areas. But laying did not proceed concentrically over the whole colony. Thus social stimulation might have been having a local effect, a synchronisation within a synchronisation. In the Brown Booby the Boatswain-bird Island birds laid in phase with those on the Stacks, which suggested that some other factor was responsible here, social stimulation being unlikely at such a distance. (Nevertheless a small/

small colony of Wideawakes on Boatswain-bird Island laid in phase with the main island population.)

Bourne (1955 and personal communication) found that in the Cape Verde Islands the different colonies of Brown Boobies were not synchronised in time of laying, although there seemed to be a general uniformity in times of breeding within each colony.

Coulson & White (1959) showed that in Kittiwake colonies, after allowing for possible effects from different physical conditions, laying was earliest where nests were most dense. Thus even in a species whose breeding season is timed primarily by climatic factors, the effect of social stimulation is still apparent. In the same way, social stimulation could be having a subsidiary effect on the laying of the boobies, but it by no means follows that this was determining the general time of breeding.

There remains the question of the food supply. The food and feeding behaviour of the two boobies is discussed later, but this study was limited in scope, and very little is known about the most important problem, the availability of food in the sea round Ascension. We could not investigate this ourselves, so the question cannot be answered conclusively, but cyclic variations in oceanic conditions might have been the first link, so to speak, of a biological chain culminating in variations in the birds' food supply. The possibility of such oceanic conditions operating at Ascension is discussed below.

#### Cyclical variation in oceanic conditions.

In some places, the food supply of seabirds is known to fail suddenly, and it may also fluctuate in the other direction, although less is known about this. The most striking and well-known cases, as mentioned earlier, occur off the west coast of South America, when the cool Humboldt Current is sometimes replaced by the warm equatorial water from the north, known as "El Nino". The seabirds, deprived of their food, die in catastrophic numbers or migrate away/

away (Murphy, 1936). Because of the commercial importance of the guano islands, these events have been recorded for nearly a hundred years, and it appears that periods of catastrophe occur on an average about every twelve years, but not regularly. Hutchinson (1950) has analysed these records, and also those from the west coast of South Africa, which because of its geographical similarities, undergoes similar phenomena; the Benguela Current, with its upwelling of cool water, provides resources which culminate in food for the seabirds nesting on the islands there. Commercial interests in the guano have again provided records of events, since 1881, the variation in the guano crop indicating fluctuations in the sea conditions. Hutchinson considered only the years in which there was a definite effect on the birds, other years, when bad crops were a result of heavy rain washing away the guano, being excluded. There seemed to be a tendency for the events on the South African coast to precede those on the South American coast; the complexity of factors involved in the South African phenomena, however, made detailed comparison unprofitable. Nevertheless there was an implication that there might be a link through some long-period oceanographic change propagated through the Antarctic Ocean. Hutchinson concludes, "If further observations confirm this very tentative suggestion, it is obvious that the phenomena will acquire extraordinary oceanographic significance". Petterson (1929), less cautious, considered that periodic changes in climate of widespread effect have a proximate cause in the outbursts of ice from the Antarctic shelf. He also considered that the Humboldt, Benguela, and West Australian Currents all had their origin in the Antarctic Ocean, and explained their periodic anomalies as being due to increases in their flow, which in turn, because of the earth's rotation, increased their deviation away from their respective coasts, the way thus being opened/

opened for the descent of the warm tropical current from the north. Bowman (1930) apparently doubted the validity of such a generalisation, but admitted that the charges that take place on so colossal a scale in the movement of ice out of the Antarctic could hardly be without climatic effect. Deacon (1933) showed that the deep ocean currents were influenced by the Antarctic Icecap as far as about  $30^{\circ}$  N. Hardy (1936) described how Deacon found in this north-moving water waves of varying salinity and oxygen content, believed to be the result of winter and summer melting of the Antarctic ice, and thus showing that the Antarctic water takes about seven years to reach the northern hemisphere.

Now Ascension lies in the path of the equatorial current which is a continuation of the Benguela Current. The tropical convergence (Deacon, 1933) runs almost diagonally across the South Atlantic between Ascension and St. Helena, roughly 200 miles south of the former. The position of this line is due to the influence of the Benguela Current in the east and the southerly Brazil Current in the west. Thus it seems reasonable to suppose that Ascension could come within the sphere of influence of these oceanic phenomena, even if only in a modified form.

The features of catastrophe years in both Humboldt and Benguela Currents appear to be similar; one of these features is unusually heavy and prolonged rainfall. Ascension is occasionally subject to periods of unusually heavy rain; one such period lasted roughly from May to July 1959, and was preceded, as will be shown, by a shortage of food for the local seabirds around September 1958. A previous period of heavy rain was recorded in 1924, when the Wideawakes' eggs were washed away (Huckle 1924); Hutchinson (op.cit.) gives 1924 as a year in which fish were scarce round the South Africa guano islands. At first sight it is tempting to correlate these events, but the reasons behind local climatic anomalies are so variable that it would be imprudent to do more than mention them here.

It/

It may be remembered, however, that unusual disturbances in the lives of the seabirds — or rather, in the sea, with consequent effects on the birds — are not likely to be detected unless they are of considerable magnitude, or of commercial importance, or the subject of a special study. Thus, although a catastrophe year would be very marked on the west coast of Africa, and although its peripheral effects, as explained above, might reach Ascension, they would be so modified as to escape notice unless revealed by a special study such as I made.

It must be stressed that such out-of-the-ordinary events, although temporarily important, need not be postulated as the permanent factor regulating breeding seasons; but they could be the extremes of a regular cycle, perhaps with its basis in the seasonal melting of the Antarctic ice. Such a regular cycle could result (although the connection is not yet clear) in a regular, though perhaps small, fluctuation in availability of food, enough to establish regular breeding seasons among the birds.

The eight-monthly cycle of the Brown Booby, however, is difficult to account for on this basis. Nevertheless, an eight-monthly cycle means that a breeding season will occur at the same time every second year, and this could be interpreted as a regular bi-annual cycle with an extra breeding season in each two-year period. If the interpolated breeding season was ever successful (and with a fairly constant food supply it might be), then selection would operate in favour of its retention. In this way the timing of the Brown Boobies' breeding could be dependant, like that of the White Boobies, on an annual cycle in the sea.

### III BREEDING, PART 2: Clutch, incubation, brooding, desertions.

#### 1. Clutch-size.

Both species laid two eggs.

On the White Booby colonies in November 1957 I found 69 clutches of one and 27 clutches of two eggs (mean 1.3), but it later appeared that any such count would give a misleading result. Both species rolled eggs into their nests from nearby, and eggs were lost. As a result, White Boobies with three eggs were occasionally seen, there were single cases of five, six, and seven eggs in a nest, and unattended eggs lay all around. Such collections of eggs were not seen in Brown Booby colonies, probably because of the topography; eggs kicked out of a Brown Booby's nest would likely break or fall over a cliff. Nevertheless I found three cases of an egg marked in one nest being incubated in another, and twice, marked chicks a few days old were found being brooded in other nearby nests.

The boobies' attachment was to the nest-site and not to the eggs or chicks, even though the nest site in many cases was hardly distinguishable from the surrounding ground. Birds whose eggs had been removed or lost returned to the nest and sat down in the incubating position, though they gave this up after about a day. Both species accepted and incubated eggs of Storm Petrels Oceanodroma castro and Frigate Birds. One pair of White Boobies was found to be incubating an egg-sized stone, and others readily accepted stones if their eggs were removed. North (1946) and Murphy (1936) have also reported this in White Boobies.

Ten White Boobies in a test rolled an egg into the nest if within beak-reach, but if beyond this the egg was ignored. The number of eggs already in the nest apparently did not matter; one female continued to roll in eggs from 15 cms. until she was sitting on seven, when she became restless.

Brown/

Brown Boobies took instant flight from the incubating position when alarmed, and eggs must sometimes have been kicked out by the push of launching. This would however not account for the many eggs lost when the birds were not alarmed by our presence, or for the numerous losses of White Boobies' eggs which were laid on level ground.

One Brown Booby only was definitely known to lay three eggs, its nest being close to a rock face such that an egg could not have got into it from elsewhere.

Summarising, both Brown and White Boobies laid two eggs, probably very rarely three, but it would be misleading to give the clutch-size as a fraction. Eggs were lost from nests and others were rolled in to augment or replace the clutch, thus making the estimation of clutch-size by sampling impossible.

## 2. Incubation.

a) Incubating behaviour: Neither species has a brood-patch; the eggs are clasped between the feet and the incubating bird rests on its tarsi, which are flat on the ground. The outer toe of each foot is also on the ground, the other toes and webs being spread over the eggs. Clearly it would be difficult to incubate more than two eggs in this way, and a clutch of three is rare in the Sulidae; the Gannets (Morus spp. - Peters, 1931) lay only one egg, possibly because they breed in cool climates and could not easily keep two eggs warm. During incubation the webs of both Brown and White Boobies were more vascularised than at other times. This method of incubating is similar to that described in the Gannet (Gurney, 1913, and Witherby et al., 1940) and in the White Booby (Murphy, 1936); presumably it is common to all the Sulidae. I do not know of it in any other family, and neither Phaëton nor Fregata, the only other genera of Pelecaniformes on Ascension, incubated in this way. The Shag Phalacrocorax aristotelis incubates with the eggs on top of the feet (Snow, 1960).

Incubation/

Incubation began as soon as the first egg was laid, and lasted 42-46 days in the White Booby and 43-47 in the Brown. Kendeigh (1952) gives 42-45 days as the probable incubation period in the Sula species. The second egg was laid, and consequently hatched, about five (occasionally four or six) days after the first.

b) Attentive spells: On the average, male and female took equal shares of the incubation, but the length of attentive spells was very variable and over a short time one partner might be present for much longer intervals than the other. For instance, a male White Booby with an 18-day-old chick spent three spells with it of 10, 15, and 15 hours, while the two intervening spells by the female were of only five hours each. Similar cases occurred in both species during incubation of eggs.

1) Methods of observation.

Six nests of the White Booby were observed during August and September, and again from November 1958 until January 1959. The details of the attentive spells, dates of laying and hatching, are given in Appendix E. Four different pairs were involved, two of them twice. In August and September, all four pairs deserted about half way through the incubation period, and so most of the information comes from the two pairs that nested successfully in November; from other shorter observations in the colony it was clear that these two pairs were ~~not~~ unusual in their incubation rhythm. Three of the four pairs that deserted provided interesting information, discussed in the next section.

Eight Brown Boobies' nests were observed, involving five different pairs, three of which made second attempts after failure. The clutches were laid in March (1), April (1), June (2), July (1), and December (3) of 1958. There were three desertions before hatching, of which two occurred during observations but were not caused by them.

Nests were checked at about three-hourly intervals during the day and until about 2300 hrs., but not between then and 0700 hrs. except/

except on 18 occasions when checks were made before sunrise to see if change-overs took place in the latter half of the night. The times of sunrise and sunset varied slightly throughout the year, but for present purposes are taken to have been at approximately 0700 and 1900 hrs. respectively.<sup>1</sup>

Greatest activity at Brown Booby nests was always at dawn, and where a change-over was found to have taken place between 2300 and 0700 hrs. it could certainly be assumed to have occurred at dawn. This was not however true of the White Booby and no assumptions could be made about that species. The lengths of the incubation spells, and the times at which change-overs occurred, are therefore accurate to about three hours, except where a change-over was actually witnessed. Accuracy of this order was sufficient to indicate the pattern of the incubating rhythm. A spell of incubation was taken to have begun when the bird was first seen on the nest and to have ended when the other partner was first seen, except where the change was witnessed.

Interrupted visits to the colonies meant that records of incubation could not be continuous. More observations were obtained about Brown Boobies because their spells on the nest were shorter than those of the White.

#### ii) Results.

The White Boobies' attentive spells varied from 13 to 48 hours, with extremes of 54 and 63 hours; but there were no very short spells and three-quarters of the 28 spells observed were of 24 hours or more (Table 5). In the Brown Booby, on the other hand, although the length again varied greatly (from one hour to 37), only four of the 135 spells observed were longer than

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<sup>1</sup> Ascension lies at Longitude 14° W and is therefore one hour behind Greenwich Mean Time which is kept locally; the correct local times of sunrise and sunset would of course be 0600 and 1800 hrs.

**Table 5.** Duration of incubation spells, White and Brown Booby.

White Booby		Brown Booby	
Length in hours	No. of spells	Length in hours	No. of spells
13-18	4	1-6	38
21-24	7	7-12	35
28-31	5	13-18	33
33-34	2	19-24	24
43-48	7	25-30	4
54	1	37	1
63	1	-	-
Means: 32 hrs.	Total 27	Means: 12 hrs.	Total 135

- Notes:
1. The White Booby figures include 12 incomplete spells of 18 hrs. or more; none of the Brown Booby spells were incomplete.
  2. The White Booby figures are derived from six nests -- four pairs and second attempts by two or them; the Brown Booby figures from eight nests -- five pairs and second attempts by three of them.
  3. Male and female took roughly equal shares of incubation and are therefore not distinguished in the table.
  4. Spells were timed from when the bird was first seen on the nest to when the partner was first seen, unless the change-over was actually witnessed. The times are therefore accurate to about three hours.
  5. Spells immediately prior to desertion are excluded.

**Table 6.** Times of change-over during incubation, White and Brown Booby.

	No. of changes:	
	White Booby	Brown Booby
At dawn (0630-0730)	11	48
Morning (0800-1230)	3	39
Afternoon (1300-1800)	17	34
At dusk (1830-1930)	14	20
During darkness (2000-0600)	11	2
Totals	56	143

- Notes:
1. Daytime checks were made at roughly three-hourly intervals; 18 checks were made between 2300 and 0700 hrs. Activity at Brown Booby nests was greatest around dawn, and change-overs between 2300 and 0700 were taken to have occurred then. When White Boobies changed during the night this assumption could not be made and only known times have been included in the table.
  2. All changes, even after short spells, have been included.
  3. Change-overs were not different after hatching and changes during brooding have been included.

24 hours. This striking difference between the two species is further emphasised by the fact that the mean length of incubation spells in the White Booby was more than twice that in the Brown (Table 5).

There was also a difference, though less marked, in the time of day at which change-overs occurred. In the White Booby this could be at any time of day or night, but was least frequent during the morning (Table 6). In the Brown Booby, that same period in the morning, together with the period around dawn, was when most (61%) of the changes occurred. In the White Booby 20% of the changes were during the night, whereas in the Brown very few occurred at that time. After their eggs had hatched, the White Boobies tended to change over more often in the night and morning, but the Brown showed no difference, and all change-overs are included in Table 6. This change in the White Boobies' behaviour was presumably related to the chick's need to be fed.

### 3. Brooding.

The chick was not brooded by clasping between the feet, at least not after the first three or four days, although the parent still sat on and completely covered it. The second egg presumably was unaffected by this slight change, and usually hatched successfully at the expected time, although the chick never survived for long (see later). The surviving chick was covered by the parent until it was ten or twelve days old, by which time it was almost clothed in white down and was too big to be brooded. The parents still attempted to brood it, but gradually gave this up and merely stood beside or partly over it, this guarding being kept up continuously until the chick was five weeks old, sometimes longer. There was no obvious attempt by the parents to shield it from the sun, nor did I see the chick clamber on to the parents' webs to keep off the hot ground, as reported by Murphy (1936). Later the chick/

chick was left alone for varying periods, up to a whole day, but rarely at night. The periods while the chick was being guarded, though not necessarily actually brooded, I shall call brooding spells.

In the White Booby the change in length of spells after the eggs hatched was striking: the longest brooding spell was 24 hours and the mean of 20 spells was 11.6 hours, as against a longest incubation spell of 63 hours and a mean of 32 hours (Appendix F). The mean figure for brooding spells is therefore close to that of the Brown Booby, whereas for incubation spells there was a considerable difference between the two species.

In the Brown Booby the brooding spells were just as variable as the incubation ones, but were generally shorter. The longest was 20 hours, and the mean of 27 records was 9.3 hours (Appendix F), contrasting with the incubation spells, of which 21 were more than 20 hours and the mean was 12 hours. The mean length of 12 spells on chicks of six to ten days old was 12.4 hours, while that of 15 spells on chicks of more than 25 days old was 6.8 hours. Hence not only were brooding spells shorter than incubating ones, but they also tended to become even shorter as the chick grew. Kendeigh (1952) found that in most species of birds attentive periods were generally shorter after hatching, and brooding attentiveness declined as the young grew older.

The difference between the two species in length of incubation spells probably indicates a difference in feeding range on the part of the adults. The importance of this is discussed later.

#### 4. Desertion.

Information was obtained from three pairs of White Boobies and two Brown which deserted during observations on incubation spells. The desertions were clearly not caused, nor were the birds apparently affected in any way, by what little disturbance the/

the observations necessitated. The desertions were not exceptional, because many others occurred at about the same time, and therefore the following accounts are considered to be representative of a widespread phenomenon.

The most important cases in the White Booby were nests DA and DB2 (Appendix E). In the first, the male was present when observations began and remained on the eggs for a further 70 hours, when he stopped incubating but stood over the eggs for a further six hours and then left. Three hours later he was seen 25 yards from the nest, and 12 hours after that in company with the female in the same place. He was again seen there three days later, but the nest was clearly deserted. In the second case, the male was again incubating at the start of observations, but was relieved after a further 48 hours; this in itself was not an unusually long spell, but he might have been incubating for some time prior to the first observation. The female incubated continuously for 72 hours, then left. This was the longest spell ever recorded. The male returned 24 hours later, i.e. after an absence of 96 hours, and incubated for at least 42 hours, at the end of which observations had to stop. The nest was deserted by my next visit. The third case (DB) was less striking: the male, after an off-duty spell of 38 hours, incubated for at least 46 and possibly 63 hours, then left. (There was a gap of 17 hours in the observations before he was noticed to be absent.) Neither bird was present during the following 33 hours, and then both were seen nearby, but not incubating. Both were nearby again the following day; but by my next visit the nest was deserted. 46 hours was a longer than average spell, but not an outstanding one.

In the two cases of desertion by Brown Boobies, the behaviour was similar. In the first, the 41st day of incubation had been reached, i.e. the egg was due to hatch in four days. The male was incubating when observations started, went on for a further 22 hours, then left; returned three hours later, but did not incubate/

incubate, and left again. 24 hours later he returned but incubated for only half an hour before leaving again. Six hours after this, i.e. 33 hours after his first departure and at least 55 hours after he began his spell, the female returned. She incubated for 45 hours, then left. The longest complete normal spell for this species was 37 hours. Two hours later both she and the male were present at the nest but not incubating, and four hours later both had gone; by my next visit the nest was clearly deserted. In the second case, the female was incubating on the 18th day when observations started, but left nine hours later. Neither bird was present for a further 48 hours, when the female returned, incubated for 26 hours, then left again. By my next visit the nest was deserted. The male was seen subsequently, so desertion was not due to his death. In one other case, a female had a spell of 24 hours (22nd day of incubation), then the male one of twelve hours; the female's next spell lasted 39 hours before she was relieved, and at my next visit the nest was deserted. 39 hours is more than three times the average normal length. Again both members of the pair were known to be alive, and bred the next season.

It is clear that in both species there was a limit to the length of time a bird would incubate without relief, and this was longer in the White Booby than the Brown.

Griffin & Hock (1949) found that a Gannet whose mate had been removed stayed on the nest for three days, the average normal spell being about 24 hours. Matthews (1954) found that Manx Shearwaters Procellaria puffinus, whose incubation spells averaged five days, would incubate for twice and sometimes three times that time when the mate had been removed. King Penguins Aptenodytes patagonica, whose normal spells were two to three weeks, extended their/

their stays to 34 and 35 days before deserting, the partners never returning (Stonehouse, 1957). The boobies' behaviour therefore conformed to this pattern, the difference being that their mates were not prevented from returning either by artificial means or death.

Some of my observations showed that the birds awaiting relief appeared to undergo conflicting drives. For instance, the male White Booby which incubated for 70 hours, stood over the eggs for six hours, then left but returned in three hours, was presumably hungry but at the same time unwilling to leave his nest.

It was impossible to say definitely that hunger was the cause of the desertions, but it seems very likely, from the evidence. Difficulty in finding food, or the necessity to go far afield for it, would certainly result in the absent partner being away from the nest for longer than usual. Lack (1956) found this in the Swift Apus apus, the length of incubation spells being increased in bad weather, i.e. when food was more difficult to find, and the relieving bird therefore delayed its return. Desertions also occurred when food was short (Lack, personal communication). Southern (1959) suggested that Tawny Owl clutches failed to hatch in rodent "crash" years because the cock was unable to find enough food for the incubating hen, who was thus forced to leave the eggs and hunt for herself, allowing the eggs to become chilled. This would certainly result in eventual desertion, but Southern has confirmed (personal communication) that eggs were also deserted before the incubation period was completed. As already mentioned, Hutchinson (1950) described how on the guano islands off the west coast of South Africa the Cormorants and other seabirds deserted their eggs when fish were scarce in the surrounding areas. Presumably similar events follow the effects of the warm current which brings disaster to the Peruvian guano islands, but the desertion of nests has not actually been described in this connection. However Vogt (1942) found that some nests of the Piquero Sula variegata on the island/

island of Lobos de Tierra were all abandoned during his observation of them, although the season was not a conspicuously disastrous one; he thought lack of food was the cause.

That the long absences of my boobies was not due to their deserting through fear or disturbance was shown when the birds returned and incubated although their partner had already given up and left.

I conclude that the most likely explanation of the desertions was shortage of food, the boobies' behaviour being entirely consistent with that of the other species under such circumstances. The evidence from the study of desertions was circumstantial, but more direct evidence was obtained from the growth of chicks and is discussed later.

The arrival at the above conclusion was not straightforward, and four points require some mention. Firstly, it was not clear why the food shortage should suddenly have manifested itself in the form of long spells of incubation between 11 and 14 September 1958. Possibly the White Boobies were experiencing a particularly acute shortage just at that time. As mentioned earlier, the desertions were not exceptional; in Hut Area, for instance, 18 out of 22 clutches being incubated at the beginning of August failed to hatch. Nine of these had disappeared by the end of August, i.e. before the above-mentioned critical period, but nine of the remaining 13 came to grief in September. Details of what happened were not obtained, most of the nests simply being found empty and the eggs lying in the vicinity; a deserted nest would quickly be tramped over by neighbouring birds and the eggs kicked about. Presumably, therefore, desertion occurred in these in the same way as it did in the nests under observation.

Secondly, although the observed Brown Booby desertions were not exceptional either, only one of them took place in August, i.e. just before similar occurrences among the White Boobies, and during the time when many Brown Booby chicks were dying of starvation.

The/

The other desertion was in January 1959, when surviving chicks, although few in number, were showing no signs of malnutrition. However, of 89 Brown Boobies that had eggs in December and January, 51 (57%) lost their eggs. I could not say that all these losses were due to desertion, but they could hardly all have been due to accidents, and some at least must have been deserted before the eggs disappeared. In both desertions under observation, the eggs disappeared soon after incubation ceased. Shore-crabs, probably Grapsus maculatus (Catesby), which ranged the cliffs up to 100 ft. above the sea, may have been partly responsible; they were seen to carry away cracked or broken eggs and might have moved whole ones. Many Brown Booby nests, however, were in places where crabs did not go. It is possible that the food shortage in August and September continued without being noticeable until the following January and may have been responsible for the desertions and non-breeding in that season.

Thirdly, losses of eggs might have been due to predation, but as no predators were ever seen, this can be ruled out.

Lastly, Richdale (1957) found that young Yellow-eyed Penguins Megadyptes antipodes were more liable to desert before completion of incubation than older ones, and it might seem possible that some of the boobies deserted because of immaturity. This can however be ruled out because two of the three White Booby pairs and one of the two Brown Booby pairs under observation had successfully raised a chick within the previous six months, and there were too many other desertions throughout the colonies for immaturity to be wholly responsible.

Summing up, a food shortage would account for the desertions more satisfactorily than any other factors, although some of the evidence for it was indirect.

IV BREEDING, PART 3: The chick; growth, feeding, abnormal growth and food shortage, asynchronous hatching and consequences.

1. Changes in appearance of chick during growth.

In both species the development of the chick was accompanied by changes in its appearance which were classified as follows:

<u>Age in days</u>	<u>Appearance.</u>
1-8	Naked.
9-13	Down appearing on back.
14-26	"Downing", i.e. down beginning to cover the whole body, the chick thus becoming white.
27-36	"Half-down", i.e. chick completely covered with down but the down not yet fully grown, and the chick only about half the size of the parent.
37-46	"Full-down", i.e. the chick entirely covered by down of the full length and almost as big as its parents, beak full-grown, but no sign of primaries or retrices yet.  <u>At 37-40 days the primaries erupted, but were hidden beneath the down for a few days.</u>
47-60	"Half-feathered", i.e. the primaries and retrices now visible through the down to a gradually increasing extent; thus this stage can be described as early or late.
c. 85	" $\frac{3}{4}$ -feathered", i.e. down remaining only on head, neck, and flanks.
c.105	"Fully-feathered", i.e. down disappeared, but chick not yet flying to sea. (This event was easily determined from the cleanness of the legs and feet).

These stages were determined from five Brown Booby chicks, all of which agreed fairly closely, and also agreed approximately with a White Booby chick that was followed through in the same way. The White Booby was slightly slower in development, but not enough to alter the age-groups. Gibson-Hill (1947) described the stages in Brown Booby chicks on Christmas Island in a similar way, and it is clear that they developed at the same rate as the Ascension birds, except that/

that the latter were about ten days later in beginning to fly. This scheme could be used for making a quick estimation of the age-composition of the chicks in a colony of either species, when there is insufficient time to take measurements of a significant sample. From this the approximate date of the peak of egg-laying could be calculated. The method is more precise than those which result in such generalised statements as "mostly well-grown chicks". It would have to be used with caution in other parts of the world where the growth rates might not be the same as on Ascension, although the Christmas Island birds show that variation between even widely separated populations can be small.

## 2. Care of the chick.

In both species one parent remained with the chick continuously until it was about five weeks old, after which time it was left alone for periods of up to a day, but not at night. The chick did not go to sea until it was about 120 days old, until when it must have been entirely dependent on its parents for food. Even after that, a chick would often beg for food and would be fed, but whether this was merely to supplement what it was catching for itself, or whether it was still dependent on the parents for food, I could not tell.

## 3. Method of feeding the chick.

This was the same in both species. Small chicks of up to two weeks old begged weakly, only raising and waving the head and uttering a faint but continuous "tip-tip-tipping" noise. If the adult was prepared to deliver food, it stood over the chick and pointed its closed beak downwards. The beak was then slightly opened and pointed further backwards, towards the feet. The chick then put its head inside the beak, stretching its neck and pushing right up to the base of the adult's gape. The adult assisted by lowering/

lowering its head still further, the beak by this time being pointed backwards underneath its breast. If the chick was large, of course, the adult did not have to lower its head at all. The adult then regurgitated, a bulge appearing in its neck if the bolus was large enough. (Plate 2). The food-begging of the chick is described more fully in the section on Behaviour.

If the chick was small, the amount regurgitated was small, and appeared to be delivered in controlled quantities. It was also well digested. The chick gobbled the food while its head was still inside the adult's throat.

At this stage I noticed an extraordinary dilation of the gape, in both adult and chick, presumably an adaptation for swallowing large fish and for enabling regurgitation without damage to the buccal cavity from fins and bones coming up backwards. The process was also strikingly demonstrated when the bird yawned. As the lower jaw opened, the proximal parts of the rami drew apart, this being possible partly because of an elastic fold of skin across the inter-ramal area and partly because of the mechanical arrangement of the articulating facets. (This was observed by manipulating the lower mandible of a dead bird). When the beak of a dead bird is opened, the articulating surfaces of the two rami are forced apart, and since the two rami are held together at their distal ends, i.e. at the tip of the mandible, this forcing-apart causes the incompletely ossified junction between the surangular bone and the dentary to hinge. A gap thus appears between the two surangular parts of the rami. One is reminded of a snake's ability to separate the two halves of its lower jaw. When a booby yawned, the two proximal parts of the rami came together again as the beak closed. The bird appeared to close the rami before shutting its beak, but this may have been an illusion. To obtain the full details of this mechanism it would be necessary to examine the articulation of the bones and also to have a film of the yawning movement. Presumably many birds that/

that feed their young by regurgitation can perform this movement. Gurney (1913) noticed that the Gannet had a "hinge across the lower jaw, probably to increase the width of the gape when feeding the young". I have found no other reference to the matter.

Large chicks were insistent in their attempts to force open the adult's beak and immediately inserted the whole head into the parent's gape. The efficiency of the above-mentioned gaping mechanism was clear, for even a full-grown chick could put its whole head inside the parent's gape, as seen in Plate 2.

As soon as the chick had obtained food, it withdrew its head, sometimes about half of the fish protruding, and swallowed, while the adult gulped back the remainder of the regurgitated food. If the food was well digested, the chick usually swallowed before withdrawing, and one could not see what was being passed.

#### 4. Measurement of growth.

Measurements of wing and culmen-length were made on many chicks of both species and were used as a means of calculating age. At intervals measurements were also made on chicks of known age. Growth curves were drawn for these and for weight, and the measurements from the chicks of unknown age could be fitted on to them.

The curves for weight were the most interesting in view of the food shortage that developed. Weights varied more, and thus were a better indication of the chick's condition than the dimensions of wing and culmen. The growth of wing and culmen was of course slowed during starvation, but less markedly than weight.

Because many of the chicks under observation suffered from starvation (discussed fully later), and because our visits to the colonies were intermittent, much of the information about growth has necessarily been compiled from what may seem confusing sources, e.g. experiments with twins, and chicks hatched at different times. Straightforward collection of data on growth was not possible. In presenting/

presenting the results I have had to keep the sources in mind, and thus the argument is more complicated than I should have liked.

## 5. Normal growth.

### a) White Booby.

i) Weight: The increase of weight with age is shown on a logarithmic scale in Fig. 8. Six chicks, whose hatching dates were known, were weighed at intervals; also included are the weights of two chicks whose ages were calculated from wing and culmen measurements at four and seven days, and five others whose ages were similarly calculated when they were between 15 and 20 days old. The points on the curve are therefore derived from 13 chicks. All were hatched early in 1958, i. e. before there was any hint of food shortage.

Also shown on Fig. 8 are points derived from two other chicks (A and B) of known age which for some unknown reason grew more slowly than the others. Clearly these were abnormal, since their growth-curves are distinctly different from the others. A was hatched at the same time as the others, B in October 1958, i. e. after the well-marked period of food shortage mentioned earlier. It was the only chick on the colony at that time.

The point X on Fig. 8 was the weight of a chick 85 days old on 29 September; it is discussed, together with points Y and Z, in the section on abnormal growth below.

ii) Wing and culmen: The growth curves for wing and culmen are shown on Fig. 9. The same birds were used. Again A is clearly separated, the critical period in its life apparently being between 20 and 30 days, when it fell behind the normal; the culmen length was obviously the least affected of the three measurements. Generally speaking, up to 30 days old there was little variation between individuals in wing and culmen length, so these two measurements taken in conjunction were used to determine the ages of other chicks.

Summary: /

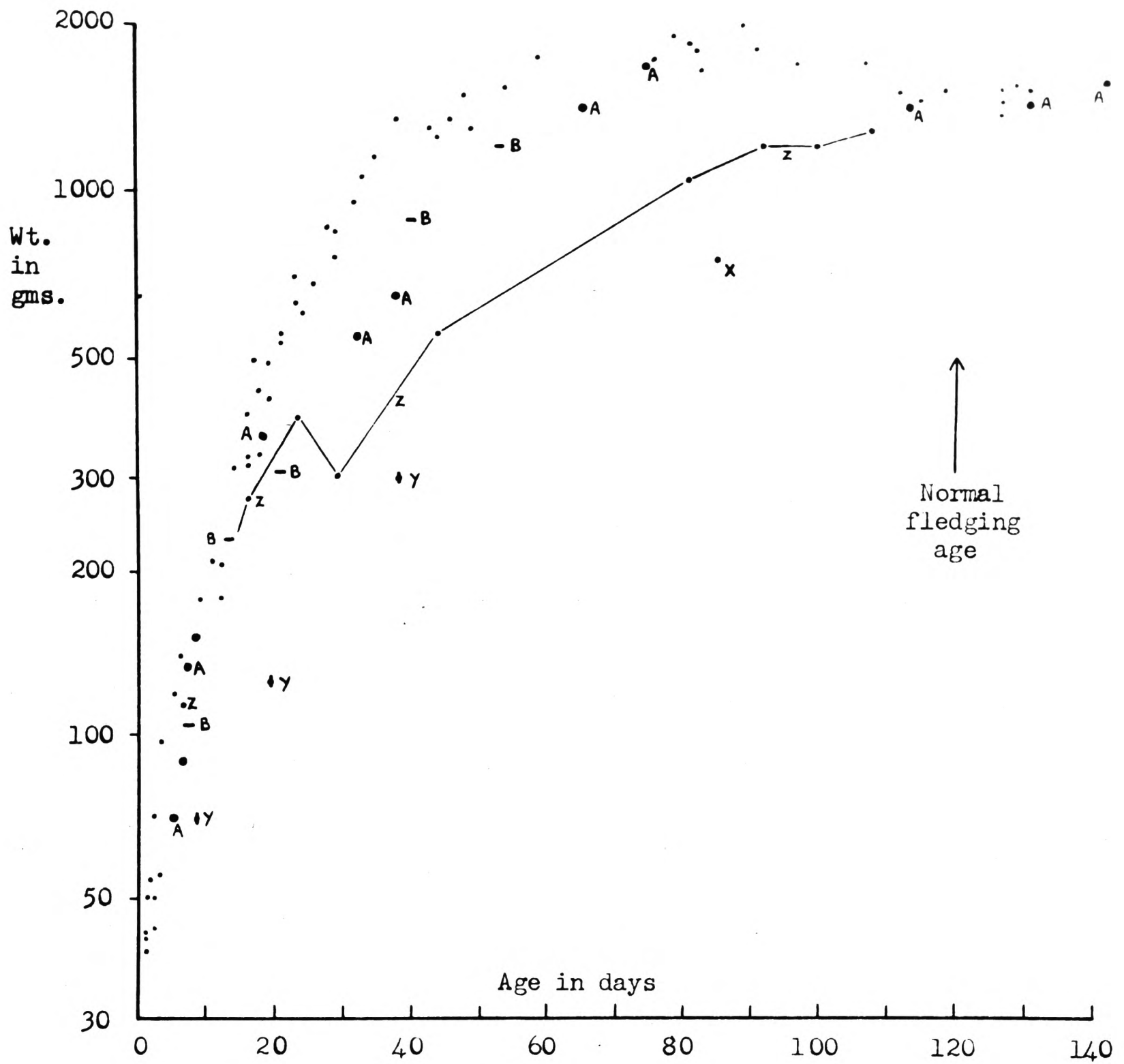


Fig. 8. Increase in weight with age of White Booby chicks.

From 13 normal chicks.

A, B, X, Y, and Z abnormal -- see text.

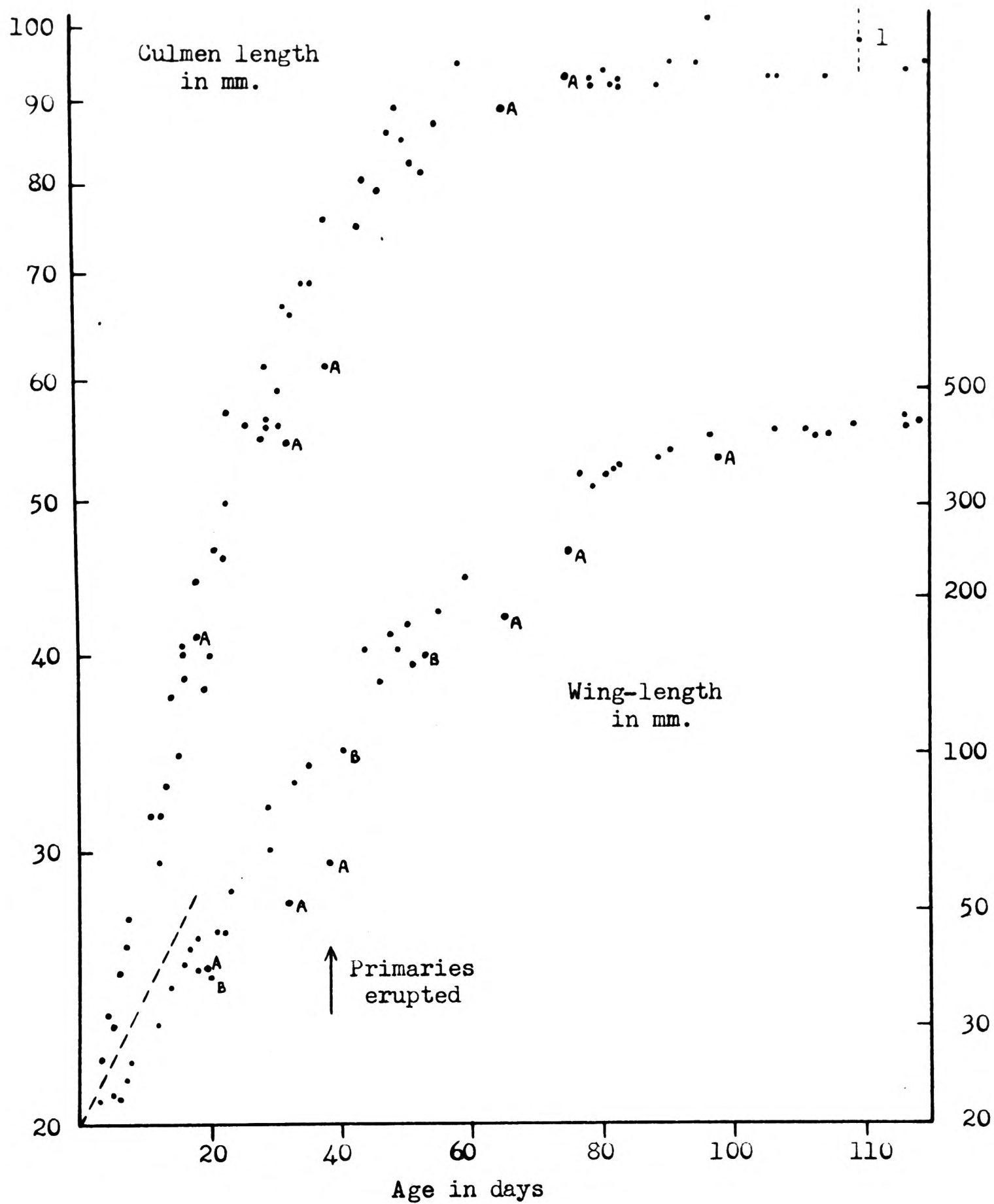


Fig. 9. Growth of culmen and wing in White Booby chicks.

- Notes: 1. Measurements from 13 chicks.  
 2. A and B abnormal -- see text.  
 3. Logarithmic scale.

<sup>1</sup> Mean of seven measurements, extremes indicated.

Summary: Weight increase slowed at about 40 days, and stopped at 80-90 days, after which weight was lost until about 100 days. Thereafter the weight remained more or less constant, most chicks fledging at about 120 days; minor variations presumably depended on when the weighing was made in relation to the last feeding. The length of the wing increased until about the 80th day, when growth slowed suddenly and reached a stop by about the 100th day. The growth rate did not alter appreciably on the eruption of the primaries, as is shown by the shape of the curve before and after the 37th day. (After eruption, the wing was measured to the tip of the longest feather).

Growth of the culmen stopped earlier, at about 60 days. Probably early development of the beak is advantageous, so that the chick can defend itself when the parents are absent.

The variation in length of both wing and culmen after growth has stopped is probably due to manifestation of the size difference between the sexes. At this age of course the chicks could not be sexed.

#### b) Brown Booby.

In the Brown Booby, the pattern of growth was very similar (Fig 10). The weight curve was complicated by some of the records being made during the time of food shortage, and discrepancies appeared in the latter part of the curve. Weights in this case are therefore presented in table form (Table 7). While discrepancies were noticeable in the weight, they were less so in wing and culmen measurement, showing again that these two are more reliable than weight for estimating age, especially up to 60 days.

Although the weight curves for the Brown Booby were nearly all aberrant, they nevertheless provided quantitative information about the effects of food shortage, discussed later under abnormal growth. Only one chick was followed through without setback; it was 100 days old before the critical period of food shortage and showed/

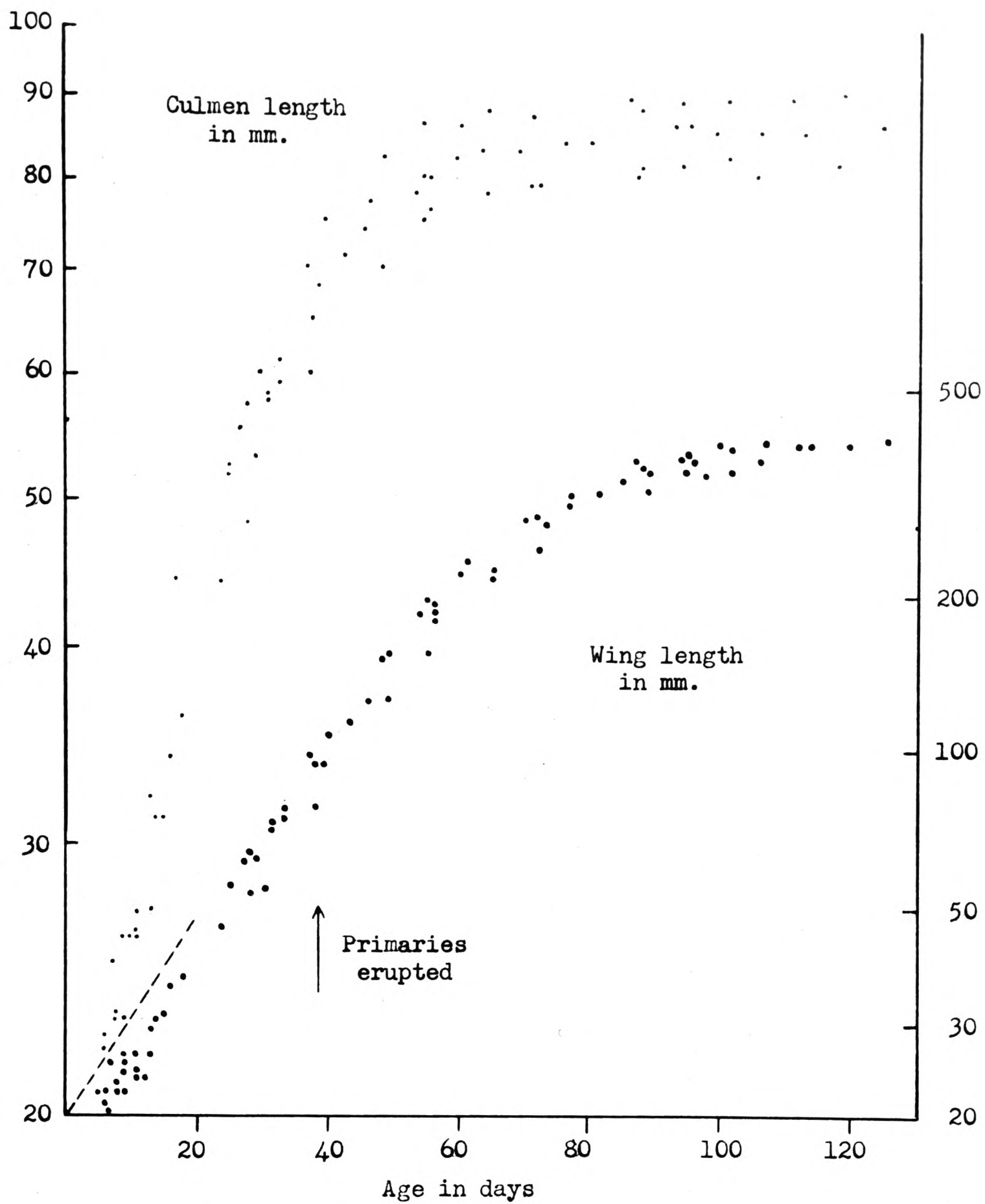


Fig 10. Growth of culmen and wing in Brown Booby chicks.

- Notes: 1. From 14 chicks.  
2. Logarithmic scale.

Table 7. Weights of Brown Booby chicks against age in days, showing normal and abnormal growth.

		CHICK NUMBER																			
		1		2		3		4		5		6		7		8		9		10	
Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.	Age	Wt.
6	82	8	102	8	99	6	72					7	72	6	53	6	65	4	54		
11	138	10	125	10	109	9	113	9	115			9	107					11	118		
14	205	14	194	14	192	13	205	16	210			13	165								
18	300	25	609*	25	389*	25	564	27	485			24	409	16	240	16	270				
29	595	29	639	29	474	28	704	31	515 <sup>1</sup>			28	500	20	360	20	375	21	200 <sup>2</sup>		
33	674					37	975	38	825 <sup>1</sup>			38	600	33	560	33	575	26	dead		
43	1025	40	925	40	700	49	1175	46	770			49	975	58	840	58	1000				
54	1175					55	1225	48	850			55	925								
60	1350	57	1375	57	1050	65	1250	56	950			65	950								
70	1400	67	1300	67	1200	89	1175	73	850 <sup>3</sup>			89	1100	69	660 <sup>2</sup>	69	890 <sup>2</sup>				
94	1290	90	1240	90	1100	95	1025 <sup>1</sup>	88	675			95	900 <sup>1</sup>	72	dead	79	dead				
100	1225 <sup>1</sup>	103	940 <sup>2</sup>	103	1000 <sup>2</sup>	102	900 <sup>2</sup>	106	800												
107	1140	113	1000	113	1000	112	800	119	750			102	640								
		121	900	121	900	120	950	133	1000			103	dead								

For notes see overleaf.

FOOTNOTES and NOTES TO TABLE 7.

\* Chicks 2 and 3, which were twins up to this point, separated.

1 3 August, 1958.

2 10 August, 1958.

3 14 September, 1958.

Notes:

1. Chick 1 was normal, 2 and 3 were normal up to 103 days, the remainder were abnormal.
  2. Weights showing abnormality are underlined.
  3. Chick 1, normal at 107 days, may have lost weight like the others after 3 August, but it was flying by then and could not be checked. It was apparently normal when caught 2 months later.
  4. Chick 6 was late in fledging but was apparently normal when caught 2½ months later.
-

showed abnormalities (Table 7, Chick 1.) Two other series of measurements (Chicks 2 & 3, Table 7) were obtained from chicks that were initially placed together in a nest as a "twin" experiment. Both grew normally for 14 days; on the 23rd day one had got into a neighbouring nest and was being fostered. Both continued to grow normally, except that Chick 3 (the fostered one) was slightly slower than the other, and were 96 days old by the critical period; up to this point they are considered as normal, and their subsequent history is discussed later. Three other chicks of known age on the Stacks were measured (but not weighed) on eleven occasions, and these points are included in the curves on Fig.10.

Thus it can be seen that the normal growth curves for the Brown Booby closely resembled those for the White Booby.

#### 6. Abnormal growth.

Abnormalities in the growth-rate are described here because they gave very clear evidence that a shortage of food occurred in August and September 1958.

##### a) White Booby.

Most of the evidence of food shortage in this species came not from weighings but from the number of deaths of chicks and desertions of eggs. The shortage began about the time of the peak of hatchings, i.e. August 1958, and there were many deaths of chicks shortly afterwards. This interfered with the programme of weighings and also with the experiments on twinning, which at that time were regarded as being of first importance and had to be done when there were chicks of like ages most readily available.

The details recorded in Figs.8 and 9 were obtained before the start of the main breeding season, and so can be used as a standard for comparison with abnormalities. Two other chicks, A and B, were not raised during the food shortage period and have already been discussed./

discussed. Chicks X, Y, and Z which appear on Fig.8, were growing during the food shortage.

X was 85 days old on 29 September 1958. It was clearly below normal weight and died shortly afterwards. Not having weighed it previously, I could not tell when it first deviated from the normal, but probably it did so in August, thereafter steadily losing weight until its death.

The situation with regard to Y was complicated by its being initially used in a twinning experiment. At 19 days, its twin, though smaller, was still alive and up to this date might have been competing for food, causing Y's growth to be slower than normal. But by the 32nd day this twin had died, and thereafter Y should have grown normally. By the 38th day, however, its weight was still below normal and by my next visit it was missing, presumed dead. It was hatched on 10 September, which was during the food-shortage, and this might account for its slowness in the early stages. But other chicks were known to grow normally in October, and in theory Y ought not to have died. Y is comparable with B, which hatched early in October and likewise grew slowly.

Z was also one of two experimental twins; they were paired on 30 July at two days old. As can be seen in Fig 8, its growth up to 12 days was normal; moreover, by this time its twin had died and subsequent events should not have been influenced by the experiment. Between 23 and 29 days Z's weight fell, but unlike many other chicks it did not die, and it continued to grow, though abnormally slowly. There was a gap in the weighings between 44 and 81 days, by which time it was still well below the normal but apparently quite fit. Three weighings at ten-day intervals after this suggested that the 40-day gap was spanned as drawn on the curve, although there could have been another drop and recovery. By 127 days it was up to fledging weight, but was still at the " $\frac{3}{4}$ -feathered" stage. (Most normal chicks were flying at 120 days). By 141 days it was fully feathered but not flying. Thus its fledging period was extended by  
at/

at least 20 days, presumably because of its setback in feeding. This setback occurred between 20 and 26 August.

b) Brown Booby.

The evidence of food shortage amongst the Brown Boobies was the same as in the White. I was weighing a number of chicks which had successfully passed the early stages, when it became apparent that something was wrong, and weighings were carefully followed.

Chick 4 (Table 7) was normal, by comparison with Chick 1, until 95 days, then its weight dropped sharply to 112 days, when it was noted as being weak. It recovered and fledged successfully at about the normal age. The date of the dip was 3-20 August.

Chick 5 also followed the normal course until it was 27 days old, then its rate of growth suddenly slowed. It too subsequently recovered and fledged, although it never reached the normal "ceiling". Its falling-off was between 30 July and 10 August. It had another small loss of weight about 14 September.

The weights of the next two chicks give even clearer evidence of lack of food. Chick 6 followed the normal course until it was 39 days old, when it suddenly lost weight, but gradually picked up to normal, or nearly normal, at 81 days. Its weight had dropped considerably by 85 days, and again but more slowly by 96 and 114 days; by 123 days it had picked up nearly to normal again. In the end the chick fledged, but it was at least two weeks later than normal in doing so. The dates of the two losses in weight were 3 August and 18 September.

Chicks 7-10 suffered setbacks from which they did not recover. A drop in Chick 7's weight apparently occurred at 38 days (7 June) but since at the next weighing it was back to normal, this may have been an error in recording. Another drop occurred on 24 June, from which there was a gradual recovery to 89 days, when its weight was nearly/

nearly back to normal. But by 95 days its weight had dropped steeply, and still further by 102 days. The next day it died, emaciated. The last drop in weight began on 28 July, and its death occurred on 11 August.

Chicks 8 and 9 started off as a twin experiment, but became separated at 16 days and thereafter lived independently. Both grew at the same rate for the next 18 days and probably for longer, the next weighing not being for another 25 days after that. By then Chick 9 was heavier than Chick 8, but both were below normal. There may have been a drop and a recovery in one of the gaps between weighings, but this could not be detected and anyway does not affect the argument which is mainly concerned with the next phase in their life. 11 days later both had dropped steeply to far below the normal weight; in three days Chick 8 was dead, and seven days after that Chick 9 also died. Their decline started on 30 July or shortly after, and their deaths were on 13 and 20 August respectively.

Chick 10 was of normal weight at 11 days but by 21 days had fallen off slightly. Five days later it died, the date being 25 August.

Chick 11 (not shown in Table 7) was weighed at 9 days old and was normal. It was not weighed again until it was 98 days old, on 14 September, by which time it was 900 grammes, only slightly below normal. It had apparently survived the period in August which had affected other chicks so seriously, but it could have dropped in weight and recovered without my knowledge. Four days later, however, its weight had fallen by 200 grammes, and 11 days after that it was dead, and very thin.

There is one further piece of evidence in Table 7. Chick 1 showed a gradual fall in weight after 70 days; as it had reached 100 days of age before 3 August, I believe that this gradual fall was normal and unaffected by the food shortage. Chicks 2 and 3, on the other hand, showed a slightly irregular and more marked fall. The dates of this were from 3 to 20 August, which is consistent with the/

the events described above. Both of these chicks, as mentioned earlier, were the subject of a twinning experiment to begin with (though they later separated) and their weights were slightly below normal earlier as well, probably as a result of the experiment.

c) Summary.

Losses in weight, or reductions in growth-rate, occurred at varying times in the lives of individual chicks (as was particularly evident in the Brown Booby), but nevertheless it was noticeable that all individuals of both species were affected at roughly the same date. There were two periods when these events occurred, one in the first week of August, and another, less important, about the middle of September. Between these there was some recovery of weight by the chicks, if they survived the first period. All these facts point to a lack of food during the two periods.

Not all the losses in weight were sudden, and the slower ones could have been the result of adults staying away from the chicks for unusually long times; this can be correlated with the lengthening of incubation spells mentioned earlier, which occurred about the same date.

Other evidence concerning the food-shortage will be discussed after the breeding success has been described.

7. Asynchronous hatching and its consequences.

One of the most striking features of the breeding biology of both White and Brown Boobies was that although they laid two eggs they never raised more than one chick.

This is not peculiar to the Ascension populations. It is widely reported for the White Booby, e.g. from Ile Tromelin (Brygoo, 1955), Goenoeng Api (Hoogerwerf, 1939), Mait Island (North, 1946), and North Keeling (Gibson-Hill, 1950a) in the Indian Ocean area; and from Laysan (Fisher, 1904), Canton (Murphy et al., 1954),  
Willis/

Willis Is. (Reithmuller, 1931) and the Galapagos (Rothschild & Hartert, 1902) in the Pacific. Murphy (1936) said that two eggs but one chick was general in the White Booby, and suggested that the adults were ill-conditioned to the presence of more than one chick in the nest, concentrating on one with the result that the other died of neglect. However, it has been shown that in other species whose eggs hatch asynchronously, e.g. the Heron Ardea cinerea (Owen 1955) and some Corvidae (Lockie 1955), when there is a lack of food the youngest chicks always die first because they are prevented from obtaining food by their nest-mates, not because of selection by the parents. Vesey-Fitzgerald (1957) said that in the White Pelican Pelecanus onocrotalus the younger chick was bullied to death by the older, two chicks never surviving in one nest.

Reithmuller (op. cit.) observed on Willis Is. that three days was the longest that two White Booby chicks survived together. He considered that the older managed to get more food and pushed the younger out into the sun. As will be seen, my own observations were similar.

Brygoo (op. cit.) is the only author I have found to mention a White Booby's nest with more than one chick. This was a single example among 31 nests on Ile Tromelin (350 miles north of Réunion). His photograph shows two chicks about 40 days old (by my reckoning) with an adult at what seems to be an isolated nest. On Ascension two chicks occasionally wandered together when their parents were absent, and they might be attended, even preened, by a non-breeding bird for a short time, thus appearing to be a brood of two. As Brygoo's nests were apparently widely dispersed, such an explanation is less likely in his case.

The situation in the Brown Booby is similar, also throughout its range. There are records of two eggs but only one surviving chick from Christmas Island (Indian Ocean) (Gibson Hill, 1947) the Barrier/

Barrier Reef (Napier, 1928), Canton (Murphy et al., op. cit.), Hawaii (Richardson and Fisher, 1950), the Bahamas (Chapman, 1908), and the Cape Verdes (Bourne, 1955). Bourne, however, said that two nests out of 15 had two living chicks, although he did not record their age and one might have died later. Chapman found two chicks in two nests out of 740, and a photograph of one example shows that they must have been about 40 days old.

One possible case of two chicks almost succeeding occurred on Ascension. On 19 May 1958, two Brown Booby chicks were found together in a small gully on Stack 4. I could not observe whether these were both fed by one pair of adults, because all the birds on the stack fled when I landed and remained away until I left again. Two nests had not been previously recorded in that gully. There was no means of telling whether both chicks were hatched from the same clutch; a chick from outside might have fallen into the gully and been fostered. By measurement of wing and culmen I estimated them as 16 and 10 days old when first found. Since five or six days normally elapsed between hatching of the first and second eggs, this suggested that they were siblings. The two chicks continued to grow at a rate consistent with their estimated age. The larger was slightly above normal and fledged in due course, apparently without any setbacks, in August. The smaller was normal in weight and measurements at 20 days and again at 34 days, indicating that the age estimation was correct. It was particularly remarkable that it should have maintained its rate of growth, while living with a larger chick. At 62 days, however, (7 August) it was dead. Wing and culmen lengths were normal, but it was thin. Many other chicks were dying of starvation in early August 1958.

This appears to be a genuine case of two chicks surviving for 34 days, and one might assume that both would have fledged had the food shortage not intervened. But it should be treated with reserve, for there is no proof that they were siblings, or that they were fed by only one set of parents. In the other 95 cases in which two chicks hatched, only one of each pair was raised to a month or more.

*Incidentally/*

Incidentally, it was notable that the larger chick in this case apparently survived the period of food shortage without any setback. If the parents were able to feed both chicks until then, it is possible that when the availability of food was reduced, they could still feed one but not the other.

Apart from this instance, the pattern of events after the hatching of the second chick was invariable, and the same in both Brown and White Booby; the smaller chick soon died. Often it was found lying dead beside the nest, occasionally still in the nest but trampled, and sometimes outside the nest, still alive but in a weakened condition. If replaced in the nest, it was accepted by the adult, but was later found outside again. This strongly suggested that the chick was somehow ejected from the nest. It seemed unlikely that the parent was responsible, because an adult was never seen to discriminate between the chicks, preening both of them, for instance, turn about. Adults also did not discriminate between their own chicks and others introduced into the nest. Chicks up to eight days old were accepted as twins, and twice, Brown Booby chicks were found in neighbouring nests after ejection from their own. Adults would not tolerate in their territory chicks that could walk about (i.e. from about 40 days old onwards), and they must have been able to recognise their own chicks at this stage because these often moved away from the territory while the parents were absent at sea. No experiments were done to find out at what age this recognition was achieved. It is reasonable to conclude that the adults were not responsible for the removal or ejection of the smaller chick.

In many cases, the second chick to hatch disappeared without trace between my visits, presumably taken by a Frigate Bird, as would be any small chick that happened to be lying unprotected in the colony. Several times I saw a Frigate Bird pick up regurgitated White Booby food, and once saw one take an unattended chick of its own species. Frigate Birds regularly took unattended chicks of the Wideawake Terns from the ground.

Eventually I came to the conclusion that the older chick was responsible./

responsible. I watched a nest in which a six-day old chick was being brooded along with a newly-hatched one. The former was old enough to hold up its head and push with its feet, whereas the latter was weak and incapable of such movement. Each time the parent stood up, the larger chick began to push the smaller about, and sometimes gripped in its beak the smaller one's neck or wing; this achieved, it pushed with its feet. However, it did not seem to be strong enough to push the smaller chick out of the nest, and certainly not so far that the parent could not retrieve the chick if it made the attempt. But in such a situation adults were never seen to try to retrieve a chick, in contrast to their behaviour, described earlier, in retrieving a misplaced egg.

Summing up, the smaller chick was expelled from the nest soon after hatching, apparently as a result of the efforts of the larger chick, and died.

#### S. Experiments with twins.

The normal growth of the chick, asynchronous hatching, and the circumstances of the loss of the second chick having been discussed, we can now consider artificial situations involving twins.

Although the experiments were not fully conclusive for various reasons discussed below, they did suggest that the adults were well able to feed two chicks, at least for some days.

A more striking result was that there was still a tendency for one chick to establish a supremacy, even though it was only very slightly the larger.

Methods: First I found a chick of (preferably) one to three days old, then searched the colonies for another of similar size to put with it, removing the other chick or egg as the case might be. Both chicks were weighed and their right wing and culmen measured.

The adult now had its own chick and another of the same size from outside. There was a possibility that it would discriminate in favour of its own chick. I soon found that this was not the case  
at/

at all. Both were accepted, and invariably the larger survived longest, whether it was the parents' own chick or not. I also found that parents of, say, a week-old chick would accept two newly-hatched ones, or one whose chick was newly-hatched would accept two five-day-old ones. In this respect conditions were not the same at the start of each experiment, especially in the Brown Booby, but there was no indication from the results that this mattered. Gibson-Hill (1947), changed Brown Booby chicks from one nest to another, and they were always accepted, even when the new chick's age was up to three or four weeks different from that of the original one. It was not possible to find enough Brown Booby chicks of exactly the same age to make the experiments uniform.

Results: Generally speaking, in both the White and the Brown Booby, one of the chicks proceeded to follow the normal growth curve (weight was the most useful as an indicator) while the other lost weight and disappeared after a few days in the usual manner. Ejection from the nest was again seen.

In two of the Brown Booby experiments an unusual thing happened. The twins grew together at the same rate until between two and three weeks old. Then one of them was found in another nest. In one case the distance between the old and the new nest was only about three feet, but in the other it was six feet; so the chick must either have moved by its own effort the whole way, or been helped into the new nest by the brooding parent. As already mentioned, this was unlikely. In both cases all the chicks were marked. White Booby chicks did change nests too, but in the twin experiments this happened only once (see v) below).

a) White Booby. The White Booby results were severely complicated because all the experiments were conducted either during or close to the period which subsequently turned out to have been one of food shortage. Desertion and/or death of the chick was probably in/

in many cases due to the food shortage. Disturbance as a result of the experiment seems unlikely because some of the desertions took place after one of the twins had died; furthermore there were many other desertions of similar and undisturbed chicks nearby at the same time.

Sixteen experiments were performed. In nine cases the experiment ended quickly, the details being as follows: i) One chick, actually slightly the heavier of the two, though smaller in culmen and wing, had disappeared by my next visit four days later. ii) The parents deserted after two days. iii) & iv) The slightly smaller chick was dead outside the nest after one day. It could hardly have starved to death in that time, and death was probably due to exposure after ejection. v) One of the chicks (slightly the heavier) was out of the nest after one day; it was replaced, but on the following day the other chick was found in a neighbouring nest; it was replaced in the original nest, but three days later both were dead. In this case probably the experiment was started too late, both chicks being 12 days old.

In the four other cases one of the two chicks in each case survived four days or less after the start of the experiment. Curiously, in all four, the smaller of the two, the one that died, was not far below the normal measurements for its age when it died. In two of these cases, the larger chick was up to the normal rate of growth while the other was alive, but it subsequently died, one at 20 days old, the other at 30, presumably for the same reason as others were dying on the colony at that time.

Thus there were seven remaining cases in which the effects of having two chicks in the nest could be observed. These are detailed in Appendix G. They show that in some cases the parents were able to raise both chicks for two weeks and more without detriment to either (as against two or three days where the second to hatch was six days behind the other), but that in other cases both chicks/

chicks suffered. This could have been due not to the experiment but to other factors. Likewise, the failure of all the twins to survive longer than 23 days need not have been due to the experiment; there were other cases in which chicks, apparently well up to that time, suddenly died. Desertion with subsequent exposure was a likely cause.

Whatever the shortcomings, the experiments did show that twins could survive together much longer than two chicks hatched in the normal way.

b) Brown Booby. The results here were not upset as in the White Booby, although here again the experiments were not entirely conclusive.

Eight sets of twins were started. In two of these the chicks separated, one in each case going to a foster parent and successfully surviving, but fortunately this did not happen until after they were six days old in one case and 14 days in the other, so that some of their progress together was observed. (Appendix G, Nests 1 and 2).

In four of the remaining six sets, the larger chick quickly established a supremacy and grew normally, while the small died or disappeared. (Appendix G, Nests 3-7).

Nest 8 was anomalous. Neither chick gained weight at all for the first three days of the experiment, probably because I weighed them twice daily and thus disturbed the parents too much. On the 18th day, which was the time of my next visit, one chick had disappeared and the other was normal.

All these experiments were done in May and early June 1958, i.e. when there was not yet any sign of anything unusual in other parts of the colony.

Summing up, four sets of twins behaved as if the chicks had been of unequal size, the larger surviving after quickly gaining on the smaller, while two behaved more like the White Boobies, the twins surviving together at almost the same rate before one ejected/

the other.

These results for both species therefore emphasise two important points: that the older chick's ability to establish its supremacy was so strong as to operate even when the chicks were of nearly the same size; and that the parents were apparently able to provide enough food for normal growth to two chicks, at least for a period of about two weeks. These two points stress that asynchronous hatching and its consequences have important effects. There is apparently no possibility of the weaker chick surviving. The parents' effort is quickly channelled in a single direction - the successful raising of one chick.

#### 9. Discussion.

Why were two eggs laid, and why did the second chick never survive? It seemed unlikely, as shown by the experiments with twins, that the parents could not provide enough food for two small chicks. If the smaller chick of a normal brood was not fed because the larger was hungry and took all the food, again it is difficult to believe that the parents could not supply more than enough food to satisfy a week-old chick, since its requirements must have been much greater when older. If, on the other hand, the parents were not likely to be able to raise more than one chick in the end, of course it would be to the larger chick's advantage to get rid of competition from the smaller one as quickly as possible. The behaviour of the larger chick could have evolved in this way.

It thus appears that the important factor here is the innate behaviour of the larger chick and not shortage of food, as is the case in the Corvidae, for instance, where the largest chick takes up the most advantageous position and therefore gets most food from the visiting parents while the others get less and may starve. It would be possible to argue, however, that even in the Corvidae one would have thought the parents could supply enough food for a whole brood of small chicks; this does sometimes happen, where the smallest chick/

chick survives for some time before dying, and it is more evident in the Heron (Lockie, 1955, and Owen, 1955).

If the smaller booby chick, then, is doomed whatever the availability of food, it is difficult to see what else the extra egg can be but an "insurance policy" against loss of one during incubation. It is perhaps important in this connection to note that of all the tropical boobies only the Redfooted and Abbott's (Gibson-Hill, 1950b) lay one egg, and they are also the only ones that build a nest off the ground. Brown Boobies are able to build nests (but not off the ground) in some places; there is no published information about egg-losses, but they might be lower under such circumstances than they were at Ascension.

If the "insurance policy" of laying an extra egg is even occasionally successful, selection will favour the retention of the habit in the species, provided that the strain of laying an extra egg is not so disadvantageous as to offset the occasional success. This seems unlikely as the eggs of the boobies were relatively small. Infertility might be another factor resulting in the laying of an "insurance" egg, but I found no evidence that this was important. It might even be suggested that in the past the White and Brown Boobies were able to raise more than one chick because of a better food supply than at present, and that the tendency to lay two eggs has not yet been selected out; but this is rather speculative and would not account for the behaviour of the older chick.

A comparison must be drawn with the Blue-footed Booby Sula nebouxi and the Piquero S. variegata, which lay more eggs than the White and Brown Boobies and appear to be able to raise more than one chick. Probably this is because their food is more abundant, but it would be particularly interesting to know what goes on in their nests when two or more chicks are hatched. The behaviour of the chicks may be different from that of the White and Brown Boobies.

Beebe/

Beebe (1924) reported that in the Galapagos Blue-footed Booby chicks were in pairs, although Gifford (1913) had observed that seldom more than one survived to the feathered stage. Off Peru, where the species is more abundant, the clutch is two, sometimes three, and two is a common number of young in the nest (Murphy, 1936). Murphy added that Piqueros frequently laid three eggs and three chicks also survived, in contrast to the situation in White and Brown Boobies. But Vogt (1942), referring to the same species in the same part of its range, described a bad season in which virtually no chicks at all were reared, and there were other seasons when the birds did not lay at all. It is well known, as has been mentioned, that off the west coast of South America the guano-birds' food supply is extremely variable.

Possibly the White and Brown Boobies are also subject to such variations, on a lesser scale, in their food supply; Hoogerwerf (1939), for instance, saw starving Brown Booby chicks, resembling those seen on Ascension, on Goenoeng Api in the Banda Sea. Fluctuation in the food supply is clearly a factor that would result in the birds laying a higher clutch than they could in most years bring to success, provided there was no disadvantage in the "over-laying". As described above, however, it seemed that in the Ascension boobies the behaviour of the larger chick was more important, in affecting the survival of the smaller, than was the abundance of food.

## V BREEDING, PART 4: Breeding success.

Accurate figures about breeding success were not obtained, for reasons discussed below, but sufficient pairs were studied to conclude that in general the success was low and that big losses of eggs and chicks of the White Booby occurred in August and September 1958.

### 1. White Booby.

#### a) Hatching success.

No useful conclusions could be drawn about this. For instance, I found several cases of birds incubating two marked eggs, one their own and the other an addled one from nearby. Again, a bird found incubating two eggs might have only one chick at my next visit; the assumption would be that the second chick had hatched and been ejected, but there could be no proof of this. Various possibilities of this sort could arise from the boobies' habit of losing eggs and rolling in others, and from the regular death of the smaller chick soon after hatching. Hence figures for hatching success on the basis of intermittent visits would be meaningless. There was no reason to believe that there was a high proportion of infertile eggs. Many of the eggs probably failed to hatch because they were deserted, perhaps only for a short time, and not because they were infertile. Lack (1954) concluded that nidicolous species generally have a high hatching success.

#### b) Breeding success.

As mentioned earlier, two separate parts of the colony were studied. Far Area consisted of 35 squares, 10 x 10 yards, and the contents of each was checked each month. Hut Area was roughly triangular in shape, with sides of about 15 yards; each nest was marked and more regular checks were made as time permitted. The two areas are therefore treated separately in this analysis.

Far /

Far Area: Between the beginning of May and the end of September 631 clutches were laid. A chick was known to have hatched successfully in 234 nests. There were, doubtless, other chicks which were deserted when small and vanished because they were eaten by Frigate Birds. Hence 234 is probably too small a figure. Of the 234 chicks known to have hatched, 56 fledged (24%). Thus of 631 pairs which attempted to breed, only 56 (9%) succeeded in raising a chick (Table 8). In addition, 206 unmarked abandoned eggs were found lying in the colony, but these could not be assigned to nests. Some of these were probably two eggs of a clutch, others perhaps only singles, and yet others might have been laid at random. These 206 eggs therefore represent at least 103 further attempts at breeding, and probably more.

Table 9a shows the months in which the clutches were laid, and the number of eggs found abandoned. Again it should be remembered that the 457 eggs found abandoned could have come from half that number of clutches, although some may have been single eggs from a nest in which the other egg was retained. It can be seen that the greatest number of new clutches was in July, while the greatest number of eggs were abandoned in August. Hence in August some factor must have been causing large numbers of desertions. I believe this was food shortage.

Table 9a also shows that while at the end of July there were 95 chicks alive, and no dead ones, at the end of August the position had changed considerably. In spite of the number of new chicks that should have hatched, the number of living chicks had increased only to 148, and there were 38 dead ones. This small increase in the number of chicks would be partly accounted for by the deserted eggs. By the end of September, the number of living chicks had fallen to 58, and another 96 were dead. Many more deaths, therefore, occurred in September. This, together with the evidence from chicks which were being weighed, indicated that there was a second period of food shortage about the middle of September.

Table/

**Table 8. White Booby: breeding success, 1958.**

	No. of clutches laid.	No. of chicks known to have hatched.	No. of chicks fledged.	Chicks fledged Clutches laid x 100
Far Area	631	234 (37%)	56 (24%)	9
Hut Area	68	38 (56%)	12 (32%)	18

- Notes: 1. The total number of clutches laid in Far Area is a minimum figure because eggs found abandoned were not included as clutches. There were 206 of these.
2. The number of chicks known to have hatched is a minimum in both areas because small chicks could have been eaten by Frigate Birds before my censuses. The figure for Hut Area is relatively high because my checks there were more frequent.
3. As the smaller chick of a brood died soon after hatching (see text), it is assumed that each clutch resulted in only one chick; thus Columns 1 and 2 are comparable. If two chicks were taken to have hatched per clutch, the figures in Column 2 would be doubled and the % survival of hatched chicks would be halved.

**Table 9a. White Booby. Number of eggs abandoned and chicks found dead per month, Far Area, 1958.**

Month	No. of clutches laid	No. of eggs abandoned	No. of chicks found alive	No. of chicks found dead
May	50	0	0	0
June	123	1	15	0
July	<u>358</u>	<u>54</u>	95	0
August	96	<u>275</u>	<u>148</u>	<u>38</u>
September	2	127	58	<u>96</u>
October	2	0	56	5

Note: The census from which these figures are derived was taken at the end of each month. See also notes for Table 1.

**Table 9b. White Booby: breeding success, Hut Area, 1958.**

Month	No. of clutches laid	No. of desertions	No. of chicks alive	No. of chicks that died.
May	15	1	0	0
June	<u>24</u>	3	6	0
July	<u>22</u>	9	25	<u>1</u>
August	6	<u>13</u>	20	<u>18</u>
September	1	7	12	5

Note: Of the 24 deaths, 21 were chicks of less than 40 days old.

**Table 10. Approximate ages of White Booby chicks found dead, Far Area.**

<u>Age of chick</u>	<u>No. found dead in:</u>	
	<u>August</u>	<u>September</u>
1 week	5	17
2 weeks	0	1
3-4 weeks	30	45
5 weeks	0	21
over 6 weeks	3	12

**Note:** Ages were estimated by inspection, as described on page 56.

Table 10 shows the ages, estimated as described on page 56, of the chicks found dead in August and September. Most chicks died when 3-4 weeks old. This is probably their most critical age, when the adults first begin to leave them alone (although normally only for short periods), and also when their growth rate increases. Adults leaving their chicks alone for the first time might stay away longer than usual if food was difficult to find. The chicks might then die of exposure, since at that age they have not yet attained their full covering of down. Hence a general food shortage could become quickly manifested by the deaths of chicks 3-4 weeks old.

Hut Area: Since each nest in this area was marked, it was known to be deserted if found empty, whereas in Far Area the number of desertions had to be inferred from the number of abandoned eggs. All the eggs in Hut Area were marked, so that it was known where abandoned eggs came from, although both eggs disappeared without trace from nearly all the deserted nests, probably through rolling down the sloping ground and out of the study area. Eggs from four deserted nests were found in others, and in four out of six other cases in which one egg was lost, the second disappeared later as well.

Apart from these points, the information obtained from Hut Area was similar to that from Far Area. Between the beginning of May and the end of September 68 clutches were laid (Table 8). From them, 38 chicks were known to have hatched, and 12 of these fledged. The success (18%) therefore appeared to be higher here than in Far Area. It was, however, noticeable that in this area more clutches were laid earlier than in Far Area, and the chicks which fledged successfully were hatched from clutches laid early in the season (10 out of the 12 in May and June). These chicks were probably old enough to survive by the time that the food shortage began. Unfortunately I had no records of their weights, which might, like those discussed earlier, have shown abnormalities.

It can be seen from Table 9b that by the end of July there had/

had been only nine desertions and one dead chick, while by the end of August there had been a further 13 desertions and 18 dead chicks.

Of the 24 chicks which died, 21 did so before they were six weeks old, which is consistent with the findings for Far Area.

Without comparative figures for other breeding seasons, it cannot be said that the low breeding success in 1958 was particularly unusual. But in December 1957 I was able to ring 47 fledglings in another area, roughly half the size of Far Area; these chicks, still not flying at that late date, must have been the later part of the previous season's crop, and this suggests that decidedly more chicks fledged in 1957 than 1958.

Even without comparative figures, it was still apparent from the numbers of desertions and deaths of chicks, and the times of these, that some factor was adversely affecting the boobies' breeding success in 1958. This factor was probably the same as the one whose effects have already been discussed in connection with the lengthened incubation spells, desertions, and abnormalities in the growth of chicks, namely a shortage of food.

## 2. Brown Booby.

### a) Hatching success.

For the same reasons as given for the White Booby, no conclusions could be drawn about this. Again I had no reason to believe that there was a high proportion of infertile eggs.

### b) Breeding success.

Two breeding seasons were studied. The total number of nests observed and their distribution over the months have already been examined, and only the nests started during the months around the peak of laying are considered here, so that success in the two seasons may be compared. Thus Season II is considered to consist of the nests begun in March, April, and May 1958, and Season III of the nests/

nests begun in the following November, December, January, and part of February. My last visit to the colony was on 5 April 1959, and no nests which resulted in chicks hatching later than mid-February have been included, since the chicks would have been less than a month old at the final visit. As will be explained later, I believe that chicks which reached the age of one month were likely to survive to fledging.

The results are set out in Table 11.

In Season II there were 185 clutches. Of these, 71 (38%) were known to hatch a chick. The remainder were recorded as having failed to hatch, although only 96 were known for certain to have failed before hatching, the other 18 being nests in which a chick may have hatched but disappeared between my visits. Of the 71 chicks known to have hatched, 36 lived to the age of one month or more. These 36 were all alive at the beginning of August, i. e. before the food shortage began, but by the end of August 18 of them had died. The other 18 fledged successfully, although as described earlier those that were being weighed showed losses in weight and retardation of development. Thus from 185 clutches only 18 chicks (10%) fledged. It should be remembered that each clutch consisted of two eggs, and that two chicks probably hatched in each case, the younger one quickly dying as happened in the White Booby. Again I have considered the raising of one chick a success, regardless of whether the second hatched or not.

In Season III there were 150 clutches. Of these, 60 (40%) were known to hatch a chick. The number of known failures before hatching was smaller than in the previous season, probably only due to a slight difference in recording. 39 chicks survived to the age of one month or more, half of them being 2-2½ months old. The chicks that survived the food shortage of the previous season were all more than a month old at the start of it, 13 out of 18 being more than two months old. This is not an adequate proof, but I believe that the 39 chicks that reached the age of one month/

Table 11. Breeding success in the Brown Booby.

<u>Season</u>	<u>No. of clutches laid</u>	<u>No. of chicks hatched</u>	<u>No. of clutches that failed to hatch</u> <sup>1</sup>			<u>No. of chicks that lived to one month or more.</u>	<u>No. of chicks fledged</u>	<u>Fledgings</u> x 100 <u>Clutches</u>
			<u>Known</u>	<u>Probable</u>	<u>Total</u>			
II	185	71 (38%)	96	18	114 (62%)	36	18	10%
III	150	60 (40%)	39	51	90 (60%)	39	39 <sup>2</sup>	26%

**Notes: 1.** The number of clutches that failed to hatch (columns 3-5) includes clutches which may have hatched but the chick disappeared shortly afterwards, i.e. probable failures could have been early losses of chicks. Column 5, the total failures, is the important one.

**2.** The number of chicks that fledged in Season III was not known, but there were 39 chicks alive at my last visit and it is assumed that most of them would be successful (see text).

month in Season III would survive to fledging, unless there was another food shortage, or other extraordinary event.

The figures for the two seasons thus agree closely up to four months after the peak of laying in each, and the breeding success to that point was 20% in Season II and 26% in Season III, the subsequent reduction in Season II probably being entirely due to the food shortage.

### 3. Summary and discussion.

Summing up, in the White Booby, in one area 9% of clutches (4½% of eggs) laid gave rise to flying young, while in another part of the colony the figure was 18% of clutches. In the Brown Booby, in one season 10% of clutches (5% of eggs) laid gave rise to flying young, while in the following season the probable figure was 26% of clutches. The first season, however, was thought to be strongly affected by food shortage.

There is little information about other birds with which these figures can be compared. Lack (1954) reviewed all available data on nesting success, but had very little for the Boobies. In nidicolous Passerines, for which there was most information, the number of young raised from eggs laid varied from 22% to 59%, with an average of about 45%. There was also considerable variation in individual species from year to year (e.g. in the Swift, one year 95% of the chicks hatched survived to fledging, in another year only 31%), and from place to place (30% to 74% in the Robin Erithacus rubecula in one year). Richdale (1957) also found variation in breeding success in the Yellow-eyed Penguin, the number of young raised from eggs laid varying from 37% to 80%, with an average of 59%, over 18 seasons. In the worst season, 45% of the young that hatched survived to fledging. He also found that of 1,475 eggs laid, only 3.75% failed to hatch due to natural causes<sup>1</sup>, a figure that is strikingly lower than the one I found for both species

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<sup>1</sup> Breakage in the nest, falls of rock, disappearances, accidental ejections, and desertions (my italics).

of booby. In four breeding seasons of the Shag Phalacrocorax aristotelis, the number of chicks fledged from eggs laid varied from 47% to 70% (calculated from figures in Snow, 1960).

Generally speaking, all my figures showed that the boobies had a markedly lower breeding success than the species mentioned above. Boobies are perhaps not strictly comparable with open-nesting nidicolous Passerines, but they are more so with penguins and certainly with Shags. Breeding success is clearly highly variable among birds, and I may have happened to witness unusually bad seasons on Ascension. In this connection it may be remembered that in some seasons on the Peruvian guano islands the breeding success is nil, with a definite correlation with the food supply. On Ascension, one of the breeding seasons of the Wideawake Tern resulted in about a 2% success (Stonehouse, 1960), but this was undoubtedly largely a result of predation.

Lack (op. cit.) concluded that in general about 8-18% of eggs gave rise to breeding adults, while Richdale's figures for the Penguins varied from 6% to 33%. I could obtain no information about post-fledging mortality in the boobies, but if this were low, the figures I obtained for their success up to fledging would bring their success up to maturity more into line with those for other species.

Finally, Lack considered that about three-quarters of nesting losses in Passerines were due to predation. The boobies had no predators of eggs at all, and the losses of small chicks to Frigate Birds were negligible, yet their nesting losses were far higher than those of the Passerines. This emphasises the importance of finding out the reasons for the desertions described earlier. However, too much importance should not be attached to comparing the boobies with other species. If the food supply, as it appeared, was the most important factor governing the boobies' breeding behaviour, i.e. egg-laying, incubation, desertions, and the care of the chick, then/

then clearly by means of these, it must also have governed the breeding success.

**Table 12. Ages of White Booby juveniles when captured after fledging.**

No. of birds at:	Ages in months				
	8-10	10-12	12-14	14-16	16-18
<b>First recovery</b>	3	5	6	9	3
<b>Second recovery</b>	0	0	5	4	1

**VI MOULT: Plumage changes and post-juvenile moult, subsequent moult cycles and their significance.**

**1. Return of juvenile White Boobies after fledging.**

Early in the study, in December 1957, 63 chicks in down were ringed, but not measured, their ages thus being known to within two months. 26 of these were caught again later, and their ages when recovered are shown in Table 12. Only one chick of less than eight months old was recaptured, and none more than 18 months, that being roughly their age when my study ended. In addition, 21 juveniles caught in the clubs were ringed; their ages, estimated by the stage of their moult (see later) were between nine and 14 months. Only four of these were recaptured at an age of more than 16 months, these four being 19-20 months old. I therefore conclude that newly-fledged birds paid a few visits to their old nest-site and the clubs, then tended to stay away from the island until they were about a year old. It was birds of this age and older that formed the major proportion of some of the clubs. Whether they remained based on the island between this first return and their first attempt to establish a territory on the breeding colonies, some two or more years later, I could not say definitely; but birds ringed in the clubs during their change from juvenile to adult plumage were not often recaptured, and as the clubs were regularly searched for such birds, I conclude their visits were probably intermittent.

**2. Moulting in the juvenile White Booby.**

It was while examining these returned juveniles that I discovered they had started their post-juvenile feather replacement, and this proved to be a useful means of estimating age. (Where possible, I shall use the terminology for plumage changes suggested by Humphrey & Parkes, 1959.)

For each bird captured, the state of moult in its primaries and rectrices was noted, and the aspect of head, neck, back and rump described./

described. It was found that changes in these followed a regular sequence, and this sequence for the primaries is shown in Table 13.

Primaries were numbered from the innermost outwards; the moult was scored by considering each primary as a number (1 to 10) and its stage of growth as a decimal of that number. Usually both wings were the same, especially in young birds, but where they were slightly different the average was taken. For example, a bird whose third primaries were both half-grown was scored 3.5; if that of the left wing was one-quarter grown and that of the right wing three-quarters grown, the average, 3.5, was again the score.

Replacement of the rectrices began at about the same time as that of the primaries, but it was found to be irregular and will not be considered further.

At five months old, chicks had fully attained their first plumage and had been on the wing for about a month. They had not then begun to shed any of the body or flight feathers. At about seven months old,<sup>1</sup> replacement of the juvenile feathers began. Birds of eight months old were found to be growing their primaries No.2, and subsequently it became clear that replacement proceeded outwards ("decendantly" — Verheyen, 1958) regularly at the rate of about one primary per month (Table 13). At the age of about 15 months, when primaries No.6 or 7 were growing, the innermost (No.1) was shed again, and thus a second cycle was started. This was the first indication that the moult of the boobies' primaries followed a remarkable course, to be described later. After this point, the rate of replacement appeared to be slower.

Throughout this sequence in the primaries there was a steady replacement of the body feathers, also commencing at about seven months of age.

The aspect of the new-fledged chick was as follows (terms as

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<sup>1</sup> Perhaps occasionally earlier; one bird of five and a half months old was found to have just shed both its innermost primaries.

Table 13. Replacement sequence of primaries in juvenile White Boobies

a. Birds of known age:

Bird no.	Age (months)	Primary score
6408	8.8	2.1
6576	9.5	3.25
6420	10.0	4.0
6326	11.1	4.75
6325	11.6	4.75
6399	11.8	5.1
6420	12.1	5.5
6408	12.4	5.0
6325	13.4	6.1
6326	15.2	8.1, 1.25

Note: The primary score was obtained by taking the number of each growing feather and expressing its stage of growth by a decimal (see text)

b. Birds of estimated age.

No. birds in group	Age (months)	Primary score		
		Max	Min	Mean
2	8-10	2.75	2.5	2.62
1	10-12			3.25
11	12-14	7.5	5.25	6.7
8	14-16	8.25	6.5	7.66 (and 1.2 <sup>1</sup> )
5	16-18	9.5	8.25	8.75 (and 1.65 <sup>2</sup> )

Note: These birds were ringed as chicks in down; the detailed aspect of each was not noted, therefore their ages are approximate to  $\pm$  1 month.

1 Average of 3 cases

2 Average of 5 cases

used in Witherby et al., 1940): the crown, forehead, hind neck, sides of neck, nape, and ear-coverts were mainly brown but with some white flecking; the scapulars, lesser and median wing-coverts were almost pure brown, but with some white flecking; the mantle, back, and rump were pure brown; the primaries, secondaries and rectrices were dark brown; the rest of the bird was white.

A change was first noticeable in the head and neck; by nine months of age the head was only slightly speckled with brown, by 13 months it was very slightly speckled (and this only detectable in the hand), and by 14-15 months it was pure white. By nine months of age the back and wing-coverts were still predominantly brown but with increasing white flecking, and they became progressively more white until by 14 months they were only slightly flecked with brown, and by 17 months were almost pure white. The rump was the last part of the bird to start changing, remaining almost pure brown until 13 months, and thereafter becoming progressively more white until by 20 months only a few brown flecks were detectable, even in the hand. These changes in the plumage were accompanied by conspicuous changes in the colour of the iris, and less conspicuous changes in the colour of the legs and facial skin: the iris was dark brown in the chick, but at about eight months began to turn green; thereafter it remained greenish, but yellowing gradually, until by 20 months it was nearly pure yellow; but the full brilliant yellow of the adult was not attained until some months later, the precise age being unknown. The legs were olive-grey in the chick, and turned gradually through flesh to orange at about 20 months, but as changes in leg colour even in adults varied (according to breeding condition), and females sometimes had almost olive grey legs, this was not a good criterion of age. The facial skin also turned gradually from the grey of the chick to the inky blue of the adult, and the bill from greyish horn to dull yellow; again this was not a reliable indication of age because/

because bill colour in adults also varied according to breeding condition.

Hence the ages of young White Boobies could be reliably estimated, on the basis of the above criteria and the stage of moult in the primaries, up to the age of about 18 months.

From this age onwards the story is more complex, and because none of my birds of known age were older than 18 months when my study ended, the evidence requires more detailing.

21 juveniles in the clubs were ringed, their ages being estimated by the above means to  $\pm$  one month. They were selected on the basis of their general brown colour, indicating that they had probably recently returned to the island after their post-fledging dispersal, and their moult and aspect was checked. 14 of them were recaptured later.

The moult in the primaries reached the outermost at about 18 months, i.e. juvenile primary No.10 was then shed. This first generation of primaries (the juvenile ones) was always clearly distinguishable from the second generation, being very worn at the tips (due to abrasion before the chick could fly) and considerably lighter in colour. Subsequent generations, however, were much less easily distinguished from one another, although new feathers were always slightly darker than old ones. For this reason, the aspect of the bird became an important guide to its age, (and also to the correct interpretation of the primary moult), as soon as the distinctive first generation of feathers had been shed.

This knowledge enabled me to use information from a further seven birds to work out (by a leap-frog method) the moult sequence up to about 24 months of age. I started with a bird of known age, A. It was recaptured first at 10 months of age, and again at 12 months, its primary moult having advanced by one and a half feathers in that time. Bird B, taken from the clubs, was at exactly the same stage as A in primary moult and aspect, showing that it must also have been twelve months old at that time. Eight months later it was recaptured, thus providing/

providing details of moult stage and aspect of a 20-month-old bird. At this point a gap in the sequence occurs, but it was bridged in the following way.

Bird C, caught in the clubs, had an aspect similar to that of the 20-months-old B; its primary moult stage was about one feather further on (moving outwards) than that of B, showing it to be slightly older. The moult stage of C's primaries appeared to be the same, surprisingly, as that of an 11-months-old bird. This apparent confusion arises from the fact that when the second cycle of the moult had reached primary No.7, a third cycle began with the shedding of No.1 for the third time, and so on. Thus what I shall call a triple cycle was established, and birds of this age and older continued to replace their primaries by this triple cycle, at certain times having three growing feathers (evenly spaced in the wing), at other times two; this remarkable system will be discussed later. Returning to consider bird C, or any bird of that age, it was possible to tell that the first generation of primaries had been shed because there were no remaining heavily-abraded feathers, but whether the wing was carrying feathers of second, third, or later generations could not be established except, as mentioned earlier, by other features of the plumage. On the basis of these, C was quite clearly not 11, but 22 months old.<sup>1</sup>

C was recaptured five months later, and its primary moult had advanced by three feathers. Thus the moult stage and aspect of a 27-month-old bird were known.

D, also taken from the clubs, was found to be half a primary advanced on the stage found in C at 22 months, and two and a half primaries behind C's stage at 27 months. D was therefore assumed to be about 23 months old. It was recaptured six months later, and thus the moult stage and aspect of a 29-month-old bird were

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<sup>1</sup> It could be argued that between the stage shown by B and that found in C there might have been a time-lag, but I had no reason to suppose that a break would occur in what had been up till then, and continued to be, a regular sequence.

established. By this time the fourth generation of the innermost primary was full grown, as was the third generation of primaries No.2 to 7, while primary No.8 had just been shed, and Nos. 9 and 10 were 'old', i.e. of the second generation. The aspect of D (29 months old) was noted as being like that of an adult female; its sex could not be determined from its voice, and presumably both sexes pass through this stage.

This bird was particularly important, because it enabled me to deduce the approximate ages of immature birds in the clubs, birds whose aspect was indistinguishable from that of adult females and whose primary moult, but for this special knowledge, might also have been indistinguishable from that of some adult females.

I now ringed a further 20 birds in the clubs, selecting those similar in appearance to D. In doing this, I ran the risk of catching birds which were indeed adult females. In several cases I did do so, but was able to reject them because their moult pattern did not fit with that of D. It is still possible that among the 20 were some adult females whose pattern of moult in the primaries by coincidence was the same as that of D, but if so I never saw them again. Adult males, selected by mistake, were at once recognised by their voices and discarded. The 20 birds were conspicuously marked with red paint on the head, and in the following three months the breeding colonies were regularly searched for such birds. (Any adult females marked by accident would have been seen on these searches, as an earlier marking experiment showed that adults in the clubs were on the colonies at other times.) The marked birds of D's age were subsequently seen many times in the clubs, but only one (see below) was found on the breeding colonies, where it was clearly a newcomer.

My purpose in marking these birds of about 29 months old was to see if they would go into the colony and breed, thus revealing to me the completion of the sequence in plumage changes from fledging to breeding. This was not however entirely successful.

I did not attempt to catch these marked birds for moult checking, as I knew they would not have changed much in the remaining three months of my study, and I did not wish to disturb them and thereby perhaps affect their behaviour in attempting to establish themselves on the colony. One bird, E, was taken two and a half months afterwards, its age being then about 31 months, and its primary moult had, as expected, advanced by about one and a half feathers. F was a similar bird, recaptured when its moult was about mid-way between the two stages of E, its age therefore being about 30 months. It was recaptured at about 32 months. G was another bird from the clubs, whose moult was just between those of E and F at their second recoveries, and thus its age was about 32 months. G was captured two months later, i.e. when it was about 34 months old, on the colony in company with a male; after handling it fled, and did not return. In the light of my previous experience of the behaviour of birds which were in the early stages of establishing themselves in the breeding colony and trying to find a mate (see section on behaviour), I was sure that G was making just such an attempt. This was the last observation in the series.

The time then was April, when there was very little breeding activity on the colonies and only a few pairs had eggs. The peak of the laying season came in the following July 1959, after I had left. I had found from the previous season that the greatest activity of unmated birds was at the end of the main laying season; hence it was not surprising that my marked birds did not appear on the colonies. Since one of them did, however, it is possible that others also did after I had left; observations from the previous season suggested that if they did, they probably would not succeed in breeding that season, although some of them might establish territories and find mates. In July 1959 they would be about 36 months old. Hence I conclude that White Boobies do not breed before they are three years old; they may do so at four years of age, but there might be a further delay between their first entering the colonies and successful/

successful breeding.

Summing up, I found that replacement of the juvenile plumage began at about seven months of age; in the primaries this was regular, symmetrical, and from the innermost outwards; in the rectrices it was irregular and asymmetrical, although it started at about the same time as in the primaries. These changes were accompanied by a gradual replacement of the feathers of all parts of the body (growing feathers were also found on the breast and belly, although there was no change in colour of these parts), and a gradual assumption of a pure white plumage everywhere except primaries, secondaries (which were not studied), and rectrices. At the same time the iris changed from brown through green to yellow, the legs from olive-grey through flesh to a dull orange, the face from grey to dark blue, and the bill from horn to yellow. The juvenile voice was retained, at least until about 30 months of age, and even at 34 months there was no definite evidence that the male voice had been assumed. The second cycle of replacement of the primaries began with the innermost at about 14 months of age, the first cycle having by this time reached about primary No.7; when the second cycle had reached this feather the bird then being about 27 months old, a third cycle began again at primary No.1.

By 32-33 months of age these various changes had brought the bird to an adult appearance, only its voice remaining more or less unaltered.

### 3. Molt of primaries in unmated White Boobies.

Unmated birds were studied from about August 1958 until March 1959, but as their behaviour was my main interest I handled them as little as possible. Two birds, however, were caught and their molt checked on more than one occasion, and their primary replacement proved to be following the same sequence as has been described in juveniles (Table 14). Bird (1) proceeded from primary No.4 to No.7 and from No.8 to No.10 between September and March, while over the same period/

Table 14. Moulting cycle of primaries in two unmated White Boobies.

Bird (i)		Bird (ii)	
Date	Score	Date	Score
12 Aug	no moult	29 Oct	1.0, 6.75
14 Sep	4.75, (8.9)	25 Nov	1.5, 7.1
16 Dec	5.25, 9.25	19 Dec	1.9, 7.5
29 Mar	7.25, 10.5	4 Feb	(2.9), 8.5
15 Jul	no moult	27 Mar	3.75, 9.5

- Notes: 1. The score was obtained as described in the notes to Table 13.
2. The figures in brackets indicate that these feathers were full-grown but the next had not yet been dropped.

period Bird (ii) proceeded from Nos.1 to 3 and from 6 to 9. Although they were both unmated, I did not know if they were both young birds, and indeed this difference between the stages of their moult suggests that they were not the same age. Birds hatched in the same season theoretically ought, as described in the previous section, to follow similar patterns of moult; departures from any such uniformity could easily occur, however, and possible consequences of this will be discussed later when comparing the moult patterns of adults.

Bird (i) is of interest in another way. In August 1958 and again in July 1959, it was recorded as not being in moult. (This was true only of the primaries. One feather was missing from the tail in 1959). I believe similarities such as this between moult stages at an annual interval are important not only in determining the rate of moult but also in considering the relation between moult, breeding seasons, and the food supply, and this will be discussed further later. After being found in a no-moult condition in August, Bird (i) appeared to start moulting in September by shedding primaries Nos.4 and 9; by the end of the following March, i.e. seven months later, it had continued these cycles by growing Nos.10, 1, and four-fifths of No.2; and Nos.5, 6, and one-quarter of No.7; and Nos.8, 9, and one-half of No.10 (for a second time). By the following July it had reached a no-moult phase again, and I think (by analogy with other birds) in the intervening three and a half months it probably continued these cycles by completing the growth of Nos. 2, 7, and 10, then growing Nos.3 and 8, then stopping. In the three and a half months it would have ample time to do this and then pause in the no-moult condition. Then after July 1959, it would continue with the cycles by shedding Nos.4 and 9, since these would be next in sequence, and this would be just what it had done in September 1958. If all this is true, and as will be seen later, evidence from adults supports this view, then it means that a generation of feathers (primaries No.1 to 10) was completely shed and/

and replaced only once in three years, i.e. at a much slower rate than the replacement of the juvenile primaries. But because three generations were being replaced simultaneously, i.e. three cycles were running, each feather would be replaced once annually. This is explained in more detail later when describing the triple cycle in adults. It can be seen from Table 14 that this could also have been true of Bird (ii)

Finally it should be noted that the two periods of no-moult in Bird (i) occurred at the same times as the peak of laying in the colony as a whole. The significance of a cessation of moult at the time of breeding will also be discussed later.

#### 4. Moult of primaries in adult White Boobies.

All the information obtained about adults indicated that their primary moult followed the same pattern as that described above. Not all the evidence was complete, but it was possible in most cases to construe what was happening. Generally speaking, then, the primaries were moulted in three spaced, outwardly-moving cycles, each proceeding at the rate of about half a feather per month and each of the ten primaries being replaced once annually. There appeared to be some synchrony of moult throughout the population in two respects: firstly, some birds were at roughly the same stage of moult at the same time, but this was not wholly uniform and will be further explained; and secondly, during breeding, many birds paused in their otherwise continuous moult, although the pause did not come at any fixed stage in the sequence. There were, however, exceptions to this general hypothesis which were given undue prominence as a result of my paying particular attention to birds which were breeding when I first arrived, i.e. they were out of phase with the main population. Nevertheless they provided information which must be included in the detailing of the evidence below.

The/

The particulars of birds that were checked over a period of more than seven months are shown in Table 15. <sup>(p. 99).</sup> This table requires detailed explanation, necessarily involving the consideration of individual cases.

As before, only the primaries have been considered, the scoring being the same as for Table 13. The different cycles had to be scored separately, e.g. a bird which had three feathers all in some stage of growth at one time has three scores. (The tail feathers were moulted irregularly, sometimes even when none of the primaries were apparently being moulted. Some body moult was also noticed at times when the primaries were not being moulted. Neither of these aspects of the moult will be further considered here, as I could work out no relation, positive or negative, between them and the events in the primaries.)

The explanation of Table 15, and the consideration of other birds, will be dealt with under the following headings: the pattern of moult, annual interval, triple cycle, synchrony, breeding during pause in moult, moult during breeding, and interpretation.

a) The pattern of moult: In every case the moult followed the pattern now established, proceeding in sequence from the innermost primary outwards. This can be seen most easily by considering a single cycle; for example, Bird 3 (Table 15) was growing its third primary in November, its fourth in December, its fifth in February, and its sixth in March; similarly, in November it was also growing its seventh primary, and by the following July this cycle had progressed as far as its tenth primary.

All the other birds in the table can be similarly interpreted, but there are some apparent exceptions. Bird 10, for instance, was growing its first primary in November, and by the next check in December this feather was almost completely grown. In the following March, however, the same feather was growing again; it must have been shed about one month after reaching full size. Presumably the abnormal November shedding was due to injury. Supporting this explanation/

explanation was the fact that in March the first primary of the other wing was also growing, whereas in November it had not been. Bird 10 was actually even more anomalous than this; the details for its left wing are given in the table, and other details in the footnotes. These indicate that probably this bird was carrying anomalies in both wings, that in the right wing perhaps being in the eighth primary. Without more regular checks over a longer period and individually marked feathers, cases of this type could not be easily resolved.

b) Annual interval: Table 15 also shows that where the interval between checks was approximately a year, there was a similarity between the stages of the moult. (This was noted earlier in the case of an unmated bird.) Thus Bird 3 showed a moult stage scored as 4.8, 8.0 in February 1958, and 1.5, 5.1, 8.2 in February 1959. (The next stage after the 1958 check, by analogy with other birds, would probably be the shedding of the first primary.) The actual dates of the checks were 17 February 1958 and 3 February 1959, which is a fortnight less than a year, while the moult had gone slightly farther than a full circle, but the parallel is still close. Further similarities of this sort can be seen in Birds 6 (April 1958 to February 1959), 9 (March 1958 to February 1959), 10 (March to March), 11 (January 1958 to March 1959) and — the most striking case — 12, where the actual dates were 21 April 1958 (scores: 2.5, 6.2, 9.5) and 27 March 1959 (scores: 2.9, 6.0, 9.5). In two other cases (Birds 7 and 13), an extrapolation would give similar answers.

c) Triple cycle: The establishment of a triple cycle has already been explained in juveniles and unmated birds. It is clear from Table 15 that in all but Bird 7 this triple cycle was continuing to operate, in that three feathers, or two (depending on the stage of the moult), were growing at one time. This means that each cycle must take more than one year to be completed, but that each feather is replaced once annually. (It also explains the annual interval between similar moult stages, described above.) This concept is somewhat difficult/

difficult to grasp until one is familiar with the whole process and also with the reading of scores, but Bird 3 may be cited as an example: In February 1958 it was growing its fourth primary; subsequent to this the moult must have paused (see later), because by the following December this cycle had reached only the seventh primary (the November and December scores, 3.5 and 4.4, preclude any other explanation), and by the next February had reached the eighth; thus in a period of a year (February 1958 to February 1959) this particular cycle had advanced only from the fourth to the eighth primary, although all the primaries had been replaced at least once. One further point should be made here, viz. that the three cycles in adults were closer together than was the case in juveniles, where the seventh primary was growing before the next cycle began with the shedding of the innermost; from the scores of eight birds examined during March 1959 it can be seen that the primaries growing were Nos. 1 or 2, 5 or 6, and 8-10. This can almost certainly be explained as due to the inner primaries taking a shorter time to complete their growth than the outer ones. Stresemann & Stresemann (1960) found this in the Accipitridae.

d) Synchrony: The similarity between the moult stages of the above eight birds checked in March 1959 suggested that there might be a synchrony of moult in the population as a whole. Accordingly all moult checks on adults were scored, and tested for this. Only slight evidence of the anticipated effect could be shown (the figures and statistical analysis are given in Appendix H). This can be explained in the following way. The White Boobies' annual breeding season would result in an annual crop of chicks of roughly the same age. Since juvenile birds commenced their moult <sup>almost</sup> at the same age, and subsequently followed a regular cycle, when such a crop of young birds begin breeding, they should all be approximately at the same stage of moult, i.e. synchronised. But as will be seen, some adults got out of phase in their breeding and moult, and breeding was not linked to any particular moult stage; further, as has been seen, even in individuals/

individuals the two wings might be slightly different in stage of moult (although this was noticeably rare in young birds whose cycles had not had time to develop any asymmetry); thus anomalies, once established, would tend to be perpetuated rather than eliminated. Hence although the synchronised breeding season would result in batches of birds being synchronised in moult, the synchrony would tend to become less with increasing age, the effect being heightened by any individual differences in age amongst the batch of chicks, which could be considerable. But the gradual removal of the older (non-synchronised) birds from the population (by death), together with the continual addition of synchronised ones, would tend to preserve a slight synchrony. A more detailed series of observations, if possible with the ages of the birds, might show if the two effects were demonstrable.

e) Breeding during pause in moult: More details were obtained about the moult of birds which bred out of phase than about those that bred at the typical time, but the following evidence from a few individuals and the series of checks on "unknown" adults (i.e. those captured only once) strongly suggests that there was a general tendency for birds not to be moulting in August and September 1958; this was just after the main peak of laying.

Before going into this in detail, I should mention the state of the primaries recorded as "no-moult". In some cases it was possible to say which of the full-grown feathers were older and which newer, but mostly this was unreliable. This unreliability was in marked contrast to the ease with which old and new feathers could be distinguished in birds which were moulting, and this suggested to me that during this no-moult period the primaries were all subjected to the same conditions for long enough to produce a uniformity in their appearance. I therefore conclude that the progress of the moult was temporarily arrested.

Two individuals, shown in Table 15, give clear evidence of what

I mean. Firstly, in the wing of Bird 8 the sixth primary was three-quarters grown in August 1958; in October, no moult was recorded; and in November, the seventh primary (the next in sequence) had only just been shed. If, as was likely, the sixth primary took two weeks to grow from three-quarters to full size, that leaves a period of about two months in which no further progress in the moult occurred. Secondly, Bird 5 was starting to grow its third primary in July, and yet in November it had just shed its fourth primary; allowing a full month, or even two months, for the growth of the third primary, it is still clear that a pause must have occurred. Table 15 shows that all the no-moult records of the "known" birds occurred in September or October, except for two in November and one in February. Also, of 13 checks made in September and October, only four gave positive evidence of moulting.

This prompted me to analyse all the moult checks made on breeding adults, month by month, noting those that were recorded as not being in moult; the results are shown in Table 16. It is clear that in the period August-November 1958 more birds were in the no-moult condition than at any other time. It was extremely unlikely that this would have arisen by chance in the sampling ( $P \ll 0.001$ ), in spite of the variable number of birds checked.

M.Lloyd has analysed these figures further. The birds checked in the period January-April 1958 were selected because they were breeding, and so the analysis has been done only on those selected at random, i.e. in the period July 1958-March 1959. The results show that the true proportion of birds moulting in the period July-November 1958 was probably (within 95% confidence limits) between 39% and 62%, while the true proportion moulting in the period December 1958-March 1959 was between 90% and 100%. November 1958 was about two months after the main hatching period, so by that time birds that had paused during breeding might have started to moult again, thus increasing the proportion of moulting birds in the figure for July-November. Figures for July/September only would show/

13	
10.8 (Jul)	
3.0, 7.0	
1.9, 5.1, 9.1	
Egg Aug. 1958 US	

Table 15.

Table 16. All moult checks on adult White Boobies and the months in which they were made.

Month	Total no. of checks	No. of birds:		% showing no moult
		In moult	No moult	
Jan '58	6	4	2	33
Feb	29	24	5	17
Mar	6	6	0	0
Apr	14	14	0	0
May		No observations		
Jun		No observations		
Jul	5	5	0	0
Aug	5	2	3	60
Sep	33	11	22	66
Oct	20	11	9	45
Nov	14	10	4	29
Dec	17	16	1	6
Jan '59	8	8	0	0
Feb	15	15	0	0
Mar	15	15	0	0

show a smaller proportion of moulting birds. This analysis therefore shows that my hypothesis of a moult pause during the breeding season was not true of the whole population, but this could be explained by a) my possibly having sampled some non-breeding birds, b) departures from synchrony which could arise as has just been discussed, and c) some birds perhaps moulting while breeding, which did occur, although under unusual circumstances (see below).

The tendency to pause in moulting thus came slightly later than the maximum courtship and laying activity, which was in July. This could mean that the pause was timed to coincide with the presence of young chicks, when the availability of food would be more important than at any other time of year. The full implication of this will be discussed later. It must be borne in mind, however, that August-November was also about the time that there was apparently a food shortage. Colquhoun (1951) found that in juvenile Wood Pigeons Columba palumbus a cessation of moult occurred during cold weather in the winter. If this was a result of shortage of food, it is conceivable that the boobies might have been affected in a similar way.

f) Moult during breedings: At the foot of Table 15 are details of the respective birds' breeding. All were occupying territories on the colony and behaved as adults and have been assumed to be so. It can be seen that although in some cases breeding occurred while the primary moult was in progress, all the individuals concerned were abnormal in breeding when the majority of the population was not doing so. Bird 3, for example, laid in January 1958 and was found to be growing its fourth and eighth primaries in February, although by that time the clutch was deserted. Bird 5 was growing primaries No. 3, 6, and 10 in July 1958, and laid in August. It could, however, have finished growing the incomplete feathers and thus reached a stage of no-moult just before laying. It laid again in the following November (well after the main peak), shed its fourth primary about the same time, and continued moulting its primaries throughout the/

the successful raising of the chick. Bird 10, the male partner of 9, was not moulting its primaries in September 1958, i.e. shortly after its unsuccessful August clutch was laid, but it started moulting them in November, about the same time as its mate laid again. Bird 11 was also found to be moulting while incubating. There is no doubt, then, that at least some individuals were able to breed and moult at the same time, although these particular birds were unusual in breeding at a time when very few others were doing so, this being what brought them to my attention.

In passing it may be noted that the male and female of a pair were in no case in exactly the same phase as regards their primary moult, although the members of pairs 1 & 2, 3 & 4, and 7 & 8 were fairly close to each other.

g) Interpretation: It was suggested to me that the moult of the White Booby might be interpreted as a post-breeding shedding of the primaries starting at two points. The outer four, because of their greater size, would grow more slowly than the inner six. A double commencement in this way would ensure enough time for a complete change of feathers in one year as well as allowing for a pause during breeding. There are, however, two arguments against this view; firstly, that there was undoubtedly a third cycle operating, and secondly, that this system did not operate in juveniles<sup>1</sup>. One further point is that if this interpretation were correct, at least in the adults, their moult would presumably start off, after breeding, at the same points in all individuals, regardless of the point reached at the end of the previous moult. There was no evidence of this except that a slight synchrony was indicated by analysis of all moult checks, and this has already been discussed.

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<sup>1</sup> Stresemann & Stresemann (1960), however, found that in some Accipitridae the primary moult of juveniles was regular while in adults it appeared to be irregular.

##### 5. Moulting in Brown Boobies.

The little information obtained about Brown Boobies indicated that their moulting was similar to that of the White. The information was difficult to obtain for two reasons: firstly, the juveniles rarely returned to the island, even then not congregating in clubs as did the White Booby juveniles, and therefore could not be caught; and secondly, the adults tended to stay away from the island when not breeding, or if present, were very wary.

One Brown Booby chick of known age returned to its birthplace when nine months old; it had not by then shed any feathers, and its entire aspect was as at fledging. It was recaptured at the same spot five weeks later, when the score for the primaries of both wings was 2.8; three weeks later the score was 3.1. This showed that the primary moulting was following the same pattern as in the juvenile White Booby and had started at roughly the same age, or slightly later. Another juvenile with a broken wing was found at Pierhead, Georgetown; because its aspect was the same as that of a chick of known age which I had recently seen (but not captured) I judged it to be about 16 months old. Its primary score was 1.5, 9.1. This suggested that a second cycle was beginning as the first neared completion, the sequence thus being similar to that in the White Booby, but with the difference that in the White Booby the second cycle started when the first had reached approximately the seventh feather, not the eighth as in this bird.

Nineteen moulting checks were made on five adults, four of which were males (Appendix I). These indicated a primary moulting starting at the innermost and working outwards in three concurrent cycles, a period of pause, and at least some breeding activity during moulting. In all these respects this species was therefore similar to the White Booby. In view of its shorter sexual cycle, however, it would be particularly interesting to know whether the moulting was also completed more quickly, and this I unfortunately have not enough data to study.

## 6. Summary and discussion.

Shedding and regrowth of the primaries from the innermost outwards, as was the case in both boobies, has been noted in the Pelecaniformes (Verheyen, 1958), but I know of no detailed information about the process in the Sulidae. The situation in the juvenile European Gannet has not been fully analysed, but is probably similar to that in the White Booby: 15-month-old Gannets were found to be growing their outer primaries (Witherby et al., 1940), and I found that White Boobies of this age were doing the same, although their second cycle would have started at the innermost primaries again by that time. Gurney (1913) noticed that a captive Gannet of about five months old was not moulting, but it began to shed feathers at about eight months old. This was about the age that I found moulting began in juvenile White Boobies. Gurney estimated that a Gannet would reach adult plumage in about two and a half years. This agrees roughly with what I worked out for the White Booby, although the adult plumage was attained gradually and a bird did not necessarily breed even when it had attained this plumage, so I could not give a definite figure. Kay (1950), on the other hand, estimated that the Gannet would not attain adult plumage until four years old.

There is likewise little published information about moult in adult Gannets. Witherby et al. found that more than 20 birds collected in September had two primaries growing, these being separated by fully-grown feathers; this strongly suggests that the moult was taking place by means of more than one cycle, as in the White Booby. They also said that adults underwent a complete moult between July and December, this sometimes extending as late as January and February. According to Gurney, the moult was between March and May, and again between August and September, i.e. (presumably) immediately before and after the breeding season. He also noticed that the moult "seemed to go on a long time" in tame birds. One can infer from this that the Gannet's moult may go on almost from the end of/

of one breeding season to the beginning of the next, which would be virtually what happened in the White Booby, if my contention (that there was a pause in the moult during breeding) is correct.

I found that the moult of the tail in boobies was highly irregular, in contrast to the regularity of that of the primaries; Gurney noticed the same thing in the Gannet. Dwight (1925) found that in the gulls (*Laridae*) the tail moult did not begin until the primaries were all or nearly all replaced, and then was irregular, although usually the central pair were the first to go. Again, therefore, the boobies are evidently not unique, and further, their peculiar tail moult need not be regarded as prejudicing the conclusions drawn about their primary moult.

The body moult of the boobies was also apparently irregular and in some birds was proceeding while the primary moult had stopped. The body moult was never found to be extensive, only a few feathers being replaced at any one time.

The relation between breeding and moulting has been rather little studied, except in northern Passerines where the moult is generally complete and post-nuptial.

Marshall (e.g. 1954) has shown that in many species interstitial exhaustion and tubule steatogenesis (in the testes) are associated with post-nuptial moult, and the general relation of the moult to this and other endocrine factors has been reviewed by Assemacher (1958); but that breeding can occur during moulting has been shown by several authors. Moreau, Wilk & Rowan (1947), for instance, reported this in an equatorial forest species which had a regular gonad cycle but an extended and apparently unrelated moult of primaries, secondaries, and rectrices. Miller (1955) found it among Passerines of an arid equatorial region, although as a general rule the moult there was post-nuptial. (This "general rule" with exceptions/

exceptions is particularly interesting since this description could be applied to the situation in the White Boobies.) Colquhoun (1951) found that Wood-pigeons had a very extended moult, during which breeding took place. Dwight (1925) found that in equatorial gulls the moult was either irregular or prolonged, and that those species with an irregular moult could be found breeding throughout so many months of the year that it was difficult to fix the peak of their moult, though probably each colony had an individual peak. He did find, however, that every species had one complete post-nuptial moult every year. Whether this involved a complete cycle of moult in the primaries, or only a replacement of each feather with more than one cycle operating at once, he did not say. The White Boobies that I found to be moulting while breeding therefore would not be unique among birds.

Three cycles of moult were operating in the White Boobies' primaries. Replacement of feathers differing from the usual method of one at a time has been noted in other species as well. For instance, Verheyen (1958) said that in birds with long wings the moult might pause for some time, and then re-start where it left off (or at the beginning again, if the pause were long), and thus the complete wing might appear to have two or even three lots of feathers of different ages. Colquhoun (1951) found that in the Wood-pigeon the moult of the primaries might stop and then start again at the beginning. Jollie (1947) observed a captive Eagle Aquila chrysaetos, in which the primaries were replaced from the innermost outwards at the rate of one per month until the seventh was shed. Then there was an unexplained nine-months' pause (June to April) before the eighth was shed, the ninth following a month later. As the eighth was shed, the first was shed again, the second being shed at the same time as the ninth. I give this in detail because it was similar to what I found in the White Booby, even to indicating that the outer feathers took longer to replace than the inner ones.

Some/

Some observations were made on moult in the other species of seabirds on Ascension, most of them showing more clearly than did the White Boobies that the moult was extended and took place between breeding. Information about the Wideawake and Black Noddy Terns is from N.P. Ashmole. Both these species, and the Fairy Tern (Appendix A), were in full plumage during the breeding season, their moult apparently occupying nearly all of the rest of the year. At the end of their breeding season, when most chicks were nearly fledged, adults could be found with their innermost primaries shed or just starting to re-grow. When birds first began to return to the nesting places for the next breeding season, some of them were found to have the outermost primaries still incompletely grown. (The Fairy Tern differed in that it was not always the outermost feathers that were still growing, and this species may well have had more than one cycle operating, like the boobies.) The terns thus had a definite post-breeding moult, differing from northern Passerines only in that the moult lasted almost until the start of the next breeding season.

In June and July 1958, Ashmole and I examined 19 Yellow-billed Tropic Birds taken from nesting holes with eggs or chicks (one a large chick); none was growing any of the primaries. 17 of them, however, were growing one or both of the <sup>inner</sup> outermost tail feathers. Whether this close synchronisation would be true of the entire population or whether the moult was tied to the breeding condition and hence the same in all the individuals we selected, we cannot tell. One bird found in a nest-hole the previous month was in company with another and presumably preparing to breed; it was growing three separate primaries in each wing. The inference from this is that the primary moult stops during breeding, the rectrices perhaps lagging behind the primaries, but much more information is required.

Finally, Ashmole and I found that about 20 Frigate Birds, all with eggs or chicks in July 1958, were in full plumage with no sign of/

of moult anywhere. They may have gone through a moult procedure similar to that of the Tropic Birds, or the terns, and completed their moult between breeding.

On rather little evidence, then, the boobies were more complex than any of these other species in their moult cycle, but like the other species they apparently tended to have a long moult with a pause during breeding. But they also tended to remain on the island when not breeding, instead of going away like the others, and so they could be periodically examined. It should be mentioned again that birds breeding at unusual times thereby received special attention, and perhaps inconsistencies have been overstressed.

The findings of this study are only partly conclusive, but they show that further work is necessary along these lines. It is evident that the moult of tropical seabirds and its relation to their breeding seasons is important, and this will be discussed in general terms later.

## VII FOOD: Feeding behaviour and prey taken.

### 1. Feeding behaviour.

No systematic study of the boobies' feeding habits could be made, but the following observations supplement the later analysis of the food taken.

Four White Boobies were once seen diving within a few hundred yards of the rocks, but the species was not otherwise seen feeding close to the shore. This was probably because the White Boobies' diet consisted mainly of Flying-fish Exocoetus volitans, which is commonly known not to approach coasts; we did not see Flying-fish on our regular trips along the two and a half miles of coast between North East Bay and Boatswain-bird Island, and only rarely off Georgetown. Brown Boobies, on the other hand, were often seen diving in the bays, usually singly. One I watched dived in 20 feet of water and emerged with a Pipefish Scomberesox saurus of 20-30 cm. held crosswise in its beak; it swallowed the fish as it flew out to sea pursued by three other Brown Boobies encountered on the way, then returned to the same spot in the bay, dived again and came up with another Pipefish. Bourne (1955) reported that the Brown Boobies in the Cape Verde Is. fed close to the shore and were never met with out of sight of land.

Large numbers of fry are occasionally found among the surf on the Ascension beaches, probably driven on shore in attempting to escape from Tunny-fish Thunnus sp. A fish obtained on one of these occasions was later identified as Selar crumenophthalmus, locally known as "Stimbras". Brown Boobies and Frigates are said by local residents to congregate to catch these fish, the boobies diving into the shallow water just outside the breakers, but White Boobies are apparently relatively rare on these occasions. Bangs (1902) reported Brown and Redfooted Boobies feeding in this way on the east coast of Florida.

Once from Boatswain-bird Island I watched a flock of boobies,  
Fairy/

Fairy Terns, Black Noddies, and Wideawakes feeding about a mile out to sea. The Brown Boobies, as on other occasions, were diving from a lower height and less vertically than the White. Brown Boobies were also seen close to the island making several successive shallow dives, although I did not know that they were actually catching fish in this way. Bryant (1859) however described Brown Boobies as fishing in this way in the Bahamas. By making frequent shallow dives, Brown Boobies might take more small fish more quickly than White Boobies, and as will be seen later one difference between the food of the two species was that the Brown Booby took a higher proportion of small fish.

As mentioned earlier, the White Boobies' incubation and brooding spells were longer than those of the Brown, which is consistent with the idea that their feeding grounds were farther from the coast.

## 2. The food.

According to Murphy (1936), flying-fish are the White Booby's principal food in the South American region, the bird's distribution apparently being the same as that of the fish. Stomachs of four birds examined contained small squids and their mandibles, together with the remains of fishes; a bird shot at sea had a flying-fish of 28 cm. inside, while another, seen on a breeding colony, regurgitated seven smaller flying-fish, and such flying-fish were said by the local lighthouse keeper to be the only recognisable part of the birds' diet that he had ever seen them disgorge.

Brown Booby chicks in the Bahamas were fed on squids and fishes (Chapman, 1908), while at another colony in the Bahamas (Bryant, 1859) the stomach of one bird contained "a great many varieties of fish, among them a cottus, a parrot-fish, flatfish of two species, and some large prawns; but their principle food seemed to be flying-fish and a species of hemirhamphus".

Little has been published since Murphy's review.

Vesey-Fitzgerald/

Vesey-Fitzgerald (1941) said that the food of the White Booby in the Seychelles consisted of pelagic fish, chiefly flying-fish Exocoetus and squids. Munro (1944), referring to White Boobies in the Hawaiian Is., said that flying-fish were plentiful near the islands and the birds almost always replete. He quoted another observer as saying that squids were also part of their diet. Gibson-Hill (1951) made observations at a Brown Booby colony on Christmas Is. (Indian Ocean); most of the eleven stomachs examined contained flying-fish Cypselurus bahiensis and squids were present to an appreciably smaller extent. No other material was identified, and he did not say over what period the stomachs were collected.

Between January 1958 and March 1959 I examined 28 food samples from White Boobies and 56 from Brown Boobies. All were regurgitations actually witnessed, but five other fish, presumably too large for chicks to swallow, were found on the ground in the colonies, and these have been included in the study. As most birds of both species regurgitated readily when alarmed, none were killed for the examination of stomach contents; three birds found soon after death had nothing in their stomachs, although injuries received in fighting might have prevented their fishing for some time prior to death. Only a very few of the samples obtained were well digested, and these were disregarded. The more timorous birds regurgitated freely, the bolder ones not at all unless handled; in general Brown Boobies regurgitated more readily than Whites, perhaps because they nested in places from which they could make a quick getaway assisted by the jettisoning of weight, whereas the White Boobies were usually more or less immobilised in the middle of a dense colony. Frigate Birds did not seem to pursue one species rather than the other, so both species probably regurgitated equally readily in the air. I handled many White Boobies, but except in one or two cases of timorous birds which regurgitated whether their stomachs were/

were full or not, it was never possible to forecast when a regurgitation was likely. Fishermen in the Seychelles have been said to obtain their bait by "teasing" the White Boobies (Vesey-Fitzgerald, 1941) but the Ascension birds did not throw up their food so readily. Large chicks usually regurgitated if roughly handled, but as far as possible I avoided causing this because they did not pick up food from the ground as do Herons Ardea cinerea (Owen, 1955), and extensive collection of samples by this method would have affected their growth. Small chicks were fed with well-digested fragments, and samples from them were useless for identification.

I noted the species, number, and estimated lengths of the fish in each regurgitation. Examples of most of the species were preserved for later identification. Large fish had usually been swallowed head-first and had often been completely digested as far as the pectoral fins, but with practice their lengths could be estimated to  $\pm$  25 mm. As will be seen, it proved unnecessary that measurements should be more accurate for the present analysis.

The food discussed in this study must be considered as that of birds at the breeding colony, and not only as food for the young. Only 23% of the samples were actually taken from chicks, the remainder being from adults which had chicks or were incubating. My impression was that outside the breeding season both species remained based on the island, but they could still have gone to sea for long periods and might have been taking different food.

In both species the prey taken fell into two clearly defined categories, those up to 10 cm. (small) and those more than 15 cm. (large). One sample from a White Booby consisted of 38 Benthodesmus of 10 cm. length, but as these fish are very slender I have included them in the size-group 5-7 cm. (Table 17).

Nearly all the small fish were 5-7 cm. long, and of them Ophioblennius was by far the commonest. (Table 18). Only half of the/

**Table 17.** Size frequency-distribution table of fish taken by White and Brown Boobies.

		No. of fish from:	
	<u>Size</u>	<u>White Booby</u>	<u>Brown Booby</u>
	4 cm. or less	3	13
"Small"	5 - 7 cm.	355 <sup>1</sup>	425 <sup>1</sup>
	8 - 10 cm.	32	10
	c. 12 cm.	0	1
	15 - 20 cm.	35	42
"Large"	21 - 25 cm.	3	11
	26 - 30 cm.	1	1
	37 cm.	1	1

- Notes:**
1. Samples containing large numbers of small fish were counted to nearest 5.
  2. In addition there were 5 "large" fish found on the ground in the White Booby colony: 3 were 26-30 cm., 2 were 31-35 cm. In the Brown Booby colony there was a similar record: 1 fish 35 cm.

**Table 18.** Prey taken by White and Brown Boobies, their numbers, and the number of samples in which they appeared.

<u>Species</u>	<u>White Booby</u>		<u>Brown Booby</u>		
	<u>No. of fish</u>	<u>No. of samples</u>	<u>No. of fish</u>	<u>No. of samples</u>	
<i>Exocoetus volitans</i>	39	20	46	26	
<i>Scomberesox saurus</i>	1	1	1	1	
<i>Selar crumenophthalmus</i>	3	1	6	6	"Large"
<i>Benthodesmus simonyi</i>	-	-	2	1	
<i>Fistularia sp.</i>	1	1	-	-	
<i>Oxyporhamphus micropterus</i>	15	6	9	6	
<i>Ophioblennius webbi</i>	300	6	260	17	
<i>Engraulis sp.</i>	26	2	75	4	
<i>Benthodesmus simonyi</i>	38	1	34 <sup>1</sup>	3	
( Cephalopods	5	3	2	2 )	"Small"
<i>Holocentrus ascensionis</i>	2	1	38	10	
<i>Centrolophus niger</i>	1	1	20	4	
<i>Decapterus sp.</i>	-	-	10	1	
Unidentified	-	-	2 <sup>2</sup>	1	

Notes: 1. 30 of these were from 1 sample

2. No specimen collected.

the samples from White Boobies contained small fish, while nearly two-thirds of those from Brown Boobies did so. Also, only 25% of the samples from White Boobies contained exclusively small fish, while for the Brown Booby the proportion was 40%. Thus the Brown Booby appeared to have a greater preference for small fish than did the White.

Nearly all the large fish were 15-20 cm. long. More fish of 21-25 cm. appeared in the Brown Booby samples than in the White, but it is unlikely that this represents a genuine difference in size-preference. 75% of the samples from White Boobies contained large fish, 46% of them exclusively, while only 57% of those from the Brown Booby did so, 34% of them exclusively, again indicating the White Boobies' greater preference for large fish and the Brown Boobies' for small.

When only small fish were taken, the average number per sample was 50 for the White Booby and 20 for the Brown. When only large fish were taken, usually only one or two were present, the mean being 1.6 for both species.

Few of the small fish were young individuals of the large species; when catching the large species, therefore, the boobies appeared to select the large individuals. Yet smaller individuals were available because they turned up in samples from Fairy Terns, Wideawakes, and both species of Noddies. Perhaps, then, the boobies went for small prey only when it was common.

The species of fish taken, their numbers, and the number of samples in which they appeared, are shown in Table 18. The Brown Booby took two more species of small fish than the White, and all but three samples of large fish from White Boobies consisted of Flying-fish Exocoetus volitans exclusively.

The distribution of samples and species over the months is shown in Table 19. Most of the samples from White Boobies were taken between January and March 1958, when adults with eggs or chicks were being handled; during the following breeding season (July to September), although as many adults were handled, fewer of/

**Table 19.** Distribution of samples and of the two main prey species over the months.

<u>Month</u>	<u>No. of samples</u>	<u>White</u>		<u>No. of samples</u>	<u>Brown</u>	
		<u>Exocoetus</u>	<u>Ophioblennius</u>		<u>Exocoetus</u>	<u>Ophioblennius</u>
Jan '58	7	3	4	5	1	1
Feb	5	5	0	3	1	1
Mar	5	4	2	3	0	2
Apr	2	2	0	2	1	1
May	1	1	0	21	18	6
Jun	-	-	-	2	2	0
Jul	2	2	0	3	0	0
Aug	1	0	0	1	0	0
Sep	2	1	0	3	0	0
Oct	-	-	-	-	-	-
Nov	2	2	0	2	0	2
Dec	-	-	-	5	0	5
Jan	1	1	0	3	0	1
Feb	-	-	-	-	-	-
Mar	-	-	-	3	1	0
Total 28		Total 56				

**Note:** The figures in the species columns represent the number of samples in which the fish appeared.

of them had eggs or chicks and fewer samples were obtained. Most of the samples from Brown Boobies were obtained in May 1958, when there were most chicks in the nest. There was a slight increase again during the following breeding season, from November to January.

The availability of the various food species throughout the period of study could not be assessed because my samples appeared at irregular intervals, and furthermore the birds were clearly selective in their fishing. Nevertheless the occurrence of some of the important prey species may be inferred from their appearance in the samples (Table 18). White Boobies took flying fish in all the months for which there were records, except August, and there was only one sample in that month. Brown Boobies, however, took no Flying-fish in March, from July to September, and from November to January. The other important fish, Ophioblennius, appeared much less regularly: White Boobies produced them in six out of 17 samples between January and March 1958 and not at all subsequently, while Brown Boobies produced them in 11 out of 34 samples between January and May 1958, not at all in the nine samples from then until September, and in eight out of 11 samples between November and January 1959. Either this species was not present outside these times or was present but in insufficient numbers to attract the boobies. When taken, it was taken more frequently by Brown Boobies than by White, and then formed a greater proportion of their diet than Flying-fish. Engraulis figured in the food of both boobies for a short time. One of the two samples from White Boobies in September consisted of 22 of these fish, and four out of six samples from Brown Boobies in July and September consisted wholly of them, no Flying-fish at all appearing in the diet during this time. All the Engraulis examined had obviously been eating -- apparently exclusively -- a bright red Copepod (later identified as Eucheta marina), and in the period when Engraulis was appearing in the food samples, the faeces of both boobies all over the colonies were dark red in colour, indicating that many birds, if not all, were feeding extensively on this fish. There might, however, have been other species/

species of fish also feeding on this common Copepod and then being eaten by the birds, but if so none appeared in the samples. Holocentrus appeared in half of the 20 samples from Brown Boobies in May and once in June (two samples), but not at any other time, and it was not present in the sample from a White Booby at that time.

Some of the small fish taken by the boobies were also taken by Black and Brown Noddies, Wideawakes, and Fairy Terns (see Appendix A). Small specimens of Flying-fish Exocoetus, and Ophioblennius, Engraulis, and Holocentrus were found in samples from all the terns at times when they were found in the samples from boobies.

As has been mentioned, previous information about the food of boobies has come from isolated records. If isolated samples, or a small series over a short time, had been taken from the Ascension boobies, the resulting picture of their food would have varied according to the time when the samples were taken. For instance, between July and September, none of the seven samples from Brown Boobies contained any Flying-fish, although three of the five from White Boobies did. Furthermore, only two of the seven samples from Brown Boobies contained any large fish. Again, four of the first nine samples I obtained from White Boobies were made up of 260 Ophioblennius (with some squids included), the other five being Flying-fish; and of the first five samples from Brown Boobies, three contained a single large specimen of Selar crumenophthalmus, one consisted of 22 Ophioblennius, and the other contained Flying-fish and squid fragments. Hence many more samples had to be obtained before the relative importance of the various prey species began to emerge.

From the published accounts, squids appeared to be an important part of the boobies' diet, but this was apparently not true of the Ascension birds, since only five samples contained squids, all of these being taken in the first four months of the study. Owen and Phillips (1956) found that regurgitations of chicks of the Purple Heron/

Heron Ardea purpurea contained many fewer insect remains than had been recorded by previous workers analysing stomach contents, and they considered this was due to the slow rate of digestion of insect parts in a Heron's stomach. Similarly, boobies probably digest squid jaws only slowly, and an analysis of stomach contents alone would over-emphasise the proportion of squids in the diet. In some places, however, squids may form a prominent part of the boobies' food, although this was not so at Ascension.

Summarising, Flying-fish were prominent in the diet of both boobies, but the birds also took other small fish, sometimes in large numbers and, particularly in the Brown Booby, to the exclusion of Flying-fish. White Boobies concentrated more on large Flying-fish, and Brown Boobies took a higher proportion of small fish of more species, and also a slightly greater variety of large fish when they did take these. Squids were recorded from both species, but were clearly unimportant as a food.

Were these two closely-related birds, living and feeding in the same area, competing? On the above evidence, there was a considerable overlap in their food, but they appeared to differ both in their feeding methods and in the variety of species taken, as well as showing a difference in size-preference. As Ascension is the only possible breeding station in a vast area of ocean, it might be argued that the two species have developed an overlap in their feeding subsequent to colonisation of the island. (Lockley and Fisher, 1954, have suggested that the Atlantic was colonised from other oceans). There are many examples of several species of birds feeding on the same type of food in the same area during a temporary abundance (Lack, 1946). I found, however, that in 1958 far from there being a superabundance of food, there was a shortage of it, and I am inclined to think that the two Ascension boobies are probably more different in their feeding than my study was able to show.

## VIII BEHAVIOUR.

## 1. Introduction.

My purpose in watching behaviour was to find out about differences between mated and unmated birds, the establishment of territories by young birds, the mechanism of pairing, and the permanence of pair-bonds and territories, and thereby to build up a picture of the structure of the colonies, which has already been outlined. The study revealed a number of behaviour patterns that have not been described before, and this section is an account of these. Closer observation might have resulted in more details of the postures and their derivation, but I have emphasised description rather than analytical interpretation.

Behaviour patterns in the Gannets Morus spp. (Peters, 1931) have been described by Armstrong (1947), Gibson-Hill (1948), Warham (1958), and Barlee (in litt.), and as they clearly differ from those of the boobies, will be discussed only where relevant.

The behaviour of boobies has been described only incidentally. Vogt (1942) briefly described the courtship of the Piquero Sula variegata, and comparison with my own observations on the White Booby shows that the two are probably similar in pair-formation, advertisement display (except that the Piquero has a "marking-time" movement of the feet, not seen in the White Booby), fighting, nest-building, and mutual preening. He said that the advertisement display of the male was similar to that of the Blue-footed Booby, and this is borne out by brief descriptions of the latter species by Rothschild and Hartert (1902) and by Murphy (1936). Since both these species nest in dense colonies on the ground like the White Booby, it is not surprising that all three should show behavioural similarities, and this, together with their morphological similarities, suggests that the three are probably more closely related to each other than to the Redfooted or the Brown Booby. As far as I know, none of the behaviour of the Redfooted Booby has been described, and therefore

I/

I include below a description of the advertisement display of this species, witnessed on only one occasion. Some of the courtship of the Brown Boobies of Christmas Island was described by Gibson-Hill (1947), but his observations differed somewhat from mine; I know of no other account. The only other species, Abbott's Booby Sula abbottii now apparently nests only in tall jungle trees on Christmas Island in the Indian Ocean (Gibson-hill, 1950b), and little is known about it. My impression from examining the five skins of this species in the British Museum is that it is closely related to the White Booby, but because of its nesting habits it may have behavioural similarities to the Redfooted.

## 2. Methods.

White Boobies were studied mostly by sitting in the colony within a few yards of the birds, which were unaffected by my presence, and field glasses were unnecessary. Brown Boobies were less accommodating, and studies were confined to a few bold pairs, supplemented by observation of others through field-glasses at a range of about 30 yards. Fewer observations were made on Brown Boobies than on White, largely because they were more often absent from the island.

About 130 days were spent at the colony island, spread over 15 months. During that time the notes on which this study are based were made as opportunity arose in the course of other lines of investigation, with occasional days or parts of days devoted wholly to watching behaviour.

The techniques/whereby individual birds were recognised have already been described; rings and paint-marks were most useful, and the birds' habit of frequenting the same spot was also helpful. A few individuals could be recognised by peculiarities of voice or plumage, but other methods were more reliable and easier to use. A few observations were made on unmarked birds. White Boobies could be caught and the ring-number checked; they were not generally upset/

upset by this and soon carried on as if nothing had happened. Sometimes the ring-numbers of birds involved in a sequence of behaviour could be checked by catching them after it was finished. Unmated White Boobies without a territory, however, tended to leave the colony after handling, and might not return for a few hours, or perhaps not at all. Such birds were therefore usually marked by splashing with paint, as this alarmed them only temporarily.

### 3. Observations.

Twelve behaviour patterns or postures of the White Booby will be described and some of them have necessarily been given new names. Briefly, events were as follows: Unmated males regularly performed an advertisement display, Sky-pointing, to which unmated females walking about in the colony responded by approaching; unmated males approached by these females might attack, or both might perform a Head-wagging movement, which was also seen during territorial disputes between established pairs. Fighting often occurred between neighbouring pairs, and a milder Sparring between members of a pair or between unmated males and females. Birds defeated in a fight (usually those that did not have a territory) might run away in a Bill-tucking posture. This and another apparently appeasing posture, Bill-up-face-away, usually occurred between unmated males and females when they came together without actually fighting. Bill-tucking was clearly related to an elaborate Bill-hiding done by chicks when attacked by wandering birds. Bill-touching occurred between members of an established pair or temporary association, i.e. a pair formed by an advertising male and a wandering female, which might later break up, and Nest-building either followed the coming-together of two unmated birds, or was performed (less frequently) by established pairs. Established pairs regularly indulged in Mutual-preening, but this also occurred between members of a temporary association, between chicks, and in the clubs. Copulation and its attendant/

attendant movements was seen more frequently among temporarily associating birds than established pairs. Two other postures, unrelated to the above events on the colony, will be described: Food-begging began soon after hatching and developed greatly as the chick grew, and in older chicks was seen to be similar to the Head-wagging of adults; and Sunbathing occurred in adults, such a peculiar position being adopted that it merited special description.

Many of these postures had extremely similar counterparts in the Brown Booby, although some appeared to be absent. Some of the observations on one species, particularly those concerned with Sky-pointing, Nest-building, and Bill-tucking, helped in the interpretation of similar behaviour in the other, and therefore the behaviour patterns of <sup>the</sup> two species will be discussed together, the White Booby being considered first in each case.

Most of the birds in the White Booby colony were mated pairs or single mated birds in an established territory, the mate being temporarily absent. Unmated birds, presumably young ones, were also in the colonies, in the proportion of about four of each sex to 100 established pairs. They were easily distinguishable from birds of established pairs by their greater activity, and but for them it would sometimes have been difficult to interpret what the less demonstrative birds of established pairs were doing. I first noticed unmated birds when most of the others had eggs or chicks, i.e. at a fairly late stage in the breeding season. Unmated males were the only ones doing the Sky-pointing display. They had no fixed territory, and moved about, but within a restricted area of about 20 yards square. An unmated male sometimes took up its station in the territory of an established pair when they were absent, behaving for the time being as if he were established, but fleeing to a nearby vacant area when the owners returned. Unmated birds never won in a fight with established ones. Besides these unmated males, there were unmated females which, by contrast, did not/

did not take up stations but walked about, apparently uneasily, in the colony. The unmated males obviously recognised them too, sometimes at distances of 30 yards, and never displayed at mated females, even if the latter were alone. Very occasionally they also displayed to a bird flying overhead, but I did not know whether such females were unmated, or even if they were females, or how such males recognised them. Once a male had seen a wandering female, he turned to fix his gaze upon her and stretched his neck upwards. Then followed the Sky-pointing display: His neck remained at full stretch, and as he threw his head back until the beak pointed vertically, he uttered a characteristic drawn-out whistle, a note that I never heard in any other context. At the same time the humeri were lifted so that the wing-tips were raised together above the tail, which was pointed up; the beak remained closed (Plates 3 & 4 and Fig. 11). After the climax he subsided again, the whole movement lasting about two seconds. The display was repeated more or less frequently (but not more frequently than every five seconds) depending on whether the female moved towards or away from him. Between displays he continued to stare at her. If she went to another male he resumed the relaxed position and appeared to lose interest in her, but would display again if she began to wander about once more. Two or three males at once might be staring at and displaying to one female. Sky-pointing males never moved from their station unless driven away; only the females moved about. Although unmated males Sky-pointed repeatedly, I saw only three birds do it when females were beside them: one Sky-pointed three times while a female was asleep at his feet, but the display was not directed at her or any other female and she did not even remove her head from under her wing; on a second occasion a male Sky-pointed at his mate in their territory, but I had not seen this male do so before and did not see him do it subsequently, the pair being under observation for more than two months; and on the third occasion the situation was/

was similar, the pair being one which I knew to have formed six months previously as a result of the male's repeated displaying. On none of these occasions did I see a stimulus that might have triggered-off the displays. All of them occurred about four months before the start of the breeding season on the colony as a whole, so it seems unlikely that impending mating was involved; and none of the pairs showed other courtship activities or laid eggs, as far as I knew, until much later.

Females Sky-pointed, to my knowledge, on only about a dozen occasions in my 15 months of study. The only difference from the male's display was that the accompanying note was a long hoarse "aaaaaah", noticeably distinct from the babble of other noises in the colony. The female was always difficult to locate, in spite of the note being so conspicuous, partly because she displayed only two or three times, and partly because her subsequent behaviour was apparently never distinctive, or if so not maintained; but I managed to see the bird concerned on three occasions: once the female was alone, and though she displayed several times, was not pointing towards any other bird and no male went to her as a result; on the second occasion a male was standing beside the female as she displayed, upon which he walked away and another male Sky-pointed at her, she then responding by going to him; and on the third occasion a female Sky-pointed several times to a bird circling overhead, following which a male (presumably the same bird) landed beside her and they preened. Once I saw a six-week-old chick throw its head into the Sky-pointing position and utter a long call like that of the female, but it was not apparently directed at any other bird.

Summing up, I conclude that these incidents were exceptional, that Sky-pointing was normally a display exclusive to males, and that its function was to attract a mate.

Once/

Once two birds had come together, they proceeded to perform other courtship activities (described below), and often copulated, but frequently they split up again and the male began Sky-pointing once more. By marking a number of unmated birds, I was able to watch Sky-pointing males form temporary associations with several different females intermittently over periods of months, and likewise unmated females did the same with different males. This went on throughout the breeding of the other established pairs. One such temporary association became permanent and the pair subsequently laid eggs, but in other cases it lasted only a day, or less.<sup>1</sup> The pair that became established did so in time for their eggs to be laid at the peak of laying amongst the other pairs; perhaps the others would have obtained mates in time for the breeding season in the July following the end of my observations in April 1959.

Sky-pointing in the Brown Booby (Plates 5 and 6) was very much the same as in the White, except that a) it often happened when the male and female of an established pair were together, and even occurred once immediately after copulation, another time while the female was incubating; b) the wings were not raised at all, only the humeri being held slightly out from the body; c) it was<sup>a</sup> faster movement throughout and was usually repeated more frequently than in the White Booby; and d) it was performed in the air, which I never saw in the White Booby. Aerial Sky-pointing was common during the period prior to egg-laying, when the pair were together at the nest site. The female would fly from the nest site, followed by the male, who while gliding would throw back his head and utter the wheezy call; often the pair flew round in a circle and returned to the nest. It would be difficult for a pair of White Boobies to take off in this way from a dense colony, and this may be the reason why the aerial display was apparently absent in that species.

Fewer observations were obtained about pair formation in the Brown Booby than in the White, but from the following evidence I

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<sup>1</sup> Details of some sample observations are given in Appendix J.

think that the process was similar in the two species:

A male (M) and two females (F1 and F2) were on an area of flat rock, each about 20 feet apart, when observations began. F2 walked away and M Sky-pointed at her, then he walked to F1 and billed with her, then picked up a feather, walked back to his original place and put it down. Then he Sky-pointed twice at F2, looking sharply at F1 after each and she at him. Then he walked past F2 to the cliff-edge, flew off, and arrived back carrying a feather which he gave to F1. He then left her, went to the cliff edge nearby, Sky-pointed several times at her, appeared to sleep (head under wing) for two or three minutes, then Sky-pointed again at her, upon which she walked to him and both walked back to his original place, which looked as if it might have been his selected nest site, from the number of pebbles lying there. Meanwhile F2 was preening. F1 flew off; M picked up and put down a pebble; then he Sky-pointed three times at F2, who looked at him but did not move. Then he went to the cliff edge, away from F2, yawned, began to preen, and paid no attention while two other males stole stones from his place. Then both he and F2 walked to his place and began nest-building and billing. Next he walked away and appeared to sleep again, while F2 began sunning. After 15 minutes, both suddenly stretched their necks up and stared at each other, presumably roused by something I did not see, M Sky-pointed several times at F2, then began to preen. There was no further incident, and eventually all flew away.

The male M must have been an unmated bird, and presumably the females were too; his display was clearly advertising and achieved responses from both females, and yet the associations he formed with them were fleeting. On other occasions I saw males Sky-pointing immediately after a female had left them, the display apparently elicited by her departure. Two single males were seen repeatedly Sky-pointing at a single female between them, and another male was seen/

seen to display to a female in flight.

Clearly, then, Sky-pointing was important in the Brown Booby in the same sort of way as in the White, i.e. as an advertisement by males, but there were differences in the details of pair-formation which cannot be fully analysed from my observations.

Sky-pointing in the Redfooted Booby was seen only on one occasion at close range. A male and female were perched about two feet apart on a steep face some 25 yards from me. Basically the posture was the same as that described for the White and Brown Booby, with head and bill raised vertically, tail up and humeri lifted, but with the difference that the wing-tips were held not above the tail as in the White Booby, but out from the body; i.e. as well as being raised, the wings were also about a quarter opened. Another difference was that the accompanying call was a throaty rasping, not a whistle; this was to be expected, as the voice of the Redfooted Booby heard on other occasions was more harsh than that of the other two species. After displaying thus two or three times, the male flew out from the cliff in a wide circle and landed again momentarily, repeating this twice. He did not display while in the air. Then the female flew round in the same way, but the male did not follow. As she landed, he Sky-pointed, and continued this for the next minute, repeating the display at about two-second intervals. Both then flew off. They were not seen again at this spot, which could not possibly have been a nesting-site, although there might have been suitable ledges for building the nest not far away. These observations suggested that the Redfooted Boobies were behaving more like the Brown Booby than the White, in that the advertisement display was performed by a male in a position which could hardly have been a territory and certainly not a nest-site; and in that the display was repeated rapidly and while the female was close.

The other behaviour patterns of the White and Brown Booby occurred/

occurred amongst established pairs as well as temporary ones, and were not apparently so important in pair-formation as the Sky-pointing.

Head-wagging was done by both sexes of the White Booby immediately before or after a fight or near-fight, but only to neighbouring antagonists, never to the other member of the pair or temporary partner. A bird would stand facing its opponent, body slightly crouched and tilted forwards, the neck withdrawn and the head pointed upwards at 45 degrees (Plate 7). The head was turned from side to side and the bill simultaneously wagged up and down rapidly and with a small amplitude, as if (anthropomorphically speaking) the bird were indicating a slow "no" and a vigorous "yes" at the same time. The posture was very similar to that of the food-begging chick (see later), except that the chick also held out its wings and called. Vogt (1942) said that Piqueros defended their territories by waving the beak at an intruder in a figure-8 movement; this is probably homologous with Head-wagging in the White Booby, although strictly in the latter it was not used in defending the territory but by birds which had been or were likely to be inferior in a fight, for example when a single bird was fighting with a pair. Head-wagging was never seen in the Brown Booby, possibly because such situations as required it would rarely arise, the territories not being close together, or because a vanquished bird would be able to make a quick getaway, or both.

In Fighting, opposing birds lunged at each other with open bills, occasionally clashing them; sometimes they grasped each other's mandibles, and then the birds might remain locked together for a minute or more, necks extended, flat on the ground, pushing (not pulling), and each trying to get a better grip. The wings were usually held out during lunging, but were never used to strike. If two pairs were fighting, they lined up male to male and female to female; fighting between the sexes was very rarely seen.

Injuries/

Injuries as a result of fighting were rare, considering the strength and sharpness of the birds' bills, but one White Booby picked up dead in the sea was found on dissection to have its sternum neatly punctured and two small wounds in the left ventricle.

Brown Boobies seemed to fight less than Whites, although in the same manner, and pairs were not seen to line up against each other; doubtless this was again because the territories were on uneven terrain and not usually close to each other, and in places where escape was easy.

Sparring, a mild form of fighting in White Boobies, occurred between male and female of a pair, more frequently if the pair was a temporary one. Sometimes a Sky-pointing male would spar with an unmated female when she first came up to him. The two sparring birds leaned forwards toward each other and rattled their open bills, but rarely for more than a second at a time, and without gripping or lunging. Bill-touching, seen only in White Boobies, was probably a mild form of Sparring, and occurred between members of a pair while Mutual-preening or Nest-building (see later) in their territory, when there was an alarm or fight among nearby pairs. Suddenly both stretched up their necks and turned to face each other, bills slightly open and tips touching (Plate 3); then they relaxed again and resumed whatever they had been doing.

Brown Boobies Spurred as above, but in this species Sparring was generally preceded or followed by Bill-pushing, when two birds, standing close together, pushed back and forwards, only their necks moving, as if to probe each other in the eye (Plates 9 & 10). Sometimes there was no more than a touching of bills (Plate 11). Probably in both species all these movements are hostile, with a decrease in aggressiveness from Sparring to Bill-touching.

Bill-up-face-away and Bill-tucking nearly always occurred together and were seen most frequently in unmated White Boobies, but also in established Brown Booby pairs. They might be done by either/

either partner when the two were separated by a short distance, e.g. when the male was returning to his mate after a short excursion to attack a neighbour, or when a female was approaching a male in response to his Sky-pointing, or when a female had left such a male to resume her wandering but turned back. The situation thus was basically one in which a walking bird approached a standing partner; the neck was suddenly stretched upwards, head tilted upwards and turned away (Plate 12). Sometimes the walk changed direction at that point. The movement reminded me of Head-flagging in the Black-headed Gull Larus ridibundus, (described by Tinbergen and Moynihan, 1952), except that the face was held up and away from the partner rather than suddenly flagged. The Bill-up-face-away occupied only three or four steps, then the bird resumed the normal walking posture and went straight in to stand beside its partner. I did not notice any posture in the stationary partner that might have caused the Bill-up-face-away, nor any following it. Sometimes the posturing bird walked in a half-circle round the partner, as if avoiding stepping within range of attack.

Bill-tucking always occurred in the same sort of situation, and sometimes alternated with the Bill-up-face-away. The neck was coiled back, Pelican-like, and the bill tucked sharply and momentarily down to the breast (Plate 13). Again the standing bird seemed to make no corresponding movements.

This same tucking of the bill occurred when birds defeated in a fight, e.g. Sky-pointing males routed from their station by established birds, were running to the edge of the colony to take flight. They were attacked by all the owners of the territories through or near which they had to pass. Unless actually gripped by a beak, they never attempted to fight back. In this posture the neck was again drawn back, chin tucked in to neck, bill pointed down (Plate 14). It was noticeable that the posture was kept up until the bird took flight or was free of attack, and was not momentary as in the Bill-tuck.

Captured/

Captured birds very often went into this form of Bill-tucking as they ran away after being released. It was noticeable that this running form of the posture was never seen in the Brown Booby, although Bill-tucking was common, and again probably this was because Brown Boobies beaten in a fight could easily escape.

The Bill-hiding of White Booby chicks was clearly related to the above postures. Occasionally an unmated male would stand beside a chick whose parents were absent, and either preened it, behaving like a guarding parent, or violently attacked it. I did not see any behaviour on the part of the chick that might have caused the one or the other, and sometimes the adult alternated between them. The adult lunged at the chick's head, upon which the chick tucked its face and bill right under its breast (Plate 15), and the attacker then usually gripped and shook the back of the chick's neck. Some chicks, whose heads were raw and stripped of down, had obviously been frequently attacked. As soon as the chick hid its bill, the attacking stopped, and sometimes no attack followed the Bill-hiding. Chicks never attempted to run away, remaining in the posture for several minutes or until the attacker went away; indeed they had no alternative, for every time they raised their heads the attack was renewed. If an attacking male had found a temporary partner, the female might also attack the chick, or both might guard and preen it. Sometimes adults stood on a Bill-hiding chick, and twice I saw a male attempt copulation with one. Warham (1958) saw both Bill-hiding and attempted copulation in similar situations in the Cape Gannet.

In the Brown Booby, Bill-up-face-away and Bill-tucking were very much the same as in the White, and likewise were seen only between members of a pair. (~~Plates 16 & 17~~). I noticed them most in males, Bill-tucking exclusively so, except once when a female Bill-tucked after sparring with another female. The reason for this might have been either that males most often walked away from the nest, e.g. to collect material, or that the male was relatively smaller than the female/

female compared to the White Booby, and therefore more readily employed an appeasement posture. It was noticeable also that in Bill-pushing the female did more pushing than the male. Bill-tucking regularly occurred after a male walking near his partner had to make a small jump on to a rock (Plate 16); at such a moment he would be off-balance and at a slight disadvantage if attacked, and I think this further indicates that Bill-tucking was an appeasement posture.

Bill-hiding was never seen in Brown Booby chicks, perhaps because wandering birds apparently did not visit nests and the necessity for it thus did not arise. Cullen (personal communication) tried attacking Brown Booby chicks and could not elicit the Bill-hiding response from them, although he could do so from White Booby chicks.

From the above evidence, I conclude that the bill, always used in fighting, has an aggressive signalling function, and that hiding it, or turning it away, reduced the likelihood of its invoking an attack. Warham (1958) saw that Australian Gannets landing on the edge of a colony -- where presumably they might be afraid -- tucked their beaks, and Cullen (personal communication) has seen in the Cormorant a movement similar to that of the male Brown Booby when Bill-tucking after a jump. A further comparison with the Black-headed Gull can be drawn; Tinbergen and Moynihan (op. cit.) interpreted Head-flagging as opposite in function to the Forward-aggressive posture in which the face and bill are presented to another bird, and likewise Bill-up-face-away is probably opposite in function to the forward-lunging seen when boobies are fighting, when the conspicuous face is presented to the opponent. The White Booby's orange-yellow bill and the brilliant yellow eyes are set in the inky-black gular and facial skin, the whole surrounded by the white head. The Brown Booby's face is also conspicuous, and it seems no accident that its blue eye-rim and strong yellow gular skin (especially pronounced in the nuptial period) are set in the background of/

of a chocolate-brown head and neck (Fig.12). As the main aim in fighting appeared to be the grasping of the opponent's bill, to hide the bill and turn away the conspicuous face is presumably appeasing. Cullen (1957) interpreted the hiding of the bill by the Kittiwake Rissa tridactyla in the same way.

Nest-building, especially the collection of material, was done mainly by the male of both species. In the White Booby, the male left the female and walked away from the territory, (generally only a few steps, but up to 10 yards was once seen when he was not attacked by neighbours) picked up a minute granule of guano, or feather or fish-bone, in the tip of his bill, and paced back to the female with it, placing it in front of her in a deliberate manner. She bowed her head and the tips of their beaks almost touched as the object was deposited. This deliberate bowing movement was characteristic of the incident, and sometimes occurred even although no object was being deposited. Sometimes bowing was not preceded by the male's walking away, and the pair might simply bow to touch some tiny object near the male's feet, their bills close together (Plate 17). Sometimes the female took an object such as a feather from the male's bill and herself deposited it, but usually the object was too small for this. The depression that formed the nest could not have been made in this way, but clearly the activities were important in strengthening the pair-bond. No scraping with the feet was ever seen, and I never found out how the nest was actually made; in some nests the hard surface-crust of guano had been broken, and this might have been done by the feet. Occasionally I saw a bird at a nest site go into a posture like the above bow, with the tips of the bill open near the ground, but there was no up-and-down striking movement of the head that would indicate digging, only a slight quivering which was also seen sometimes as objects were deposited at the end of the bow, and I do not think this movement helped to make the nest depression. Cullen (personal communication) thought this movement closely resembled one seen in the/

the Cormorant, which is a good nest-builder. None of the White Boobies' nests were on very sloping ground, so that a nest of any sort was rarely important for the safety of the eggs (though many were lost, as mentioned earlier, probably because of desertion), and hence the Nest-building activities just described could have become largely ritualised.

Nest-building was also a prominent feature of courtship in the Brown Booby. Males made repeated visits to the sea to collect feathers, which were placed on the nest-site or taken from the bill by the females, the depositing always being a joint bowing movement like that of the White Booby. The movement resulted in a posture that resembled the female's copulatory position, because the neck was slightly arched and the bill quivered as the object was deposited; copulation sometimes did immediately follow the bow of Nest-building, and once I saw it while the female was holding a feather (Plate 18). Quivering of the bill might be the only remaining traces of a movement that would assist the fitting of material into the nest, as it does in other birds, but the Brown Boobies' nests were all so rudimentary that the movement could hardly be important in this connection. Nests were very variable in size, depending on the availability of heavy material and the exposure of the site, because feathers, although assiduously collected at times, were usually blown away; for instance two nests on the flat top of the island were heaps of bones, feathers, and shreds of old guano bags, 18 inches across and with a depression in the middle in which the eggs were laid, while in other places eggs were laid on bare rock with only a few small stones round them. I put a pile of stones and feathers near one such nest before the eggs were laid, and immediately the male ceremoniously carried each object over to the female, even accepting a feather from my hand.

Nest-building, then, was more functional in the Brown Booby than the White, in that more material was used and pebbles at least could be useful in preventing the eggs rolling away, but it was also clearly highly ritualised in courtship.

Mutual-preening/

Mutual-preening was very common between members of established pairs in the White Booby, but less so between partners of a temporary association. It also occurred occasionally between a parent and its chick, amongst groups of larger chicks which formed when their parents had left them for long periods, and between adjacent juveniles and adults in the clubs, irrespective of age or sex. Mutual preening could not therefore be described as purely a courtship ceremony, although it was clearly important in courtship. The two birds involved rapidly nibbled each other delicately but searchingly about the head and neck, rarely elsewhere, and if one bird began the partner almost invariably reciprocated (Plate 19). Bouts of Mutual-preening usually lasted for several minutes, and were often preceded or followed by self-preening. Mutual-preening is performed by many birds (Armstrong, 1947), usually about the head and neck, and Goodwin (1956) suggested this might be because of head-infesting ectoparasites, but the subject has been little studied. Certainly the White Boobies were infested, and usually on the neck and throat, by Hippoboscid flies, Olfersia aenescens C. G. Thomson.

Mutual preening was not seen in Brown Boobies, which were also infested by the same Hippoboscids. In view of its prominence amongst the White Boobies, this is extraordinary, especially as there seemed to be ample opportunity for the members of established pairs to preen each other. As has been mentioned, Brown Boobies were never seen to congregate in clubs as did White Boobies, and in White Boobies Mutual-preening might conceivably have started as a social behaviour pattern in these clubs and later become incorporated into courtship, while such a development could not take place in the Brown Boobies. It would however be difficult to support this argument with evidence from other species; for instance male and female Fairy Terns regularly preened each other while sitting on their nesting ledge prior to laying, and Fairy Terns certainly had no clubs or other social gatherings.

#### Copulation/

Copulation in the White Booby occurred between temporarily associating birds as well as between mates. Mounting was not regularly preceded by any display or posture; the pair could be Nest-building or Bill-Touching or Mutual-preening, but most often the pair appeared to be simply standing together. The copulatory posture of the female has already been mentioned, and the male attempted to mount as soon as the female adopted this. Occasionally a male would lift a foot and stretch his neck over the female's without her being in this posture, but mounting never followed this, or if so was momentary and ended in a bout of Sparring. Usually the first indication of an impending copulation was the male's lifting a foot to paw the female's back, but closer observations showed that the female was already in her posture before he began this. As the male mounted, his neck was stretched over the female's, and when in position on her back his neck was arched over her shoulder, bringing their heads side by side. During copulation the male did not trample, or grip the female's neck, but as she raised her tail he wagged his sideways until a momentary cloacal contact was made, upon which he raised his head backwards; dismounting followed immediately. There was no regular post-copulatory movement; the female adopted her normal stance, and the pair either touched bills or fiddled with granules of guano or nest-material, or bowed, or began Mutual-preening, or Spurred.

The above description applies equally to copulation in the Brown Booby, except that it was sometimes followed by a short spell of Bill-pushing.

Two other postures, Food-begging of chicks and Sunbathing of adults were not apparently connected with any of the behaviour sequences described above, (except Head-wagging, see below), but they have not been described before in boobies, and so will be dealt with here.

Food-begging/

Food-begging was the same in both species. Naked chicks of a day or two old weakly raised and waved their heads, this being accompanied by a faint tip-tip-tipping. Intensity was greater in older chicks. In fully-feathered chicks it was more intensive still, sometimes violent. Such chicks sometimes begged quietly but continuously even when the parent was absent, the begging increasing in vigour when the parent arrived. If a chick was being fed, other chicks nearby sometimes started begging, mildly, but did not face the feeding adult. A begging chick crouched, head held back and bill pointing up; the head was turned from side to side, the bill at the same time being bobbed up and down, the call being uttered continuously. At high intensity the whole movement was much faster and the noise louder, and then the wings were held out, and waved up and down, primaries almost touching the ground (Plate 20). At low intensity, the wings were not held out, and then the posture was indistinguishable from the Head-wagging of the adult White Booby. The chick was not necessarily facing its parent, although it might wave its head more in that general direction, nor did it move towards the parent while actually begging. If the parent was a little distance away the chick stopped begging momentarily, but kept its wings out, and flopped towards the adult, resuming begging at closer range. It then made occasional lunges at the adult's beak, sometimes striking with its wing, and sometimes succeeding in forcing its own bill inside, although this did not necessarily result in its obtaining any food. Adults were apparently quite tolerant of this persistence, and attempted to avoid the chick only by turning their heads this way and that. Curiously, Food-begging was most persistent in chicks that were able to fly.

In Sunbathing, the body was tilted forward; the head was held horizontal, the beak was opened and the gular pouch vibrated rapidly. The wings were unfolded backwards until they formed a diamond or kite-shape, the angle between humerus and ulna-radius being/

being about 120 degrees, and the wing-tips were crossed above the depressed tail (Plate 21). The bird maintained this posture as long as the sun was hot, folding its wings if a cloud passed over, and re-opening them to the kite position when the sun came out again. The position was adopted by means of a movement similar to that used when stretching a wing. The gular vibration often occurred without the kite posture, especially among incubating birds. Sunbathing was seen most frequently in the clubs, although it occurred occasionally on the colonies as well, and as there were no Brown Sooty clubs, this might be one reason why Brown Boobies were seen to Sunbathe less frequently. This difference in behaviour could hardly be due to the difference in colour of the two species, because, confusingly, the dark Black Noddies Sunbathed regularly, while the white Fairy Terns did not.

#### 4. Summary and discussion.

The behaviour patterns of both species may be interpreted according to the situations in which they occurred. Fighting, Head-wagging, and Sparring clearly involved fear situations, while Bill-touching, Nest-building, and Mutual-preening (sometimes) were sexual in character. The Bill-up-face-away and the Bill-tuck, both employed by a bird liable to attack from its partner, were postures obviously based on concealing the face and bill, which, because of their conspicuous pattern and importance in fighting are presumably aggressive features. Bill-tucking while running away, and Bill-hiding by chicks when attacked, were clearly similar in function. The female's copulatory position, presumably submissive, was also slightly similar to the movement of tucking the bill.

Sky-pointing was purely an advertising display, with no obvious fleeing or attacking components. It may be derived from the position adopted prior to take-off, in which the bill is pointed upwards and the wings slightly raised and opened (Plate 22), although this/

this position is held only momentarily. If so derived, the posture has become considerably exaggerated, in that the head is thrown back, the tail cocked up, and the humeri are more raised. The position in which the wings are held during the display varies considerably in different species: in the Brown Booby they are scarcely raised at all, in the White they are held up but not out, in the Redfooted (on the basis of one series of observations) they are held both up and slightly out, and in the Blue-footed they are almost completely extended sideways (Murphy, 1936, illustration). Gibson-Hill (1948) briefly described in the Cape Gannet a posture similar to Sky-pointing and called it a sexual display, distinguishing it from that species' taking-off posture. Tinbergen (1959) saw this same head-raising in Cape Gannets, in birds that he thought were afraid but "rooted to the spot", and he related it to similar postures in the courtship of the European Gannet. Fisher and Lockley (1954), and Barlee (in litt.) described and photographed what appears to be this same posture in the European Gannet, and called it a taking-off posture, not connected with display. Thus there appears to be some confusion over the matter, but one might conclude that the postures in all these species are related, although conceivably they might have different functions. Daanje (1950) considered that a similar posture in the Cormorant was derived from an intention movement of flying-up.

Nest-building and Mutual-preening were two patterns important in strengthening the pair-bond. The former was clearly ritualised, since exaggerated movements were carried out while the material used was largely functionless for the nest. Mutual-preening was likewise probably ritualised as a courtship ceremony, being much commoner in courting and paired birds at the nest site than in others.

The differences between the behaviour of the Brown and White Boobies could be related to differences in nesting habits. Firstly, in the Brown Booby the Bill-up-face-away and Bill-tuck occurred between/

occurred between members of a pair, but no Head-wagging, nor Bill-tucking while running, nor Bill-hiding of chicks were seen; and in the White Booby the advertisement display was restricted to birds on the ground but in the Brown Booby it was aerial as well. All of these points are probably connected with the fact that the Brown Boobies' territories were in places from which they could quickly take flight and into which intruding birds were unlikely to wander.

Secondly, both the advertisement Sky-pointing and the appeasing Bill-up-face-away and Bill-tuck occurred between members of established pairs in the Brown Booby, but mostly between unmated birds in the White. Outside the breeding season, the Brown Boobies tended to be absent altogether from their territories, whereas the White Boobies were more or less permanently resident. Thus the male and female of a Brown Booby pair might have become unfamiliar to each other during absence from the nest site (although territories and mates were the same from one breeding season to the next), and advertisement and appeasement postures, clearly connected with unfamiliarity in the birds concerned, would be necessary to re-establish the pair bond.

Only the Brown Booby collected nest-material (feathers) from the sea, and although its behaviour in nest-building was otherwise similar to that of the White Booby, its use of material was greater and the nest sometimes a considerable structure.

Mutual-preening, common among White Boobies, was never seen in Brown Boobies. This may have been connected with their not congregating in clubs, but mutual preening occurs in such a number of species of varied social habits that one cannot draw conclusions from comparisons with only the White Booby.

It is just possible that the two species' differing behaviour patterns were a result of differences in nesting habits only at Ascension. On the Bahama Cays, the Brown Booby nests are dispersed widely over flat ground (Chapman, 1908) and on Goenoeng Api the nests/

nests of the White Booby are on flat spaces amongst vegetation where the territories cannot be closely juxtaposed (Hoogerwerf, 1959); I would expect the bird's<sup>02</sup> behaviour to be somewhat different in such situations from those on Ascension. It would be interesting to see in what way they differed, and a study of this would help in the understanding of how the behaviour of the two species had been evolved, and how plastic the patterns are.

## IX GENERAL CONCLUSIONS AND DISCUSSION.

It was found that both species of booby, and the Fairy Tern, had marked breeding seasons on Ascension, the White Booby and Fairy Tern breeding annually (but at different times of year), and the Brown Booby less than annually, with a sexual cycle of about eight months. Individual birds conformed to the general pattern. Presumably there would not be marked breeding seasons unless external factors were operating to control them, and this will be discussed below.

Both boobies laid two eggs but raised only one chick, and further, both had a very low breeding success, not only because chicks died, but also because many birds failed to breed at all or deserted their eggs, this being due (partly on the evidence of unusually lengthened incubation spells) to the parents' experiencing difficulty in finding food. There was, however, no evidence that adults were dying from lack of food although many chicks did so.

On the basis of these findings, it is possible to consider further what factors might be important in the regulation of the population, as well as in the control of the breeding time.

The feeding range of the boobies, and indeed of many seabirds, is relevant to the question of availability of food during the breeding season, particularly when the chick has to be fed. A shorter time was spent away from the nest after the chick had hatched than before, suggesting that the parent did not then feed as far from the colony, and possibly not farther than would enable it to return to the chick before the food it had collected was digested. (This reduction in time spent away from the nest after the chick had hatched was particularly noticeable in the White Booby). Since food was apparently carried in the stomach, it is reasonable to suppose that the adult could not suspend digestion.

I found that food was often delivered to the booby chicks in a well-digested state even when they were able to, and at other times did, take food that was hardly digested at all. The question is open to further investigation, however, as the boobies might conceivably have been able to hold their food in a distended oesophagus, or have had some inhibitory power over their digestion, but I do not think this was likely.

Assuming that digestion cannot be inhibited, it follows that the birds must have had to get back to the colony before the food collected was digested, and certainly before the chick began to starve. In the case of the Fairy Tern, which carried food in the bill, birds would have to get back to their chicks before the food dried up. Hence the area in which food could be obtained would be reduced to an area determined by the birds' "digestion range" as soon as the chick had hatched.

Now in a species of seabird with a vast area of ocean at its disposal for finding food, it is at first difficult to see how adult mortality (and hence the population) could be controlled by the availability of food. (Extrinsic factors, such as predators and disease, may be excluded from this discussion, as neither boobies nor Fairy Terns had any predators; see also Lack, 1954, and Wynne-Edwards, 1955). But the birds' numbers and the time of their breeding, could be controlled by variation (perhaps only slight) in the food supply near the colony during the breeding season. In times of shortage, accentuated by the restriction in foraging range, the adults would have a low breeding success, resulting in a small recruitment to the population. The adults themselves would normally be able to survive by giving up their attempt to breed and then utilising the food still available to free-ranging birds. It should be noted that the breeding success would be density-dependent under this system; for example, if the breeding population were high and the availability of food low, the over-exploitation of that food by the adults attempting to breed would reduce/

reduce the over-all breeding success of the colony; while if the population were lower, breeding success would be higher, even though the total amount of food available was the same.

It may be generally true that the food supply of tropical seabirds is not normally very variable, i.e. is not abundant for a short period as is well known in temperate land-birds, and therefore the raising of even one chick may be difficult. In such circumstances, selection would favour a long growing period of the chick, a small clutch, or a brood that could easily be reduced to the minimum if conditions demanded; these features were clearly seen in the boobies. Wynne-Edwards (op.cit.) has pointed out that such features are characteristic of many seabirds; as a rule they tend to have a small clutch, tend not to replace lost eggs, have a slow-growing chick, and sometimes a long reproductive cycle; all these could have been imposed upon them (i.e. selected for) by food not being sufficiently abundant at any one time to allow of a short, highly-productive breeding season.

In this way the adult population could be maintained at a relatively constant level, fluctuations in availability of food resulting primarily not in variability of adult mortality but in variability of number of young raised and hence recruitment. Paludan (1951) concluded this about the Herring Gull Larus argentatus, in which two forms of the same species had very different adult mortality rates but the numbers were maintained at a constant level in each by a difference in the mortality of the chicks. The same result would be achieved if the mortality was not only amongst the chicks but also took the form of desertions or failures to attempt breeding, as happened among boobies, and as mentioned earlier has also been shown by Southern (1959) for the Tawny Owl.

At this point the significance of the moult cycles must be considered. Pitelka (1959) has suggested that in the Steller Jay Cyanocitta stelleri the timing of the moult, which imposes a considerable/

considerable physiological strain on the bird, is closely related to the time of maximum food abundance, and questioned whether the timing of the moult, not the breeding season, was more closely related to that abundance. There seems no reason why this should not apply equally to other species. In both boobies, the moult was considerably extended, appearing to go on continuously with only a pause during breeding (although some individuals breeding out of phase with the main population were moulting while in some stage of their breeding season). It is also relevant that in the Fairy Tern although the moult appeared to be irregular, not beginning and ending at fixed points, it nevertheless quite distinctly stopped throughout the breeding season (Appendix A). This prolongation of the moulting period is again consistent with the idea that the availability of food is fairly constant throughout the year; during breeding, especially during the raising of the chick, i.e. when the bird's range is restricted and its food requirements at the same time greater, the moult is stopped. This is presumably because the combination of moulting and breeding would create a greater demand in food than the supply would allow. The moult also goes on slowly throughout the remaining period presumably because at no time is food sufficiently abundant to allow of a quick moult. That three cycles of primary replacement were running simultaneously in the White Boobies (and possibly also Fairy Terns) could be due to the need to renew all the primaries each year without flight being impaired by a gap at any one point. In this connection it was unfortunate that more was not discovered about the moult of the Brown Booby, whose inter-breeding period was shorter than that of the other two.

Having considered how food might control population and the moult cycle, it remains to be seen how it might also control the timing of the breeding seasons in the Ascension species. (Other factors, of course, may be involved in these and other species elsewhere, depending on the circumstances, e.g. availability of nest/

nest sites, or periods of climatic unfavourability.) In the present case it appears that the difference in timing between the White and Brown Boobies could be attributed to differences in their feeding, just as the different timing of the Fairy Terns' breeding could be attributed to their feeding on other small fish, whose period of greatest availability might come at a different time of year. The Brown Booby's eight-month cycle, however, resulting in its breeding at about the same time as the White Booby every two years, could mean that its sexual cycle is also regulated basically by an annual variation in oceanic conditions, but that its food supply is sufficiently constant (and different from that of the White Booby) to make possible an attempt at an extra breeding season, i.e. three in two years. Thus by concentrating on different food the two species may have evolved differences in their biology which have allowed them to respond to the same underlying factors but in different ways.

If food, then, is responsible for the timing of the breeding seasons in the boobies and Fairy Tern (and possibly the other Ascension species as well), there are presumably annual variations in its availability, and these variations, although small (as has been mentioned), could be effective as regulators of the breeding time.

Variations in the marine environment which could be effective at Ascension have already been discussed (pages 41-44). Stonehouse (in press) has described the marine environment of the South Atlantic with reference to Ascension, and cites various authors who have noted areas of upwelling cool water, phosphate concentration, plankton distribution, and other related factors; but he concludes that little is known about the breeding biology of fish in tropical surface waters or of their distribution and relative abundance at different times of year. Further study might reveal a connection between these oceanic changes/

changes and availability of food for the birds, resulting in a cyclical variation that would control their times of breeding.

In conclusion I would recall the words of Hutchinson and say that if further biological observations confirm these tentative suggestions, the oceanographic phenomena will have acquired still greater significance.

## Appendix A.

The Fairy Tern Gygis alba.

## 1. Introduction.

This species was studied in parallel with the Boobies and with the same objects. A strict comparison between the two is not warranted, because they are not closely related, and therefore only a short account is given in this Appendix; a full account of the study will be published separately. There are some points, nevertheless, where similarities and differences between the Fairy Tern and the Boobies are relevant to the question of breeding, and these are dealt with here.

About five pairs of Fairy Terns nested on the horizontal boughs of a small grove of rubber trees Ficus sp. at the foot of the west slope of Green Mountain, and about 100 pairs on the inaccessible cliffs of the west face of Green Mountain and the west face of Weatherpost; scattered pairs also nested on the south east face of Weatherpost, on the sea cliffs of South East Head, and those immediately opposite Boatswain-bird Island. I think the total of these colonies was not more than about 200 pairs. The main nesting place was Boatswain-bird Island itself, where I estimated there were about 500 pairs. The estimation of numbers was everywhere difficult because the nests were often widely scattered on inaccessible and sometimes invisible ledges. My area of study included about three-quarters of all the accessible nests on Boatswain-bird Island, and these numbered about 150. My known nests numbered 110 in the first season and 103 in the second.

## 2. Breeding seasons.

It was quite clear that the Fairy Tern had an annual breeding season. Table 1 shows the number of new eggs found in each month. There was a marked peak in the number of new eggs in January of both 1958/

Appendix A Table 1.

Breeding seasons of the Fairy Tern.

	Number of new eggs laid in:									
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun-Sep	Total
Season I (1957-8)	4	8	17	32	20	21	4	4	0	110
Season II (1958-9)	1	11	14	37	27	13	-	-	-	103

Note: There were 8 known replacements in Season I and 21 in Season II, of which 11 were in March.

Appendix A Table 2.

Fairy tern: intervals between successive layings of individual pairs.

Interval	8	9	10	11	12	13	14	(Months)
No. of pairs	1	8	7	14	21	6	2	(Total 59)

Note: These intervals are between the first recorded laying in Season I and the first recorded laying in Season II. Because some of the first attempts in Season I (i.e. late 1957) were not seen, the intervals in some cases are probably too short.

1958 and 1959, although laying began in the previous Octobers and gradually built up to this. Laying continued in the two months following the peak, after which it quickly fell off. Birds were seen around the island in small numbers during the other months of the year, and a few eggs (five or ten, not more) were laid on the island in these months, but not in my study area. Ringed adults were seen at their old nesting places occasionally in August, and more frequently in September and October; it could not be said that the Fairy Terns were leaving the island entirely as did the Wideawakes, but on the other hand they were not so obviously resident as were the Boobies.

The figures in Table 1 include repeat layings after the loss of an egg. In the first season there were eight known repeats, but some of the first attempts recorded might also have been repeats from eggs lost before my arrival. In the second season 11 of the 21 repeats occurred in March, showing that laying of first eggs fell off sharply after the peak in that season.

15 pairs of birds were ringed in the first season and in all but three cases they returned with the same partner to exactly the same spot to breed in the second season. (The three apparent exceptions could have been mistakes on my part, since the birds had to be caught by netting, butterfly fashion, and usually two or three birds hovered about one's head at the same time so that the wrong one was liable to be caught). I therefore assumed that in all cases where eggs were laid in the second season on the same site as in the first, the same birds were involved. There were 59 such cases; all doubtful ones were discarded. Table 2 shows the intervals between the layings of these pairs. 35 of the 59 pairs had an interval of 11 or 12 months. The remainder may have been different through my having missed their first laying.

On the basis of the two peaks of laying a year apart and the intervals between laying of individual pairs, I conclude that at Ascension the Fairy Tern breeds annually, between December and February/

February, with some laying in the two months before and after. The species thus resembled the White Booby in respect of its sexual periodicity but differed in its season being at the "opposite" time of year; it therefore also differed from the Brown Booby in both timing of breeding and periodicity.

### 3. Clutch, incubation, brooding, and behaviour of the young chick.

Invariably one egg was laid. I found two cases of a second egg (which, judging by shape and pattern, was presumably laid by the same bird) placed very close to the first, but in both cases it was clear that the first had been deserted before the second was laid. In nearly every case the spot on which the egg was laid was so small that another egg could not have been balanced alongside it anyway. Also, the egg was relatively so large that the bird could not cover more than one, although a few individuals tried to do so if given an extra egg. The care with which a bird settled on or rose from its egg was delightful to see. It was remarkable that so many eggs were successfully balanced on such awkward places. I witnessed one case of an egg being laid precisely on the spot on which it was to remain, for it could not subsequently be moved. A series of experiments in which eggs were moved from their original site showed that the birds' attachment was more to the site than to the egg.

Both sexes incubated. The partners usually changed over at dawn (12 out of 14 observations) and the spells of incubation were of either 48 or 72 hours. (I had two definite records of 48-hour spells, one of 54 hours, and two of 72 hours; and another five incomplete records of 48 hours and two of 72 hours). In this respect the Fairy Tern had longer spells than the Brown Booby (about 24-hour spells) and also, though by a smaller margin, than the White Booby (about 48-hour spells).

The incubation period was about 36 days. I had one record of this length and another of 37-40 days. In the latter case the egg was apparently left unattended for up to two days in the early stages;

stages; it may have been incubated for short periods while I was absent, since records were taken only at about every three hours during the day and not in the middle of the night. I knew of one other case where the egg was also left unattended for unknown periods. Presumably events of this sort lengthened the apparent incubation period by varying amounts. The eggs were very well camouflaged and none was known to be predated, therefore they could probably be left unattended without danger. This was not true for the Boobies, whose territory was occupied by other birds unless guarded. Very little fighting over nest sites was seen among Fairy Terns.

The chick was brooded only for the first few days, and thereafter was left alone for long periods except at night, when one of the parents usually roosted nearby. Like the egg, the chick was well camouflaged and its efficient claws enabled it to cling safely to tiny ledges. The Boobies could not leave small chicks because of hunting Frigate Birds, but no Frigate could manoeuvre itself in the cliff winds so as to get a Fairy Tern chick, even if it could see the chick in the first place. Frigates were able, however, to develop considerable skill in picking up the cryptic Wideawake chicks from the ground.

Some of the Fairy Terns' eggs were lost through being laid in too insecure positions. One bird laid twice on a smooth ledge and lost the egg both times because a Black Noddy chose to land there; I cut a notch in the ledge and the Fairy Tern laid again in this, successfully. A few chicks also fell. Once they had fallen, the parents could not or did not find them; therefore the chick's ability to hang on had a high survival value.

#### 4. Breeding success.

The breeding success of the Fairy Tern in both seasons was higher than that of either of the two Boobies. It should be remembered/

remembered that the Boobies laid two eggs to the Fairy Terns' one, but even considering the success as per clutch, the terns' was higher. 46% and 34% of the eggs laid were known to hatch in the first and second seasons respectively (Table 3.) Nearly all the remainder disappeared without trace; in the first season, for instance, only 10% were known to be deserted or failed to hatch for other reasons, such as becoming cracked (perhaps at laying) although not falling from the ledge. It was possible that some, or perhaps many of the eggs which disappeared without trace did actually hatch, the disappearance being due to the very young chick dying or falling off, but I do not think there was a major loss of small chicks through falling, as few were found below cliffs with many nests. In the first season only nine chicks (18% of those that hatched) were known to die before fledging. Another 10 unaccountably disappeared. 67% of the chicks that hatched in the first season survived to fledging. A comparable figure was not obtained in the second season, because not all the chicks were ready to fly when I paid the final visit to the colony. Eighteen (78%) of the 23 chicks hatched were still alive at my final visit. This figure would presumably have been a little lower by the time the chicks reached the flying stage.

Largely because of the high loss of eggs, only 31% of the attempts at breeding in the first season were successful, while in the second season the figure was less than 26% (see note to Table 3). These figures were, as I said earlier, higher than those obtained for either of the Boobies, though not much higher. (14% of the White Booby clutches laid resulted in a chick fledging, while the figures for the Brown Booby were 10% and 26% in Seasons B and C respectively. The Boobies of course had two eggs per clutch).

Replacement of lost eggs has already been mentioned in connection with the peaks of laying activity. In the first season the number of replacements could not be accurately determined, but in the second, of 45 eggs or small chicks known to have been lost, 21 were replaced, seven of them being lost again and replaced a second/

Appendix A Table 3.

Breeding success of the Fairy Tern.

	No. of eggs laid	No. of young hatched	No. of young flew	Young flew: young hatched	Young flew: Eggs laid
Season I	110	51 (46%)	34	67%	31%
Season II	68	23 (34%)	18 <sup>1</sup>	78% <sup>1</sup>	26% <sup>1</sup>

Note: The number of eggs laid in Season II was actually 103, but as the success of eggs laid later than 25 February could not be known, only the eggs laid before then have been included.

1 The 18 chicks of Season II were not known to fly, hence this figure and the following two would doubtless be reduced if the final successes were known. But by analogy with the previous season they would probably not be greatly reduced.

second time. 22 other first losses were however not replaced.

#### 5. Moult.

Forty-one adults were examined for the state of moult, 98 checks in all being made. Seven birds were checked on five occasions each, these five checks spanning a year in each case. The results were puzzling and here I shall only say that there was no obvious uniformity. The following conclusions however could be drawn: a) The moult in the primaries proceeded from the innermost outwards, perhaps starting at more than one point. b) The birds were in full plumage while breeding (i.e. from about a fortnight before laying until the chick was about two months old - but this period varied), and indeed for almost the whole of their time of attachment to a nest-site. There were no exceptions to this general statement; that is to say, no birds with eggs or young chicks were found to be moulting primaries or rectrices, although in some birds a few body feathers were growing. c) Six of the seven birds checked on five occasions had feathers growing at two points and one at three; therefore either the moult was proceeding from two points or a multiple cycle was operating as in the Boobies. d) The main moult took place between the breeding seasons. This is a corollary of b) above, but there was also positive evidence of it from the seven birds examined five times each. e) There was some evidence that at the start of the breeding season the primary moult did not stop at the same point in all individuals.

#### 6. Food and feeding.

Fairy Terns were never watched feeding at close quarters, but twice I watched parties of them through binoculars at a distance of about half a mile. They were feeding in company with White and Brown Boobies, Black Noddies, and Wideawakes. The Black Noddies were practically invisible at that distance, but appeared to be feeding in the same manner as the Fairy Terns, which swooped very fast from a height of above 20 feet and seemed to pick things from just above/

above the surface, without touching the water. This behaviour was quite distinct from that of the Wideawakes, which were surface-plunging. The boobies were of course diving, and it is possible that in this instance the Fairy terns and Black Noddies were snatching the fish disturbed into leaping out of the water by the boobies. I did not see what fish were being taken. Under other circumstances Fairy Terns presumably catch fish by means of shallow plunges like other terns; a Hatchet-fish Sternopyx and a Myctophid Lamponyctus, both deep-water species by day and therefore not likely to leap out of the water like flying-fish, were taken from a Fairy tern which must have caught them by plunging early in the morning while they were still at the surface.

Fish carried by birds not actually caught were recorded if seen close enough to be recognised, but mostly the records of the Fairy Terns' food were from adults captured while carrying a fish. Once a chick had been fed the sample was irrecoverable, because chicks did not regurgitate, differing markedly from the boobies in this respect. Only one sample was regurgitated by an adult on handling. The 37 samples obtained therefore represent food brought to chicks, with the single exception. I had no reason to believe that the adults' food was in any way different, but it could have been so without my knowing. Once an adult male known to be courting (its mate laid a few weeks later) was seen carrying a fish, but nearly always birds seen with fish could be found to have chicks.<sup>1</sup> Since the breeding seasons were well defined, the majority of the food samples were also from a restricted period of the year. Thus 29 of the 37 food samples were taken from December to March in both seasons, and only three from the intervening period of June to November. Very little therefore was known of the Fairy Terns' food in that time.

The kinds of prey taken and the number of samples in which they occurred are shown in Table 4. The number of species was slightly greater than that taken by the Brown Booby, and greater again than

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<sup>1</sup> In spite of this case there was no other evidence that the carrying of fish by the male played any part in courtship as it does in other terns (Cullen, 1960), nor was courtship feeding ever observed.

that taken by the White Booby. As I had 84 samples from the Boobies and only 37 from the Fairy Tern, this suggests that the terns' diet was considerably more varied than that of the boobies. Only one Cephalopod was recorded, which was remarkable because these turned up regularly in the food of both Black Noddies and Wideawakes.

It can be seen from Table 4 that only Benthodesmus, Ophioblennius, and Oxyporhamphus (a small Flying-fish) were found in more than three samples. This suggests that these were relatively more available than other fish, but it was clear that the Fairy Terns also took other fish when they became abundant. For instance, several birds were seen to be carrying Decapterus on two days in March 1959 (three only were recorded, however,) but this fish was never seen at any other time. Black Noddies were also taking these fish then, and presumably a shoal was around. The birds may have been taking other such temporarily abundant species between my visits and therefore without my knowledge.

There was some variation in the size of prey taken. Fish of 5-8 cms were commonest, but occasional larger ones such as Scombroids and Exocoetus up to 10 cms were seen. Twice single Benthodesmus of 15-20 cms were seen to be fed to chicks; these were very slender fish. Very small chicks, however, (up to a week old) were fed with fish so small as to be invisible except at very close quarters. It has been suggested, perhaps because of this, that Fairy Terns feed their young by regurgitation at first, a thing which I never witnessed. In one case I witnessed, the near-invisible fish fed to a day-old chick was a semi-transparent Trichurio of 15-20 mm.

All the fish identified and listed in Table 4 are pelagic and not inshore species. This is consistent with the fact that Fairy Terns were never seen to fish close to the shore. The fact that the incubation spells were as long as 2-3 days also suggested that the adults might be wide-ranging in their feeding.

Finally, it may be mentioned that all the specimens of fish taken/

Appendix A. Table 4.

Prey taken by Fairy Tern.

Species	No. of fish etc.	No. of samples	Months in which they occurred
<i>Benthodesmus simonyi</i>	20	8	Feb '58 (3), Dec '58 (3) May '58, Feb '59
<i>Centrolophus niger</i>	4	4	Feb '58, Jan '59 May '58 (2)
<i>Decapterus</i> sp.	3	3	Mar '59
<i>Diaphus dumirili</i>	1	1	May '58
<i>Donichthyes rondeletii</i>	2	2	Mar '58, Feb '59
<i>Exocoetus volitans</i>	1	1	Jan '59
<i>Holocentrus ascensionis</i>	4	4	Apr '58 (4)
<i>Lamponyctis guentheri</i>	1	1	Feb '58
<i>Nomeus albula</i>	1	1	Feb '58
<i>Ophioblennius webbia</i>	7	5	Jan '58, Dec '58 May '58, Feb '59 (2)
<i>Oxyporhamphus micropterus</i>	11	6	Feb '58 (3), Oct '58 Jun '58, Feb '59
<i>Priacanthus cruentatus</i>	3	3	Jul '58, Jan '59 Feb '59
<i>Sternoptyx diaphana</i>	1	1	Jan '59
<i>Trichurio</i> (?) sp.	3	2	Jan '58, Feb '58.
Undetermined Scembroid	3	2	Mar '59 (2)
Undetermined Cephaloped	2	2	Mar '59

Note: The total number of Benthodesmus was made up of single fish except for two samples of six and eight fish each. There was one sample of six Oxyporhamphus.

taken from Fairy Terns were in excellent condition, apart from a double beak-mark behind the gills where the fish had been held. This, combined with the birds' catholicity of taste, makes them a possibly valuable means of sampling the small-fish population of an area of ocean. Certainly the Ascension Fairy Terns provided us with a presentable collection of pelagic fish that we should not otherwise have obtained.

#### 7. Summary.

1. The Fairy Tern on Ascension had an annual breeding season, with a peak of laying in January, and most individuals which were known to breed the first season bred again approximately a year later in the second.

2. The clutch was one egg, the incubation period about 36 days, and the incubation spells 2-3 days, both sexes participating.

3. Breeding success was higher than in the boobies, but there was still a considerable loss of eggs. The number of young raised from eggs laid was 31% in the first season and 26% in the second. In the second season about half of the pairs that lost their egg laid again.

4. A moult of all the feathers took place while the birds were not breeding. They did not completely desert the breeding colony like the Wideawakes, and a few records were therefore obtained for the intermittent period. These showed that the primaries were moulted from the innermost outwards, at two points (perhaps more) simultaneously, and that there was no uniformity in the population; in all respects therefore the Fairy Terns' moult resembled that of the Boobies except that some of the Boobies moulted while breeding.

5. The kind of prey taken varied, and 15 species of pelagic fish were recorded as being brought to the chicks. Some of these species appeared to be temporarily abundant. Only one Cephalopod was recorded in the total of 37 samples.

Appendix B.

Measurements of Brown Boobies.

<u>Males</u>			<u>Females</u>		
Rt. wing (mm.)	Culmen (mm.)	Weight (gms.)	Rt. wing (mm.)	Culmen (mm.)	Weight (gms.)
380	90	950	415	92	1200
395	87	900	415	95	1150
385	87	850	405	92	1450
380	89	900	410	96	1350
380	91	1000	405	91	1200
390	88	1050	400	91	1150
370	89	1050	400	99	1400
390	89	1100	400	95	1400
390	88	1100	395	94	1250
410	-	1200	400	95	1100
380	-	1200	390	91	1250
400	-	1200	410	91	1300
400	-	1100	410	95	1400
410	-	1100	400	93	1150
			420	-	1400
			400	-	1430
			400	-	1550
			410	-	1450
			390	-	1400
			410	-	1500
			420	-	1550
			400	-	1550
			420	-	1450
			410	-	1400
			400	-	1400
			420	-	1300
<u>Means</u>	<u>390</u>	<u>1050</u>	<u>406</u>	<u>93.5</u>	<u>1350</u>

For all three sets of measurements the difference between means of male and female is significant. ( $P < 0.001$  in each case, variance taken into consideration.)

Appendix C.

White Boobys intervals between layings.

<u>1st laying</u>	<u>Success</u>	<u>2nd laying</u>	<u>Interval (months)</u>
4.12.57	US	cl.8.58	8
16.11.57	S	25.8 and 11.11.58	9½ and 2½
cl5.12.57	US	mid.8.58 (US)	c 8
cl-30.9.57	S	early.8.58	10-11
1-30.9.57	S	early.8.58	10-11
11.11.57	S	6.8 and 11.11.58	8½ and 3
1-30.9.57	S	early.8.58	10-11
late.9.57	S	early.8.58	10-11
late.9.57	S	early.7.58	9-10
23.12.57	US	cl.9.58	8½
c4.12.57	US	c20.7.58	8
early.1.58	US	26.7.58	7
c9.12.57	US	25.7.58	7½
c6.12.57	US	mid.8.58	8½
c5.12.57	US	28.7.58	8
early.12.57	US	24.6.58	c6½
early.1.58	US	mid.7.58	c6½
c7.12.57	US	early.8.58	8
cl0.1.58	US	mid.8.58	c7½
c3.12.57	US	mid.8.58, 5.12.58	8½ and 3½
c5.1.58	US	25.7.58	7
cl5.1.58	US	24.9.58	8½
late.4.58	US	31.12.58	8
27.4.58	½S	24.3.59	11
2.5.58	½S	3.4.59	11
5.4.58	S	29.3.59	11
1-4.6.58	US	c20.9.58	4
1.6.58	US	2.4.59	10
1-28.2.58	S	29.11.58	c.10
mid.8.57	S	5.7.58	11½
15.12.57	S	mid.4.59	15½
c.mid.8.57	S	early.7.59	22½
late.5.58	US	13.9.58 US 1.5.59	3½ and 7½
mid.7.58	½S?	early.7.59	12
c30.7.58	US	early.7.59	11

Notes: S = chick fledged  
 ½S = chick lived at least 9 weeks (½ fledging period)  
 US = eggs failed to hatch or chick died.

Appendix D.

Breeding Seasons of White and Brown Boobies throughout their ranges.

Locality	Latitude	Date of Laying:		Author
		White Booby	Brown Booby	
A. Ascension	8 S	Jan 1878	-	Penrose 1879
Ascension	8 S	-	Aug 1922	Wilkins 1923
Porto Rico	18 N	-	Feb-Mar 1927	Danforth 1931
Los Hermanos	15 N	Jan 1908	Jan 1908	Lowe 1909
S. Domingo	22 N	c. Apr 1859	Feb 1859	Bryant 1859
Cay Verde	22 N	-	Jan 1907	Chapman 1908
Swan Is.	18 N	-	Feb 1929	Fisher & Wetmore 1931
Roques & Orchila	12 N	-	Feb-Jul	Phelps & Phelps 1959 a, b.
C. Verde Is.	15 N	-	Aug 1951	Bourne 1955
S. Paul's Rocks	1 N	-	Dec 1902	Micoll 1908
S. Paul's Rocks	1 N	-	Nov 1921	Wilkins 1923
Bissagos Is.	10 N	-	Oct 1938	Maclaren 1950
B. Mait Is.	11 N	Aug 1942	-	North 1946
Latham Is.	7 S	Nov 1936	-	) Moreau 1940
Latham Is.	7 S	Dec 1938	-	) Vesey-Fitzgerald 1941
Seychelles	5 S	Sept-Oct	-	Nicoll 1908
Glorioso	12 S	-	Mar 1906	Gibson-Hill 1941
Cocos Keeling	12 S	Jun 1941	Mar-May	Gibson-Hill 1947
Christmas Is.	10 S	-	Mar-Jun	Hoggerwerf 1939
Coenoeng Api	8 S	Jul 1938	c. Feb 1938	Gibson-Hill 1950 c.
Pulau Perak	6 N	-	Oct-Nov 1948	

Appendix D (contd.)

	Locality	Latitude	Date of laying:		Author
			White Booby	Brown Booby	
C.	Raine Is.	11 S	c. Oct 1958	Dec 1958	Warham pers. comm.
	Willis Is.	16 S	c. May	Apr	Reithmuller 1931
	Bunker Gp.	24 S	-	c. Oct. 1927	Napier 1928
D.	Phoenix Is.	5 S	Jun 1891	Jun 1891	Lister 1891
	Canton Is.	5 S	Apr-Aug	-	Murphy et al. 1954
	Christmas Is.	1 N	Oct-Dec 1953	-	King 1955
	Hawaii	21 N	Feb-Apr	-	Richardson 1957
	Hawaii	21 N	-	Jan	Richardson & Fisher 1950
E.		)	Dec 1898	-	Snodgrass & Heller 1904
		)	Jan 1902	-	Rothschild & Hartert 1902
		)	May 1903	-	Beck 1904
		)	Oct 1905	-	Gifford 1913
		)	Jan 1906	-	Gifford 1913
		)	Jan 1923	-	Beebe 1924
		)	Jan 1954	-	Eibl-Eibesfeldt 1959
		)	Aug 1957	-	Eibl-Eibesfeldt 1959
		)	-	Aug 1905	Gifford 1913
		)	Jun 1905	-	Gifford 1913
		)	-	Sep 1905	Gifford 1913
		)	-	-	-
		)	-	-	-
		)	-	-	-

Notes: 1. Only records stating eggs or chicks seen are included. Dates refer to time of laying, in some cases calculated from descriptions of chicks.

2. A = Atlantic and Caribbean, B = Indian Ocean and Red Sea, C = West Pacific and Australasia, D = Central Pacific, E = East Pacific.

3. Where the year is not stated, observations were over more than one year.

Appendix E.

White Booby incubation spells.

Nest DA: First egg laid 1400 hrs 25 August 1958.

Stage of incubation	Parent	Duration of spell, hrs.	Time of change.
1st day	F	1 hr	1500
	M	24-28	15-1900
	F	43+	
17th day	M	70+	
	Then M began to stand over eggs, 6 hrs later flew off. 3 hrs later seen nearby. Both present 12 hrs later. M seen 3 days later. Deserted.		

Same nest, first egg laid 11 November 1958.

2nd day	F	5+	2200-0700
	M	24+	
12th day	F	6+	2200-0700
	M	7+	
20th day	F	28+	2300-0600
	M	31+	
33rd day	F	8+	2200-0700
	M	34	1730-1900
	F	24	2100-0630
	M	13	19-2100
	F	24	2100-0700
	M	7+	
Chick 6 dys old	F	5+	14-1900
	M	22	1430-1900
	F	16	11-1400
	M	3+	
" 18 dys old	M	2+	13-1500
	F	7	19-2200
	M	9-13	22-0700
	F	4	1130-1600
	M	15	0730-1300
	F	7	1930-2230
	M	10	0930-1400
	F	5	1930-2300
	M	15	1430-1700
	F	5	1700-2200
	M	15	13-1400
	F	1+	

Nest DG5: First egg laid 1400 16 September 1958

2nd day	M	24+	
13th day	F	9+	2200-0700
	M	33	16-1830
	F	21+	

Deserted by next visit

Appendix E ctd.

White Booby incubation spells ctd.

Nest DB1 First egg laid 8 August 1958

Stage of incubation	Parent	Duration of spell, hrs.	Time of change
2nd day	M	30+	1600
	F	48	13-1600
	M	22	1400
	F	laid second egg.	
16th day	M	54	15-1900
	F	43+	
33rd day	F	22+	1300
	M	9-15	2200-0530
	F	38	1530-1900
	M	46+ then left	
	neither for 33 then F & M present. Both seen following day nearby. Deserted.		

Same nest, first egg laid 11 November 1958.

2nd day	F	28+	2100-2230
	M	8+	
13th day	F	6-15	2200-0700
	M	7+	
20th day	M	2+	18-2000
	F	47	19-2230
	M	18+	
34th day	F	1+	2200-0730
	M	63	17-1900
	F	18	1300
	M	9-17	2200-0600
	F	14	2100-0700
	M	7+	
Chick 8 dys old	M	8+	2200
	F	15	1430
	M	7	2200
	F	13	11-1400
Chick 21 dys old	F	6+	13-1900
	M	15	0700-1200
	F	4	16-1930
	M	17	15-1930
	F	24	1930-2300
	M	8	0730-1430
	neither	3-8	
both	?	2200-0800	
M	5+		

Nest DB2 First egg laid 20 August 1958

6th day	F	2+	13-1500
	M	47+	
21st day	M	48+	1530-1830
	F	c.72, then left M returned 24 hrs later, stayed 42+ Deserted by next visit.	

Appendix F.

Brooding spells, White and Brown Booby.

White Booby:			Brown Booby:		
<u>Age of chick</u>	<u>Nest</u>	<u>Duration of spell (hrs)</u>	<u>Age of chick</u>	<u>Nest</u>	<u>Duration of spell (hrs)</u>
5 days	DA	22	6 days	B59	19
		16			5
8 days	DB	15			17
		7			19
		13			6
18 days	DA	7			2
		9			15
		4	7 days	120	4
		15			20
		7			18
		10			6
		5			18
21 days	DB	15	25 days	B59	1
		4			8
		17			12
		24			2
		8			5
					3
			4		9
			36 days	B59	6
					13
					10
					12
					4
					3
					10
Total no. spells:		20	Total no. spells		27
Mean duration:		11.6 hrs	Mean duration		9.3 hrs.

Notes:

1. Only complete spells are included.
2. The age of the chick in each case is its age at the beginning of the series of observations.
3. Between the last two observations on the Brown Booby, i.e. on the B59 chick c. 39 days old, there was a period of c. 3 hours when the chick was alone.

Appendix G.

a) Case-histories of artificial twins, White Booby.

<u>Nest no.</u>	<u>Age at start.</u>	<u>Chick 1.</u>	<u>Chick 2.</u>
1	2 days	Slightly below normal at 6 days, very low at 12, died at 13.	Normal to 12 days, lost weight by 16, died before 23.
2	2 days	Slightly behind ch. 2 but nearly normal until 16 days; dead by 23.	Normal until 16 days, dead at 23.
3	1 day	Normal until 4 days but at 10 had not increased, died at 11.	Normal until 4 days, no gain by 10, but picked up by 14 and nearly normal at 21; rate fell at 27, died 29.
4	1 day	Slightly below normal until 12 days but at 17 well below and newly dead on 18.	Normal at 5 and 12 and 18 days, gone by 24.
5	2 days	Normal at 4 days; at 17 recently dead, wounded, out of nest, but nearly normal weight.	Same as Chick 1. Nest probably deserted.
6	1 day	Grew slowly until 19 days, not much behind ch. 2 but well below normal; died before 32 days.	Grew as Ch. 1 until 38 days, when it was less than a third normal weight. Disappeared.
7	1 day	Above normal at 4 days. Dead at 14 but not much smaller than Ch. 2.	Above normal at 4 days. Slightly below normal weight but not measurements at 14; dead at 15.

Appendix G ctd.

b) Case-histories of artificial twins, Brown Booby.

<u>Nest no.</u>	<u>Age at start</u>	<u>Chick 1</u>	<u>Chick 2</u>
1	8 days	Normal to 14 days, then was out of nest, but crawled back; normal at 23 days, but Ch. 2 now in nearby nest. Proceeded normally.	Normal to 14 days, normal at 23 days but now in nearby nest. Proceeded normally.
2	4 days	At 6 days below normal but growing; up to normal at 16 days, but now in nearby nest. Proceeded normally	Normal at 6 days and still so at 16, but now alone in nest. Proceeded normally.
3	8 days	Lost weight by 10 days; nest deserted by 14 days.	Gained slightly by 10 days but below normal. Deserted by 14 days.
4	3 days	Had gained no weight by 5 days, was ejected on 9th day.	Normal at 5 days and continued so.
5	10 days	By 12 days had gone. (Was the original chick of this nest.)	At 12 days was normal and continued so.
6	14 days	Gone by 16 days.	Normal at 16 days and continued so.
7	7 days	77 gms. at start, but wing and culmen same as Ch. 2. Disappeared same day.	97 gms. at start. Proceeded normally.
8	5 days	No gain in weight by 8 days (probably due to twice-daily weighings). Disappeared by 18 days.	Same as Ch. 1. at 8 days, normal at 18 days. Proceeded normally.

Appendix H.

Moult of adult White Boobies: scores for all checks; and time (in two-week periods) when they were made, Jan 1958 - Mar 1959.

<u>No. of checks</u>	<u>Time</u>	<u>Score</u>
4	Jan 2	3.75, 7.5, 8.75, 9.8
24	Feb 2	1.2, 1.5, 2.25, 2.9, 3.2, 3.4, 3.75, 4.0, 4.0, 4.1, 4.5, 4.75, 5.25, 5.5, 5.75, 6.0, 6.1, 6.2, 6.4, 6.5, 6.75, 6.9, 6.9, 7.2, 7.25, 7.9, 7.9, 8.0, 8.1, 8.75, 8.8, 9.2, 9.25, 9.75, 9.9, 9.9, 10.1, 10.1, 10.1, 10.3, 10.5, 10.9
2	Mar 1	1.5, 4.0, 6.5, 8.3
4	Mar 2	1.1, 3.1, 5.2, 7.0, 7.2, 9.0, 9.2
14	Apr 1	1.1, 1.9, 2.0, 2.0, 2.1, 2.5, 2.7, 2.75, 3.1, 3.5, 3.75, 4.9, 5.3, 5.75, 5.9, 6.2, 6.5, 6.6, 6.7, 6.75, 6.9, 6.9, 7.1, 7.3, 7.5, 9.25, 9.3, 9.5, 9.9, 9.9, 10.0, 10.4, 10.5, 10.5, 10.5, 10.9, 10.9, 10.9
3	Jul 1	2.0, 3.1, 5.5, 6.0, 6.9, 9.75, 10.1, 10.2, 10.3
2	Jul 2	5.5, 9.75, 10.75
2	Aug 1	5.9, 6.8, 10.25, 10.25
10	Sep 1	2.0, 3.75, 4.25, 4.75, 5.0, 5.5, 7.0, 7.25, 8.6, 8.8, 9.1, 9.8, 9.9, 10.25, 10.75, 10.9
1	Sep 2	10.75
5	Oct 1	3.0, 4.75, 6.25, 6.85, 7.0, 8.0, 10.75
6	Oct 2	1.25, 4.0, 4.2, 6.75, 7.0, 7.25, 7.25, 7.5
7	Nov 1	1.25, 3.0, 3.1, 3.5, 4.9, 7.0, 7.0, 8.5
3	Nov 2	1.9, 2.5, 4.0, 7.1
3	Dec 1	1.75, 3.3, 4.75, 7.9
13	Dec 2	1.1, 1.75, 1.9, 2.1, 2.9, 3.7, 3.9, 3.9, 4.4, 4.5, 4.8, 4.9, 5.0, 5.0, 5.1, 7.1, 7.3, 7.5, 7.6, 7.6, 7.75, 8.1, 8.25, 8.5, 8.9, 9.2, 9.25, 9.25, 10.9
2	Jan 1	3.75, 7.1
6	Jan 2	1.9, 3.3, 4.2, 4.25, 4.25, 4.4, 5.75, 7.6, 8.0, 8.25, 8.9, 8.9, 9.9
12	Feb 1	1.1, 1.1, 1.5, 1.75, 3.75, 4.0, 4.75, 4.9, 5.0, 5.1, 5.25, 5.5, 6.1, 6.1, 7.25, 7.3, 7.6, 7.75, 8.2, 8.5, 8.5, 8.6, 9.0, 9.75, 9.9
3	Feb 2	1.75, 2.9, 6.0, 9.6
15	Mar 2	1.1, 1.25, 1.3, 1.5, 1.6, 1.9, 2.25, 2.6, 2.7, 2.75, 2.9, 3.75, 3.75, 4.4, 4.5, 4.9, 5.0, 5.0, 5.3, 5.7, 6.0, 6.0, 6.5, 6.5, 6.75, 6.9, 7.1, 8.25, 8.5, 8.75, 8.75, 8.75, 8.9, 9.1, 9.1, 9.2, 9.5, 9.75, 10.25, 10.25, 10.25, 10.5, 10.75

Total 140

## Appendix H. ctd.

### Argument.

Adults were captured at irregular intervals and in varying numbers throughout the study, which was divided into two-week periods and all birds examined in each period grouped together. The scores of these birds were also grouped, e.g. in Mar 1, two birds were examined and their scores were 1.5, 6.5 and 4.0, 8.3 respectively; the group score for that period was therefore 1.5, 4.0, 6.5, 8.3. All scores for the whole study were plotted against time, and it appeared that there was a pattern of moult in the population, particularly after July. (This was probably because the birds examined before July had been selected because they were breeding, and <sup>as</sup> ~~has~~ already been seen, these were not in phase with the rest of the population, and their moult therefore probably not representative.) The birds' triple cycle of moult in the primaries made scoring and analysis difficult; and birds in the no moult condition could not be scored at all.

However, I erected the hypothesis that the birds examined were not moulting independently of one another but were somehow synchronised. This hypothesis was examined for me by J.F. Scott, Unit of Biometry, University of Oxford, as follows, his conclusion being that there was only ~~very~~ slight evidence of the anticipated effect.

First, it was tested whether the distribution of scores in each month could be regarded as rectangular, i.e. random throughout the range. For no month was this unlikely, nor was the composite test for all months (July 1958 - March 1959) significant,  $X^2$  with 27 degrees of freedom being 25.41.

Secondly, the scores in each month were divided into those below and above 6.0, and these were tested to see whether they followed the same pattern from month to month. If my hypothesis was right, sometimes one half should have two peaks and the other one peak, and vice-versa, hence giving an irregular pattern.

However, it was very likely that the pattern was the same,  $X^2$  with 7 d.f. being 5.82.

Finally, the same test was carried out with the scores in four groups. Certain months had to be grouped together to give large enough numbers. The result is given below.

Month	Moult score			
	1 - 3.4	3.5 - 5.9	6.0 - 8.4	8.5 - 10.9
July-Sep	3	8	5	17
Oct-Nov	7	6	12	2
Dec	7	11	9	6
Jan-Feb	8	14	12	11
Mar	11	9	8	15

$X^2$  is significant here ( $P < 0.05$ ), being 22.62 with 12 d.f. Thus there is some evidence that the pattern of moulting was not uniform from month to month.

Although it cannot therefore be said that the moult was synchronised throughout the population, at least not closely, the lack of uniformity established by the third test must indicate that not all the birds examined were moulting in an entirely unrelated manner. This has been explained in the text.

- Notes:
1. Birds found to be in a no-moult condition could not be scored and have been omitted from the above analysis.
  2. No observations were made between April 2 and July 2, i.e. over four two-week periods.
  3. 13 birds scored early in the study were scored again subsequently, so the sample is not of 140 different birds.
  4. During the first part of the study (January to March 1958) some of the birds checked were selected because they were breeding; as they were in this respect out of phase with the rest of the population, their moult may also have been unusual, and therefore the third test was done on birds caught at random after July 1958,

Appendix I

Details of moult in Brown Booby.

<u>Bird no.</u>	<u>Date</u>	<u>Moult</u>
6555 Male	28/7	R 3.8, L no moult
	29/10	no moult R & L
	3/12	R no moult, L 2.2
	5/4	R 1.0, 5.8, 9.8; L 4.8, 8.8 (Mate laid late March)
6470 Male	13/11	no moult (R 6 & 10 old).
	16/12	R 2.0, 6.3; L no moult
	16/1	R 2.9, 6.9, 10.0; L 3.8
	27/3	R 7.8, 10.9; L 1.3, 8.1, 10.9 (Mate recently laid)
6615 Male	28/10	no moult
	25/11	no moult. Mate recently laid
	3/1 & 16/1	no moult
	27/3	R 5.8, 8.8; L 1.1, 4.8, 7.8
6500 Male	28/7	no moult. Recently laid
	30/9	no moult
	24/11	R 1.3, 10.0; L 2.0, 10.0 Courting
	29/12	R & L 1.9, 6.3, 10.5 Recently laid
	17/1	R & L 6.8, 10.9
	27/3	R & L 3.0, 7.5
6344 Female	15/2/58	R 1.3, 7.3; L 6.2
	1/12	no moult. Recently laid

## Appendix J.

### Details of behaviour in unmated White Boobies.

A male (M1) was seen Sky-pointing on 7 May 1958, and again on 22 May, 25 May, and 5 June, always alone. On 6 July he was with a female (F1) and behaving as if paired to her. Two days later F1 was seen copulating with a different male at the place where M1 had been. On 30 July M1 was alone at this place, Sky-pointing again, and F1 was not present. On 11 August F1 was at this place with another unmarked male, possibly the same one as before. On 13 August M1 was again Sky-pointing there, F1 being absent. On 28 August he was found in the same place, incubating an egg, and his mate turned out to be F1. Subsequent to this, although the egg was lost by 29 September, the two birds were not seen with other partners or anywhere else but in this territory, the last observation of them being at the end of the following February.

Another male (M2) was first seen Sky-pointing on 12 August; on that day he formed a temporary association with two different females. A month later he was seen again with another unmarked female. Two months after that, having been seen three times in the interim, always alone, he was seen Sky-pointing and was joined by a ringed female (F2), and he attempted to copulate with her. A month later, he was again alone and twice was seen to display at different females. Three weeks later he was seen with F2 again; then three times alone, then in February with another ringed female, F3. M2 was thus first seen on the colony towards the end of a breeding season, and after seven and a half months of associating with at least seven different females, was still unmated.

F3 was also first seen in August, and subsequently with at least three different males, several other times alone on the colony, and was still unmated by the following March. F4, another ringed female, behaved in a very similar way over the same period.

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It is unfortunately impracticable to acknowledge by name all those who have been of assistance throughout this work in many different ways, some small, some great, but I am very grateful for all their help. I should like particularly to thank the Expeditions Committee of the British Ornithologists' Union for the opportunity to do this enjoyable work, my fellow-members on Ascension for help with field work and for a great deal of profitable and pleasant discussion, and Dr. David Lack, F.R.S., for hospitality at the Edward Grey Institute and much advice and encouragement.

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Fig. 11. White Booby Sky-pointing, extreme example.

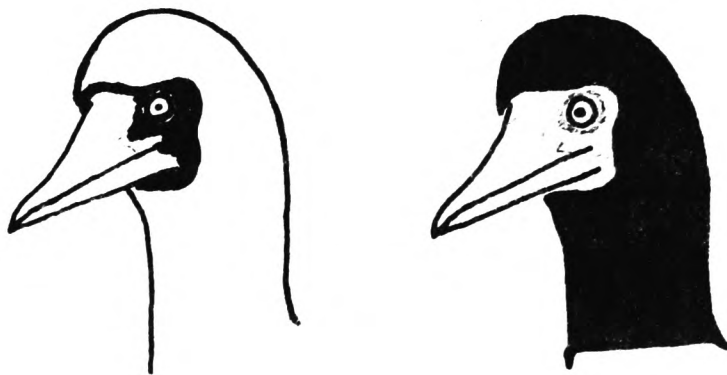


Fig. 12. White and Brown Booby face patterns.



**Plate 1. South East Head and Boatswain-Bird Island  
from Weatherpost.**



**Plate 2. White Booby chick being fed.  
Note bulge in adult's neck.**



Plate 3. White Booby Sky-pointing.



Plate 4. White Booby Sky-pointing, female on left.



**Plates 5 & 6. Brown Booby Sky-pointing.**



Plate 7. White Booby Head-wagging.



Plate 8. White Boobies Bill-touching.



Plates 9 & 10. Brown Boobies Bill-pushing; male on left.



Plate 11. Brown Boobies Bill-touching.



Plate 12. Bill-up-face-away, male White Booby.



Plate 13. Bill-tucking, male White Booby.



Plate 14. White Booby Bill-tucking while running.



Plate 15. White Booby chick Bill-hiding.



Plate 16. Male Brown Booby Bill-tucking.



Plate 17. White Boobies bowing during nest-building.



Plate 18. Brown Boobies copulating, female holding feather.



Plate 19. White Boobies Mutual-preening.



Plate 20. Brown Booby chick food-begging; male parent in foreground.

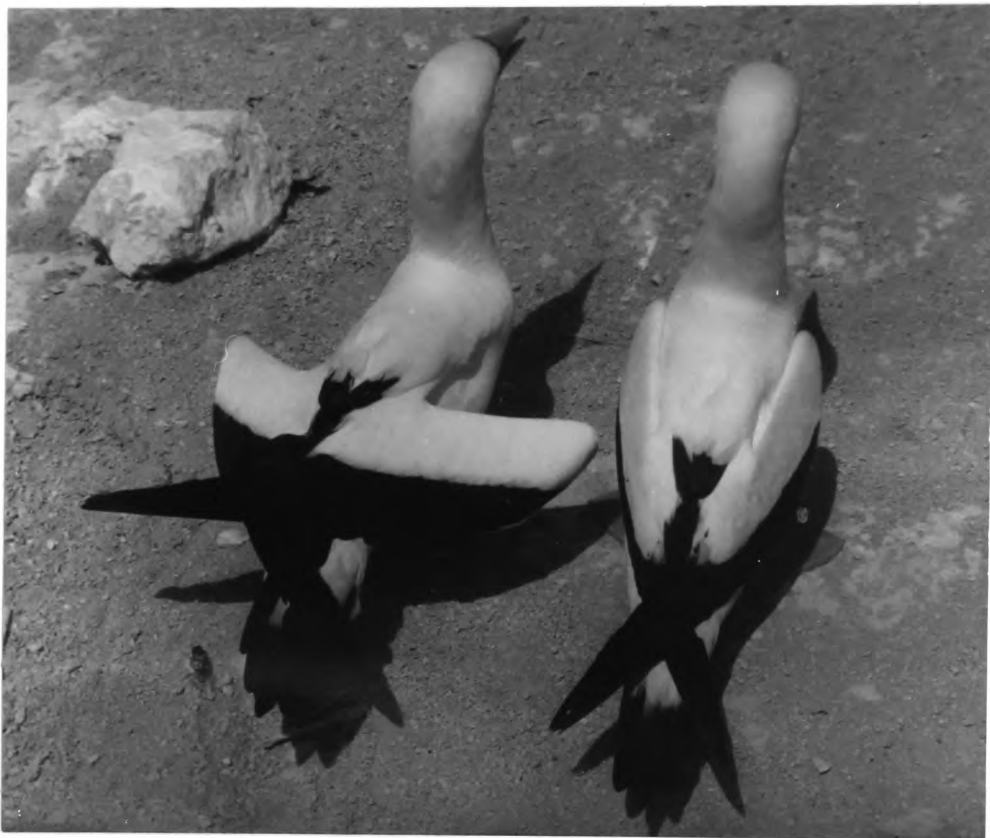


Plate 21. White Boobies Sun-bathing.



Plate 22. White Booby taking off.

