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THE BREEDING BIOLOGY OF THE GANNET (SULA BASSANA) WITH PARTICULAR REFERENCE TO BEHAVIOUR.

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- by -

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ABSTRACT

Gannets were studied on the Bass Rock (Scotland) between 1960 and 1963, and particularly in a colour ringed group (the observation colony). The account is in two parts (general breeding biology and behaviour) which are amalgamated in this brief summary.

The entire Gannet population of the Bass was estimated in June 1962 and a considerable increase over the 1949 population (last count) shown (about 4,800 pairs in 1949 to about 7,000 pairs in 1962, excluding 'club' birds). The increase in the observation colony was mapped in detail, for the period of the study.

The mid-cliff regions of the Rock are the first to be re-populated each year. In the observation colony (and presumably in all areas) old pairs return before newer ones, and males before females. The maximum seasonal stay at the breeding Colony is from late January to early November.

During this period both sexes actively defend the nest site by fierce fighting, where necessary, and a special aggressively-motivated 'ownership' display, bowing (analysed in detail). Sites are guarded continuously and males gather nest material throughout (females only after egg laying and for a much shorter period). Nest sites and mates are usually permanent, though females show less attachment to the site than do males (an attempt to separate the two effects is made).

New sites (which may be on cliff ledges of various sizes or on flatter ground) are established only by males usually four years old (beginning in April) and are held a year before breeding is attempted. Birds tend to return to the same small area of the Colony from which they originated. Site establishment normally involves fighting (discussed in detail). Pair formation takes place only at the site; the

male performs an advertising display - a modified form of bowing and females 'prospect' for such males. Males are conspicuously aggressive to females - especially in new pairs but also throughout life - and females show a high tolerance of male attack and an appeasement posture (facing-away) restricted to this situation. Males bite their mates whenever they meet on the site, and the pair then perform a prolonged 'friendly' meeting ceremony (mutual fencing). This, like male advertising, is a modified form of bowing.

Laying begins late March or early April and continues (by first-time breeders) until late June or exceptionally the first half of July. Older females lay earlier and produce heavier eggs. Greater density also probably causes earlier and more closely synchronised laying. Incubation behaviour in both sexes was, in some cases, released by donated eggs, but others were refused close to the laying date of the pairs concerned. Males take slightly longer incubation stints than females. No two-egg clutches (except the product of different females) were found, though Gannets usually replace a lost egg in 6 - 32 days (first-time breeders significantly less often than experienced females). However two eggs are incubated as successfully as one. The incubation period, 43.6 days, is the same for new and experienced birds. Eggs lose 10 - 13% in weight during incubation (underfoot). Eggshells are not systematically removed. Hatching success for birds breeding at least the third time was 86% and for first-time breeders 62.5%.

The nidicolous young may be fed immediately on hatching. Feeding, by incomplete regurgitation, continues for the entire pre-fledging period (no starvation period). The length of attendance spells drops sharply after hatching. Even during the phase of maximum chick growth, the pair spend some 15% of daylight hours together at the nest. The young reach a maximum of 150% of the adult weight. Starvation among chicks was never found during the study period.

Juveniles leave the nest at about 90 days (both from new and experienced breeders). However the former lost more small chicks and had much lower overall success (49% of eggs laid gave fledged young in new pairs, 82% in experienced pairs). The growth of young was followed in detail. Parents do not discriminate in favour of their own young and will accept substitutes, probably at any stage in the chick's growth, and even when natural and foster chicks differ markedly in age. However adults repel wandering chicks and even attack unguarded ones. Furthermore, chicks normally stay strictly on their nests. These factors prevent doubling up. Artificially twinned nests revealed that if the chicks were of about the same age both survived and were adequately fed, though fledging at about 94 days and growing slightly slower than singles. A significant age difference (three or more days) however led to the persecution of the younger by the older and hence its starvation. Excluding such cases, pairs with twins gained an 80% reproductive advantage in 1962, the year of the experiment.

The implications of the twinning results are discussed together with other factors (deferred maturity, non-breeding population, etc.) affecting recruitment rate.

Return of colour ringed adults over the three years of the study gave a 6% annual adult mortality and thus a life expectancy of 16.2 years. Mortality between fledging and returning to breed is calculated to be about 80%.

The ontogeny of behaviour in chicks is described. Juveniles show characteristic pre-leaving behaviour and fly well at the first attempt, though cannot rise for some days having alighted. They are not accompanied by parents and do not return to the nest. Adults tend to attack them on the sea. They may return to the breeding Colony in their first year, but do not normally do so until two or three years old. Immature plumage stages are described and illustrated.

Body maintenance activity (preening, sleeping, plumage shaking, etc.) is described. Rotary head shaking is a response to peripheral tactile stimulation and occurs as a probable displacement reaction in some fear situations. The ordinary sideways head shake is shown to be a simple movement which has been incorporated into several complex displays and also occurs alone, in ritualised form, in at least one signal situation.

Social behaviour away from the nesting site is discussed and contrasted (in complexity) with breeding behaviour. A special posture (sky-pointing) which precedes and accompanies movement away from the site is discussed here. Its comparative occurrence within the Sulidae is also discussed.

Finally adaptations to cliff nesting in the Gannet and Kittiwake are compared. The two show many similarities, evolved convergently, but also several important differences (apart from those inevitably resulting from dissimilar phylogeny).

The general discussion centres round the importance of the site and associated aggression in the Gannet's breeding biology.

GENERAL INTRODUCTION

This account of the breeding biology and behaviour of the North Atlantic Gannet Sula bassana L. is based on work carried out between 1960 and 1963 on the Bass Rock, Scotland. The two parts of the study, breeding biology and ethology, will be introduced separately. The following is a list of general points relevant to the study.

Study Area. (Plate 1)

The Bass Rock (Lat. 56° 04' N., Long. 2° 38' W.) in the Firth of Forth, two miles from the East Lothian coast, is a mass of hard, igneous 'trap', forming the final link in a series of volcanic outcrops stretching across the Lothians. About a mile round the base, 340 feet high and bluntly conical with a planar area of about seven acres, it rises practically sheer for 250 - 300 feet on all sides except the south-facing slope. Superficial sub-soil permits a luxuriant growth of grasses (genera Holcus, Bromus, Deschampsia, Poa, Tridactyla). Other common plant species are Lavatera arborea, Beta vulgaris, Silene maritima, Melandrium rubrum, Taraxacum officinale, Urtica dioica, Carduus spp., Rumex spp., Lamium album, Lamium purpureum, and Cochlearia officinalis.

Although only the fifth largest, the Bass is one of the oldest British gannetries and has been for centuries the locus classicus of the Gannet, to which it gives the specific name. It is an ideal study area since nesting groups on both cliffs and flatter ground are accessible and certain isolated groups are available for experimental and other purposes. In addition the presence of other species (Shag Phalacrocorax aristotelis, Herring Gull Larus argentatus, Kittiwake Rissa tridactyla, Fulmar Fulmarus glacialis, Guillemot Uria aalge, and Razorbill Alca torda) affords some inter-specific competition, though the Gannet is easily the dominant species. Guillemots and Kittiwakes, at least, are also old-established.

Plate 1. The Bass Rock, from the north.

The observation colony, above the north-west face, is marked with white arrow. Note that (i) the top of the island is almost clear of nesting Gannets, (ii) the sheer north and north-west faces are thinly populated (the ledges are narrow), (iii) east face thickly colonised (broken terrain).

Opportunities for Study.

Many definitive accounts of Gannet breeding biology and especially behaviour, including Gurney's (1913) monograph, The Handbook of British Birds (Witherby et. al. 1940), Perry (1948), Fisher & Lockley (1954), the recent Handbook of North American Birds (Palmer 1962) and many individual papers, contain errors which stem largely from the fact that the information was gathered (necessarily) during short visits to breeding Colonies. Despite the statement of Wodzicki (1953) that the North Atlantic Gannet is one of the most thoroughly studied bird species, and with the important exception of the famous population and distribution studies of Fisher, Vevers & Venables (1938 - 1951), accurate information was extremely limited at the beginning of this work. It was therefore of particular value to live at the breeding Colony and maintain a daily watch at the main observation colony throughout the breeding season - the only way in which absolutely dependable records of breeding success, rate of laying, etc. can be obtained. The periods spent on the Bass Rock were :- 1960 (July 18th. - August 18th. and October 16th. - 17th.); 1961 (February 1st., March 4th. - November 4th.); 1962 (February 19th. - October 11th.) and 1963 (March 25th. - September), with the following absences :- 1961 July 22nd. - 31st., October 16th. - 29th.; 1962 July 20th. - 30th.; 1963 July 23rd. - August 7th.; 91 effective weeks.

Methods of Study.

Trapping and marking. 171 adult Gannets were trapped with pole and noose on different areas of the Rock and ringed with individual combinations of A.C. Hughes' plastic self-coloured spiral chicken rings and British Trust for Ornithology serial monel rings. Of this number 135 were subsequently used to determine annual adult mortality. The plastic rings kept their colour very well over the three-year period of study but a few individuals lost part

or all of one or more rings, though in most cases identification was still possible.

Young were marked with B.T.O. rings and colour combinations identifying the year and, in some cases, the area of the Colony from which they fledged. Small young were marked on the crown with dye, if confusion could otherwise have arisen (e.g. in twinning experiments Chapter 4). Eggs were marked with the date of laying by waterproof dye. Nests and sites were mapped in relation to the local physiography and, in some cases, to colour-coded iron markers driven into rock crevices, and related to a card-index.

Observing. Observations were mainly made on a colony of approximately 250 nests and sites on steeply sloping ground facing N.W. (Plate 2), from two hides. This colony became apparently indifferent to the observer and it was not necessary to be escorted into the hide. Within this 'observation colony' two areas, each containing 20 nests, were demarcated by painting rock and used for systematic behaviour checks. Approximately 3,000 hours were spent in the hides.

Sexing. Behaviour differences easily established the sex of colour ringed birds, but it was also discovered that individuals could be sexed, despite close morphological similarity, by slight differences in the shade of the buff head and the greenish-blue lines running along the tops of the toes and up the tarso-metatarsus (Chapter 1).

Recording. A portable tape-recorder was used for detailing lengthy and complicated behaviour sequences. Cine-photography, using a Bolex H16 at 24 frames per second, provided records of all the main behaviour patterns. A comprehensive colour film taken jointly by Dr. N. Tinbergen and myself has been deposited with the British Film Institute and is submitted with this thesis. The line illustrations were drawn directly from enlarged images from mono-

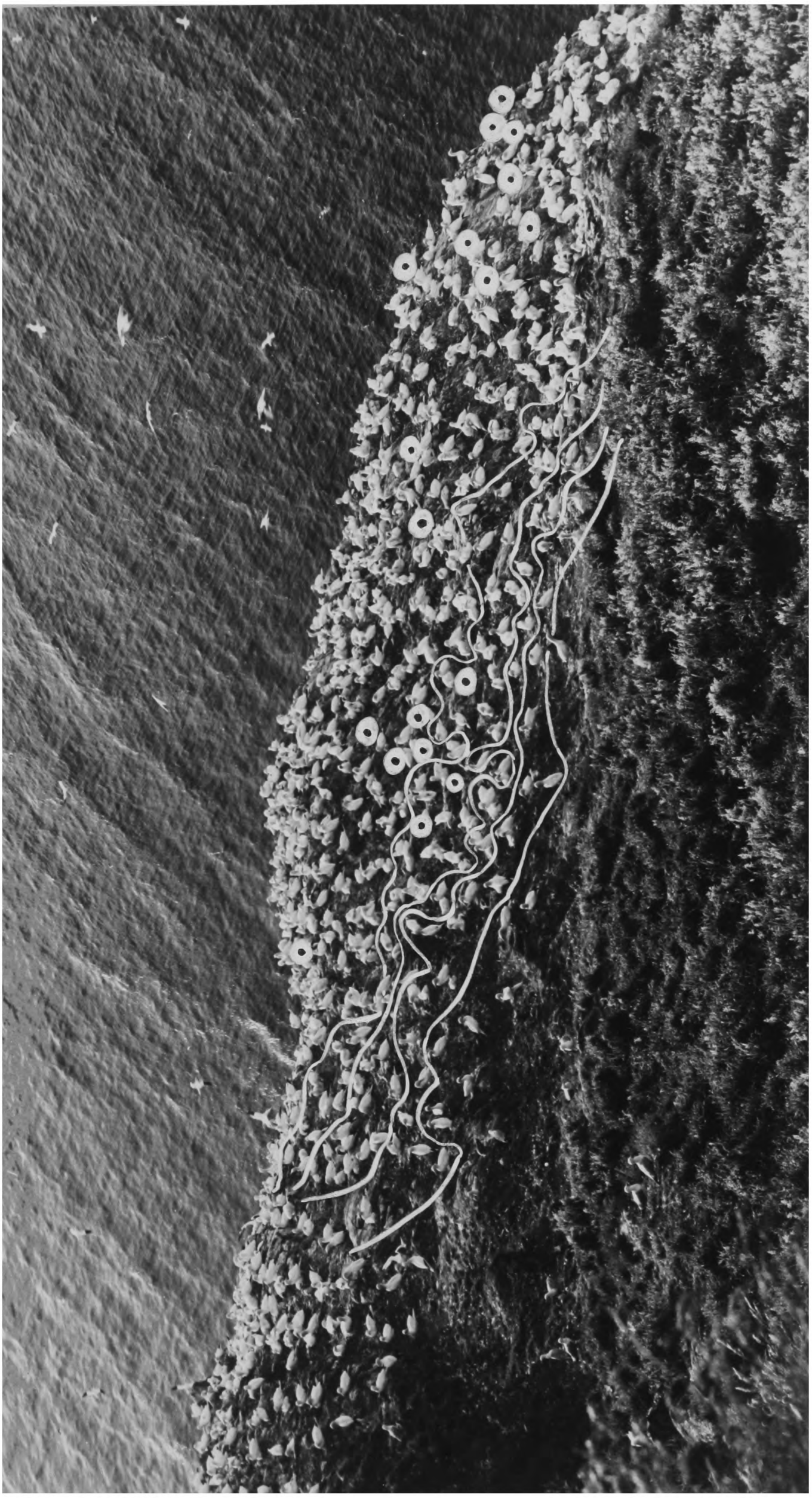


Plate 2. The observation colony, showing annual increments of breeding birds (1961, 1962, 1963). The white line nearest the cliff edge demarcates the 1960 breeding limit. Annual extensions are then shown by successive lines. Nests 'squeezed in' among the established mass are shown by white circles.

chrome cine-films. Still photographs were taken on Ilford 35mm. F.P.3., often using a 400mm. lens.

Measuring. Three spring balances (0 - 150gm., 0 - 1,000gm., 0 - 5,000gm.) were used for weighing eggs, young and adults. Culmen measurements were taken with dividers and wings with a measuring-string.

References.

Reference to the studies of Murphy (1936), J.M. Cullen (1956), E. Cullen (1957), Richdale (1957) and Dorward (1962 a & b) are so frequent that I have omitted the date after each citation of these works. Where a recent work summarises previous references (e.g. Hinde 1956 on Territory) I have often quoted merely the recent work.

For information about boobies I have amplified published work by personal communications from J.M. Cullen and D.F. Dorward.

Definitions.

The following terms are used as defined below.

Adult — Adult-plumaged, not necessarily physiologically capable of breeding.

Breeding cycle — The sequence of events followed between the return to the breeding Colony and departure from it.

Club birds — To avoid ambiguous use of the terms 'unemployed' and 'non-breeding' the mixed population of immatures and adults temporarily frequenting different non-nesting areas of the Rock throughout the summer will be referred to as 'club birds' and the problem of their precise status will be discussed under the appropriate heading.

Colony — This can mean either the entire population of the particular geographically discrete area, or a certain group within the main area. The Bass

Colony exemplifies the former, the observation colony the latter. The sense may be inferred from the context.

Established — Having held a breeding site consistently for more than a season, but not having bred.

Newly-established — Having held a breeding site consistently for at least several days, but not more than a season and not having bred.

Experienced — Having bred at least once.

Fringe — Fringing the main area where experienced birds nest are zones, usually less densely colonised, occupied by more recently established birds. The size of such a fringe will obviously vary according to the length of time it has been occupied, whether the group is expanding and how fast, and possibly other factors. Whilst any flattish ground nesting group must have an outer edge (and hence a fringe in the literal sense) it need not have a fringe in the special sense used here.

Immature — Any bird with immature plumage (from one to five years).

Nest — A small, fixed area, defended and having nest material.

Site — A small, fixed area, defended but without nest material. The spot upon which the nest will be built.

All statements refer to Bass Gannets, unless otherwise stated. It may be that some features of Gannet breeding biology differ from one breeding station to another.

GENERAL BREEDING BIOLOGY

INTRODUCTION

Detailed studies of sea-bird breeding biology have greatly increased in the last two decades, possibly stimulated by Richdale's 18-season study of the Yellow-eyed Penguin Megadyptes antipodes (1957) and 16-year study of the Royal Albatross Diomedea epomorphora (1950 & 1952), and Murphy's classic "Oceanic Birds of South America" (1936). Despite the considerable difficulties entailed in prolonged work on sea-birds, many recent studies have amassed quantitative information of a kind not previously available. The following are examples :- Emperor Penguin Aptenodytes forsteri, Prevost (1953); Stonehouse (1953); King Penguin Aptenodytes patagonica, Stonehouse (1960); Adelie Penguin Pygocelis adeliae, Sladen (1958); Black-footed Albatross Diomedea nigripes, Laysan Albatross Diomedea immutablis, Rice & Kenyon (1962); Madeiran Storm Petrel Oceanadroma castro, Allan (1962); Guillemot, Uspenski (1958); Tschanz (1959); Tuck (1960); Puffin, Fratercula arctica, Myerberget (1962); Cormorant Phalacrocorax carbo Kortlandt (1942); Shag, Snow (1960 & 1963); Red-billed Tropic Bird Phaethon aethereum, Yellow-billed Tropic Bird Phaethon lepturus, Stonehouse (1962); White Booby Sula dactylatra, Brown Booby Sula leucogaster, Dorward (1962); Kittiwake, Coulson & White (1956, 1958 & 1960); Common Tern Sterna hirundo, Austin (1942 - 49); Black Noddy Anous tenuirostris, Sooty Tern Sterna fuscata, Ashmole (1962). In addition the work of Tinbergen and his co-workers on the behaviour of the Black-headed Gull Larus ridibundus, (e.g. 1959); J.M. Cullen (1956) on the Artic Tern Sterna macrura and E. Cullen (1957) on the Kittiwake pay close attention to the general breeding biology of these species.

This is particularly desirable since, partly for convenience, much of the most important and influential work

on bird ecology - Lack's in England (1954 & refs.); Kluijver (1951) and L. Tinbergen (1960) in Holland - and particularly on the fundamental subject of reproductive rates, has been on short-lived, insectivorous passerines, notably the Great Tit Parus major. Yet it has long been recognised (Howard 1920; Wynne-Edwards 1936 & 1939) that long-lived colonial sea-birds offer many special problems connected with factors regulating their breeding success, such as territory, social behaviour, feeding, pre-maturity periods and the regularity of the breeding cycle, including non-breeding years and the effects of age and experience on breeding success.

For many reasons the Gannet is particularly suitable for long-term ecological study. Its population trends are more accurately known than for any other colonial sea-bird (Fisher & Vevers 1950); it is a specialised fish-eater; forms dense, permanent breeding colonies and permanent pairs, with conspicuous nests to which, it now seems, it remains largely faithful throughout its long breeding life and shows all the features associated with large size, longevity and low reproductive rate. Further it is possibly unique in combining two most important features; it is virtually without predators today, man excepted, and the present study shows that it seems rarely, perhaps extremely rarely, to suffer from even slight food shortage. This is very remarkable, since there is extensive evidence that a wide range of colonial sea-birds, and particularly their young, suffer from some, often severe, food shortage.

The present study is a broad-based attempt to provide information on as many aspects of the Gannet's breeding biology as possible, particularly those requiring prolonged, unbroken attendance at the Colony and a detailed knowledge of individual nests and birds. Particular attention is paid to the description of Gannet behaviour and also its motivation, function and evolutionary aspects.

To appreciate the adaptiveness of behaviour it is necessary to understand the problems facing an organism in its natural environment, and some recent studies have shown how many diverse features of an animal's ecology, behaviour and structure can be related to some major adaptive theme. Thus Von Haartman (1957) in his study of the Pied Flycatcher Muscicapa hypoleuca demonstrated the relationship between hole nesting and the species' breeding biology; E. Cullen related Kittiwake behaviour to cliff nesting; Phillips (1962) examined plunge diving in relation to the presence of white on the head and/or underparts; Crook (1962) studied pair formation in weaver bird spp. in relation to certain ecological aspects and Wickler (1959) has carried out a similar analysis for some fishes. Tinbergen and co-workers are gradually uncovering the entire anti-predator system in the Black-headed Gull, which affects many features of its behaviour (e.g. spacing out of nests, egg-shell removal, roosting habits). In the present study the implications of dense colonial nesting (mainly on cliffs) and strongly developed aggression gradually emerged as central aspects of the Gannet's breeding biology.

Since the adaptiveness of behaviour in relation to ecology may be investigated by looking at convergence between phylogenetically dissimilar species and divergence between phylogenetically related but ecologically distinct species, the studies of Cullen on the Kittiwake and Dorward on two Sula species are particularly relevant and the Gannet and Kittiwake will be compared in detail towards the end of this account.

The interaction of the external situation (presence of mate, egg, chick; status of individuals; etc.) with behaviour is also taken into account where possible. To quote Lehrman (1959) --- "many of the problems which are illuminated by knowledge of neuro-endocrinological relationships

arise from ecological work; ---- many phenomena such as prolonged mutual courtship ceremonies of colonial birds, the onset of incubation behaviour; changes in behaviour upon hatching of the egg ---- acquire a new dimension as scientific problems in the light of recent advances in physiology. The coalescence of ecology, ethology and physiology can give added stimulus to all three".

For convenience the general biology and ethology have been treated separately except where (as in the feeding behaviour of twins compared with singles) the two are integral parts of a single account. This artificial division creates problems concerning the best place for items which could logically be considered under either. However cross reference is not difficult, and unwieldy sections embracing widely differing subject matter are avoided by this method. Details of some morphological features have been included in the general section since it was thought desirable to give this information early in the account.

The order of presentation is based on the chronology of the annual breeding cycle. A short summary and, where appropriate, discussion follows each chapter. Details not immediately involved in the account have been relegated to appendices.

- 1 -

ADULT MORPHOLOGY AND VOICE

The Sulidae are a compact family divisible into the pan-tropical boobies (genus Sula) and the true gannets of temperate or relatively cool-current regions. The latter form a closely-related trio comprising the North Atlantic Gannet, the South African or Cape Gannet Sula capensis and the Pacific or Australasian Gannet Sula serrator (some authors use Morus as the generic name), and may perhaps best be regarded as three forms of the one ~~sub~~-species, though more usually given specific rank.

External Sex-differences.

Gurney (1913) and later authors give adequate descriptions of the structure and plumage of adult Gannets but say nothing about external sex-differences.

Although in several boobies (Murphy 1936; Dorward) the female is the larger sex, the reverse is true in the Gannet. Female culmens measured on average 98.9mm. (range 94 - 104, 31 measured) against the male's average 100.2mm. (range 93.5 - 110, 33 measured). Fewer (11) bill depths were measured, average 37mm. (range 34 - 40mm. in both sexes). Wing-length in the male averaged 514mm. (range 475 - 535, 5 measured) and in the female 498 mm. (range 475 - 505, 4 measured). Males weighed average 3,252gm. (range 2,880 - 3,620gm., 6 weighed) and females 3,117gm. (range 2,900 - 3,400gm., 3 weighed). These size-differences are not noticeable in the field and cannot reliably be used for sex recognition.

The colour of bill and soft parts shows sex-differences in boobies, males being usually brighter or even differently coloured. The Gannet shows no sex-differences in the colour or extent of the black facial soft parts and lines on the bill. There are also no sex-differences in iris colour or the shape of the pupil, as there are in some boobies. The body plumage is identical in both sexes. Apart from differ-

ences in behaviour, however, two morphological features (head colour and the colour of the digital lines on the webs and tarso-metatarsus) can be used with fair reliability.

Head colour. Both sexes show some shade of yellow/buff, ranging from pale yellow to deep orange-brown, on the head and neck. This colour is sometimes well marked as early as the second year, when the rest of the plumage is extremely immature, and has therefore little to do with sexual maturity. In both sexes the colour is less intense very early in the breeding season, deepens and then tends to fade during the rest of the season, particularly in the female who almost invariably becomes 'spotty' and untidy about the head and occasionally turns completely white. Males sometimes become spotty, but usually retain a smooth glossy appearance. The female's change is not due to the male's constant biting (as suggested in Fisher & Lockley 1954) since unmated females showed it. Moult is probably responsible for the spotty appearance, but not for the paling.

Despite both the variability and seasonal change, within any pair the darker bird (if there is one) will generally be the male (Fig. 1).

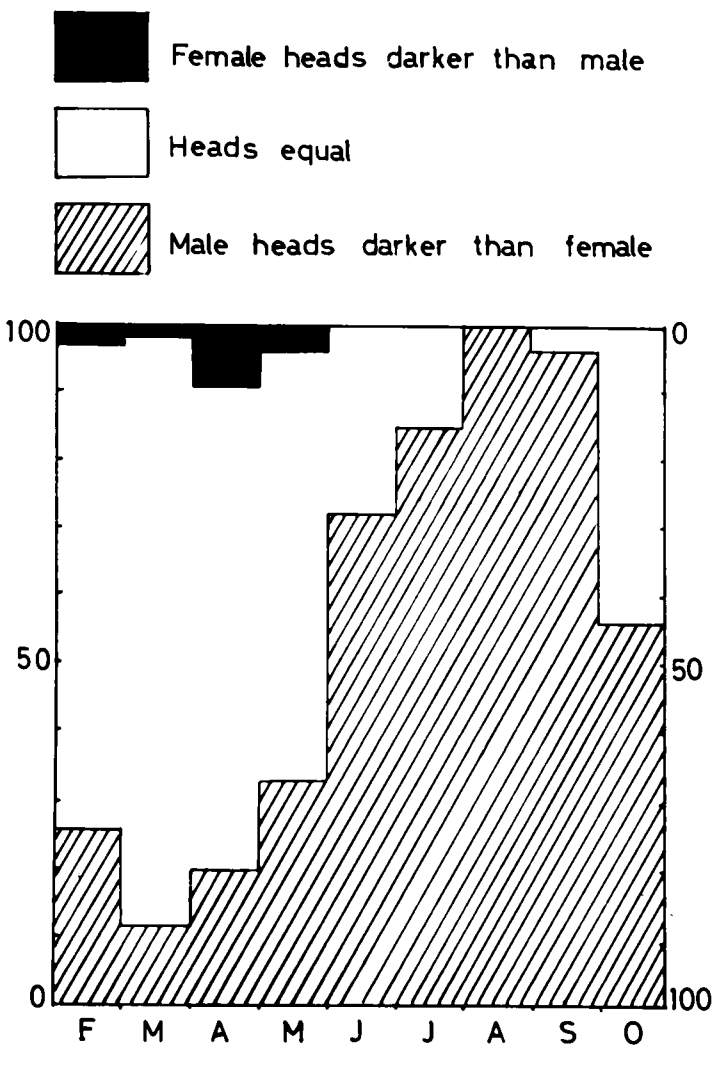


Figure 1.

Seasonal changes in head-colour differences.

At one stage in the breeding season this difference becomes extremely marked, but by October the female is darkening again. Individual colour ringed pairs occasionally showed the male darker than the female one year and vice versa the next. Murphy states that in the Blue-footed Booby Sula nebouxii the male has a darker ashy head than the female.

Function of head colour. Striking facial patterns and conspicuously contrasting head colour (Murphy) are found throughout the Sulidae, except the Piquero Sula variegata and Sula nebouxii, although only the Gannet has a yellowish head.

Conspicuous physical features have often been used as 'morphological support' for the evolution of many striking, ritualised signal movements such as the touching of specula in the Anatidae (Lorenz 1941, see also Lack 1940 on the 'Releaser Concept in Bird Behaviour'). The Gannet's yellow head colour, together with the striking pattern of lines on the beak, pigmented facial soft parts and the blue orbital ring may therefore be suspected to serve a signal function. It will be shown that much of the Gannet's social signal behaviour employs conspicuous head movements in all of which the face and head are involved in exhibition, presentation or withdrawal. The colour and face pattern may therefore enhance the value of these movements as signal characters. However, it is not yet possible to come to a positive conclusion about the function of the head colour in the Gannet, and although several interesting problems are raised, these are discussed in Appendix A.

Colour of digital lines and webs. In spite of the great variation in the shade of green in some individuals and some overlap between sexes as a whole, in every one of the pairs examined, the male's web lines were more yellowish and the female's more

bluish green, (Table 1). In the more extreme cases even single birds could be sexed by this character (as was confirmed by their subsequent behaviour).

TABLE 1. Sex-difference in the colour of digital lines.

Singles

Males		Females	
Yellow webs	Turquoise webs	Yellow webs	Turquoise webs
57	14	4	37

Pairs

Male yellow webs and female turquoise webs	Male turquoise webs and female yellow webs	Both yellow webs	Both turquoise webs
27	0	9	7

Function of web lines. Since slow raising of the feet, showing off the web lines, accompanies the striking pre-movement posture (sky-pointing) it may be suggested that they have a signal value, indicating impending movement through the colony. Together with the sky-pointing posture they might have an appeasing function, additionally plausible in view of the Gannet's strong aggression. However the evidence does not support this, in addition to which the ancestral cliff nesting habit (Chapter 15) would usually not require a departing bird to walk through others. Nevertheless some other signal function of the lines is not excluded.

A further web character, helpful in determining the status of individuals, is that birds newly-arrived at the breeding colony as site establishing males or prospecting females have pale grey webs and tarsi, whereas older birds have much darker ones. The only individuals possessing very pale webs were new to the colony, though not all apparent newcomers had them.

Voice.

The Gannet has a very limited vocabulary when compared, for example, with the gulls and perhaps even the Guillemot, though not in comparison with some other Pelecaniformes. It shows no sexual dimorphism recognisable to my ears, in strong contrast to the boobies in which sex-differences in the structure of the syrinx produce a thin piping from the male and a loud call from the female (Murphy). However, individual differences in voice enable recognition of mates and neighbours as they fly in. Male Gannets are more vocal than females, giving the aggression/fear call more readily when approached.

The main call is a strident, far-reaching 'urrah rah rah' used by both sexes at about 4/sec. when flying in to the site. The pace of the syllables accelerates, their amplitude increases and just before touch-down the pitch is slightly raised in a final 'shout' which tails off as the bird lands. Much the same call is given by both sexes during bowing (usually between 10 - 25 separate calls in 4 - 10 seconds) and mutual fencing, where it rises and falls in pitch and amplitude according to the intensity of the display. During aggression (adult fights, threats, male attacks on females or adult attacks on chicks) the call is often given, particularly during spurts of renewed aggression.

An alarm version of the same call is very loud and staccato, repeated three or four times on a slightly descending scale and graded according to the degree of fright (e.g. slight for an attack by a Herring Gull, great for a close approach by man).

During take-off and sometimes after a hop or run, a soft 'oo-ah', attenuated, sometimes disyllabic and lower on the second syllable, is uttered. This 'groan' is invariably accompanied by sky-pointing and because it is usually heard

just as the bird steps off the ledge in a contorted position with neck stretched and tail acutely depressed, it has been suggested to result from this physical distortion - perhaps by ejection of air from the thoracic air sacs. However it can certainly be produced by birds in normal pre-flight position and in a variety of other positions, and is graded in intensity inversely with the urgency of take-off, being completely absent in urgent ones. It is certainly produced ~~voluntarily.~~ under "control".

The only other sound differing in kind from the harsh 'rah' call, is an oft-repeated grunt rather like a soft Raven's croak. It occurs rarely, and from birds in fast, level flight, and appears not to have been previously recorded.

The Gannet's main call is frequently associated with aggression, as in incoming birds, fighting and threatening, bowing and mutual fencing. The absence of a complicated vocabulary is probably correlated with the relatively large number of visual signals, though perhaps these are mainly required by the combined effects of high aggression and dense colonial nesting.

- 2 -

THE BASS COLONY

The size of the Gannet population of the Bass Rock was estimated in early June 1962 (Nelson in press). Previous counts had also been made, on several occasions, of certain areas visible from other parts of the Rock. This chapter presents the results and suggests two correction factors which may be generally applicable. For details of other British gannetries see Fisher & Venables (1938); Fisher & Vevers (1943 - 44) and Fisher (1951).

Rintoul & Baxter (1935) trace the first references to probable Bass Gannets to Beowulf, who in the 6th. century mentioned Gannets in the North Sea. A Scotichronicon record (Fordun 1447) from Gurney (1913) also mentions large numbers nesting on the Bass.

Fisher & Lockley (1954) discuss the spectacular fluctuations in the 19th. century of world Gannet numbers, describing the alarming decrease from 1834 to 1894, probably due to human predation, and the equally dramatic upward trend which began towards the end of the century and seems to have continued ever since, giving an overall increase on the east side of the Atlantic from 70,000 to 82,000 pairs between 1939 and 1949 (Fisher & Vevers 1951).

There have been few counts of the Bass Colony since the descriptive impressions recorded by early authors, such as Harvey (quoted by Fleming 1847). He describes the Bass in May and June as being almost covered with "nests, eggs and young birds, so that you can scarce find free footing anywhere", and compares the birds flying about the cliffs to a "mighty swarm of bees". These remarks describe a situation which no longer exists. The whole top of the island, except one or two areas fringing the cliff tops, is now clear of nesting Gannets. However, Fleming himself (1847) proposed 5,000 breeding pairs as a reasonable estimate, which compares well with the 1929 (4147); 1936 (4,150) and 1939 (4,374) figures (J. Fisher in 'The Hand

book' Witherby et. al. 1949). In 1949 the Midlothian Ornithologists Club, led by G. Waterston, counted 4,820 nests (G. Waterston pers. comm.) - the most recent estimate. It seems that the Bass Gannet population has remained relatively stable after a slight decrease at the beginning of the century (1904 3,000 and 1913 3,250 pairs).

Methods.

Counting. Large sections of the cliffs are invisible from above and the entire Rock was therefore counted from a boat, using 7 x 50 Zeiss binoculars. Natural rock features divided the Colony into 21 groups of varying size. In small groups individual birds were counted. Larger groups which, because of broken terrain, lack of demarcating features and their density, could not be accurately counted, were estimated as mutiples of a 'unit' (i.e. a small section, or 'unit', of the larger group was accurately counted and the larger mass estimated as 'n' times the unit).

Two areas were checked by counting from vantage points on the Rock and gave results 18% less and 3% more than the sea counts. Since the land and sea checks were made on different days and the two areas were situated on awkward 'counting' terrain and their boundaries difficult to duplicate exactly, they tally reasonably well and indicate that the final figure is unlikely to err by much more than 10%.

Photography. Overlapping section-photographs were taken, but counting from these was found to be misleading as many pockets of Gannets were obscured or totally hidden and the error in dense masses would be too great. Figure 2 and Plate 1 show the distribution over much of the Rock and enable not only the main centres of population to be placed but also several discrete colonies (see Appendix B).

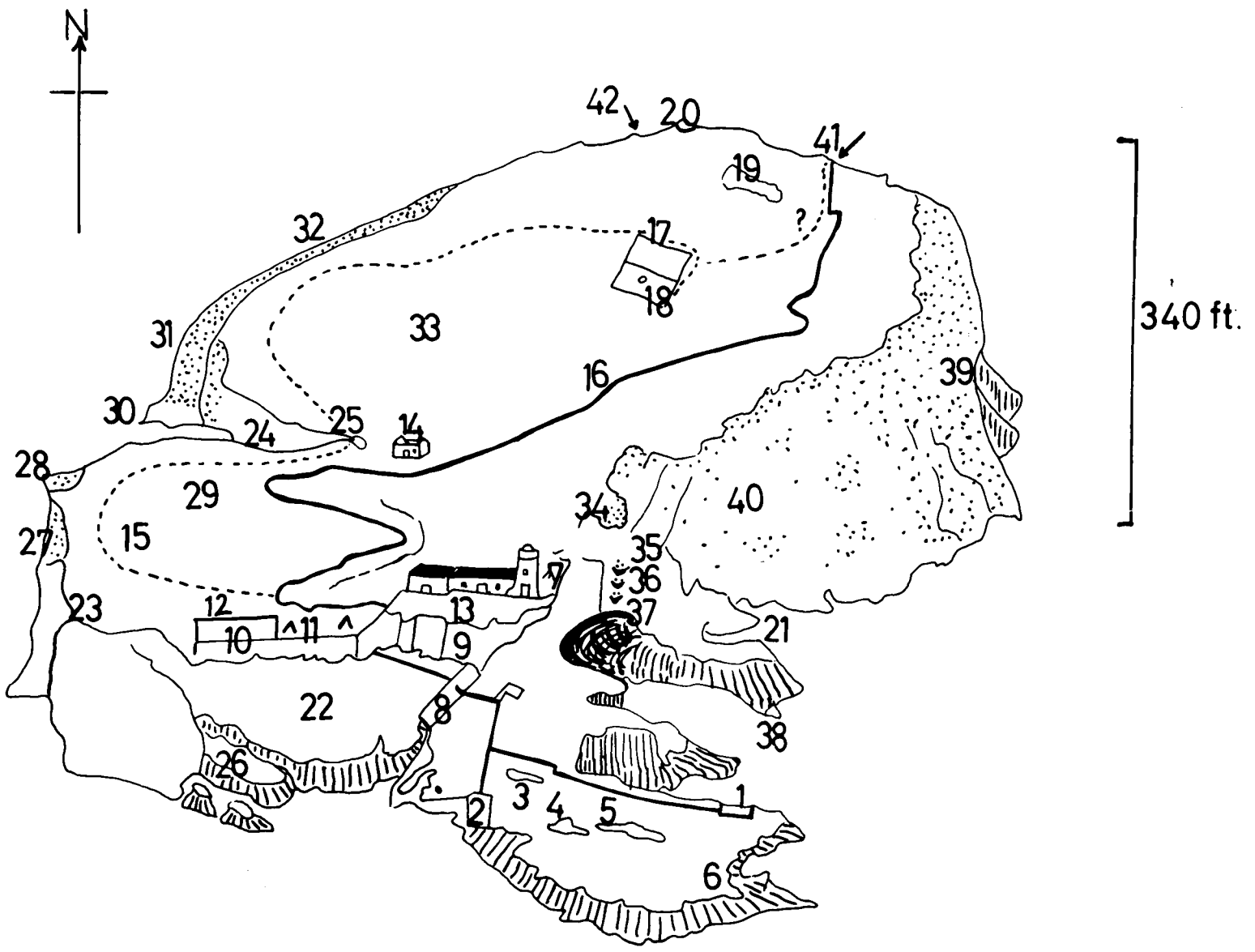


Figure 2. The Bass Rock, drawn from aerial photograph. (See Key)

Calculation of pairs and non-breeders. Two factors modify the results of a straightforward count. Prolonged observations on a large group of individually known nests revealed that some nests or sites would, at the time of the count, be occupied by non-breeding birds and some by pairs. Both considerations affect the figure for the number of breeding pairs at any Colony - a figure which cannot be taken as synonomous with either the total number of birds or the total number of nest drums. All previous estimates have been in terms of one or other of these.

Non-breeders. The total number of adult Gannets on the Rock in the middle of the breeding season includes many non-breeders, falling into two categories : (1) Young adults or slightly immature birds, four to six years old, with established sites but no egg or chick. Except when partnering an experienced bird, Gannets establish sites and form pairs

KEY TO FIGURE 2.

1. East landing (old N.E. port).
2. West landing (pld S.W. port). Actually on S. side.
3.
4. Brackish rock pools.
5.
6. Osbairn point.
7. Site of old crane.
8. Mantle wall, with four cannon embrasures.
9. Battlements of old garrison.
10. Continuation of battlements.
11. Gable ends of old garrison living quarters.
12. Lighthouse outbuildings.
13. Lighthouse buildings and compound.
14. 15th. century ruined chapel, on site of St. Baldred's 7th. century cell.
15. Route followed by old garrison path.
16. Concrete path of N. fog horn.
17. Upper walled garden.
18. Well (drainage water).
19. Top loch.
20. Summit (ruined fortification).
21. Entrances to E. caves.
22. S. slopes below battlements, covered with Tree Mallow.
23. W. turret.
24. N. side of cable gulley.
25. Gulley-head pool.
26. Shag rock.
27. Headland colony.
28. The needle.
29. The headland.
30. Low shelf - a jutting outcrop at base of W.S.W. face.
31. Nesting mass on S.W. face.
32. Nesting mass on W. face, spreading beyond cliff-top.
33. Steep rocky face above chapel.
34. Colony 6, (Lighthouse colony).
35. Upper E. face, group 3.
36. Upper E. face, group 2.
37. Upper E. face, group 1.
38. Gannet colony at base of E. face (ousting Shags).
39. Nesting mass on E. face.
40. Sparsely occupied sheer E. face.
41. North fog horn colony, facing N.
42. Observation colony, facing N.W.

for all or part of a season prior to that in which they first lay. (2) Adults and a large number of more immature birds, which settle on unoccupied parts of the Rock according to wind direction, but do not hold permanent sites. These will subsequently be referred to as 'club birds' and evidence for the view that they are non-breeders, and not off-duty breeders will be given later.

Category 1 birds not only hold sites on the outer fringe of established areas but also between established pairs where topography permits. The breeding population is therefore less than would appear from a superficial examination. For all practical purposes it may be taken that pairs which have once bred do not regularly have non-breeding years. Only long-term observations would show that these <u>never</u> occur but in the observation colony, of the 157 & 158 pairs breeding in 1960 & 1961 respectively, all but six (3 in each year) bred again the next year. Therefore the birds which are without chicks by early August belong either to categories 1 and 2 above or are failed breeders. Their proportion within the colony can be calculated and a figure for the breeding population obtained.

Figures in Table 2 were obtained by counting in early August three large and inaccessible (to eliminate the effects of disturbance) groups. The proportion of nests without a chick was recorded and represented birds that had (a) not bred, (b) lost egg or chick, (c) produced infertile eggs. In the observation colony, which was also undisturbed, over two seasons 77% and 79% respectively of eggs laid produced fledged young, leaving infertile eggs and egg or chick loss to account for the remaining 22%; (b) and (c) could then be evaluated, assuming that any egg/chick mortality would have occurred by the time the counts were made, and (a) calculated.

TABLE 2. Proportions of breeders and non-breeders (owning nests or sites) on three areas of the Bass Rock, 1962.

Area	No. of nests with chicks	No. of empty nests: Calc. egg or chick loss	No. of empty nests: Non-breeders	No. of sites. Non-breeders	% total† nests & sites of non-breeders	Adjusted* % total nests & sites of non-breeders
Part of S.W. face	75	21	19	73	49	40
	Total breeders 96		Total non-breeders 92			
Part of N.W. face	162	46	87	69	43	39
	208		156			
Observ. colony	184	52	3	26	11	-
	236		29			

† Assuming no sites to be failed breeders

* Assuming 22% of sites to be failed breeders. This is unlikely, but gives the absolute minimum figure for non-breeders.

The percentage of non-breeding site owners is seen from the Table to vary considerably, from at least 40% in the S.W. face section, to 11% in the observation colony. Certain features of the three areas could account for such variations. Thus, prior to 1961 the nesting success of the flatter observation colony would undoubtedly have been extremely low, since it was the most accessible group on the Rock and hence disturbed by visitors. The number of birds returning to establish sites would therefore be low, if one assumes that chicks return to the same local area in which they were born (see Chapter 8). It is also a very dense group and, unlike the section of the S.W. face, contains few suitable unoccupied spots. Newcomers are thus forced to the inland fringe which is possibly less inviting than, say, the S.W. face. If, therefore, a proportion of first-time breeders do not return to the area from which they hatched (for which there is some slight evidence) this proportion may be expected to be higher in the

least 'attractive' areas.

In the absence of a similar survey of all sections of the Rock it is desirable that a minimum percentage for non-breeding site owners should be used. Since the Rock is not a uniform habitat a compromise between the three proportions must be made and the figures of 40% and 39% respectively from the S.W. and N.W. faces have been taken as representative of half the Rock (in fact more than half of the terrain is of this type - cliff areas of wide, flat or gently sloping, broken ledges and plateaux) and the figure of 11% as representative of the other half. The general figure is thus $\frac{\frac{(40 + 39)}{2} + 11}{2}$ or 25%. 20% can therefore be taken as an estimated figure for non-breeding site owners.

Pairs. Several authors have allowed for the percentage of nests occupied by pairs. Their figures vary from 7% on Grassholm (Salmon & Lockley 1934) to 20% on St. Kilda (Fisher & Vevers 1943). Boyd (1961) arrived at a figure for St. Kilda of 11% using land photographs.

As it is impossible from the sea to separate pairs and singles among a nesting mass the number of individuals was estimated. To ascertain the number of nests the proportion of pairs was calculated from daily observations of some 300 nests in the observation colony. These indicated that 15% of nests would have pairs present at the time of this count. The seasonal variation in this proportion (see Fig. 22) should be taken into account if this figure is used by others.

Results of Gannet Count.

For the entire Rock a 'maximum' of 8,200 pairs was obtained, excluding non-breeders and immatures without sites, with a 'minimum' estimate of 7,700. Of these approximately 1,070 (max.) or 1,000 (min.) were 'extras' due to the presence of both members of a pair, and a further 1,420 (max.) or 1,340 (min.) represent site owners with no egg or chick, giving a

corrected figure for breeding pairs of 5,700 (max.) or 5,350 (min.). However the correction factors are themselves estimates. If the feasible maximum and minimum values for these are also taken into account the final corrected figure is 5,200 ± 700 breeding pairs. Previous counts of the Bass Rock Gannets have included site holders with the breeding pairs.

The grand total of Gannets on the Rock is set out in Table 3.

TABLE 3.

	Pairs		Singles	
Status	Max.	Min.	Max.	Min.
Breeding pairs	5700	5350		
Non-breeders with nests or sites	1420	1340		
Non-breeders without sites			2500*	2000
	7120	6690	2500	2000
Total individuals of all categories	16740	15380		

* Estimated on several separate occasions and not involved in the main count, (club birds).

Distribution. The increase undoubtedly occurring in the Bass Colony may be followed, in addition to overall counts, by recording the colonisation of new ground and the increase in certain discrete groups (see Appendix B).

Discussion.

A highly important point in the understanding of Gannet population dynamics and breeding behaviour is the availability of nest sites. The Gannet's notable aggression in site establishment (Chapter 9) implies competition and possible shortage of suitable breeding sites. However, there is at present no such shortage on the Bass Rock. Some areas now unoccupied once held nesting Gannets. One cannot sustain the suggestion that the unoccupied areas lack subtle require-

ments invisible to man. The enormous variation in physiography, aspect, distance from cliff-edge, nearness to other nesting masses, angle of slope, etc. of areas which <u>are</u> colonised by Gannets indicates their adaptability in these respects. Ashmole (1962) recorded serious competition among Black Noddies for nesting ledges, but, as with Gannets, in the presence of apparently suitable but un-used ledges elsewhere. The tendency to nest near other members of the species caused them to concentrate in areas already colonised and ignore others, but as far as the Gannet is concerned there is apparently a plentiful supply of un-used sites bordering the existing colonies which would presumably satisfy the species social tendency.

The question of the non-breeding adult population thus becomes even more intriguing. Fisher (1954)* concluded from his population studies that there was no evidence to suggest food-shortage as a factor limiting Gannet increase. My results confirm this. Not only have I failed to find a single case of chick starvation in three seasons (except where one parent disappears) but the twinning experiments (Chapter 4) also support it. If, also, it can plausibly be argued that potential nesting sites are still available, then non-breeders present a problem (Chapter 7).

The tendency to nest close to others leads to a slow, consolidated extension, which may seem like an adaptation to overcome site-shortage, since suitable breeding stacks are certainly limited, but it is at least doubtful whether the British Gannet population has ever seriously approached the level at which the supply would be saturated.

The group at the base of the east cliffs (Fig. 2, 38) displacing Shags, is a straightforward example of interspecific competition in which the smaller and less aggressive species is failing to resist encroachment. Interspecific competition becomes of great interest when two species are in genuine conflict. On the Bass, however, neither the Shag nor the

* in Fisher & Lockley.

Herring Gull (which is losing ground on the fringe of the observation colony) effectively compete. Morton Boyd (pers. comm.) considers that the Fulmar may, in at least one gannetry, successfully do so, and Fisher also records competition between Guillemots and Gannets on Noss (Fisher & Venables 1938).

Summary.

The Bass Rock Colony is increasing and held 7,000 breeding and site owning pairs in 1962. The latter, together with an allowance for nests containing both members of the pair should be taken into account when estimating the breeding pairs. It seems very probable that there is at present no lack of suitable nest sites on the Bass Rock.

- 3 -

THE BREEDING CYCLE (PART 1.)

Brief Outline.

The first individuals (usually old males) return to the Bass Colony about the third week in January, but many are several weeks later. Site attendance gradually becomes regular and copulation and nest building usually precede egg laying by at least a month in any pair; only males bring nest material in the pre-egg stage. Laying (a single-egg clutch) begins at the end of March, with a peak in the fourth week of April, and continues until the end of June, very late eggs being either replacements or belonging to first-time breeders. See Fig.3for the seasonal extent of the various parts of the breeding cycle.

Moult begins soon after egg laying and continues until August. Incubation (44days) is shared equally by both sexes and changes to brooding the egg or chick on top of the webs after the egg chips.

The chick is brooded for about three weeks, after which it is merely guarded constantly, preened and fed by both adults equally for a further ten weeks. Feeding, by regurgitation, occurs several times a day and continues until the chick's departure in mid-August at the earliest, or November at the latest. Chicks leave the nest without the participation of the parents, both of which remain on the nest for, at most, a further two to three months.

Fledged chicks stay on the water for an unknown period (probably about two to three weeks) before they are capable of flight. Chicks from the Bass swim either directly S., or N.E. before turning S.W.. Some, at least, return to the Rock in their first year, but males do not establish sites until their fourth year, breeding in their fifth. They probably live at least 15 - 20 years.

Adults are thus moulting, including flight Feathers, whilst breeding— a highly unusual situation.

Arrival, Departure and Duration of Stay.

Arrival. Adult breeding Gannets are present at the Colony from before the end of January to November, though good numbers were present on the Rock throughout the mild winter of 1934-35 (Robinson 1935). Table 4 shows the dates of first return to the Rock. Gannets, unlike for example Kittiwakes (Coulson & White 1958), Puffins (Lockley 1953) and to a lesser extent Guillemots (pers. obs.) and Manx Shearwaters Puffinus puffinus (Lockley 1942), do not congregate in rafts on the sea before returning to the breeding sites. Individuals first landing on the Rock in early January or even December stay only a few hours and may then be absent for many days.

TABLE 4. Dates of first return to the Rock.

Year	First seen near Rock	First seen on Rock	First date 1,000+ present	Last date 50% or more unguarded nests
1961	Jan. 7th.	Jan. 13th.	Jan. 22nd.	April 8th.
1962	No record	Jan. 14th.	Jan. 24th.	April 11th.
1963	Jan. 1st.	Jan. 18th.	Jan. 27th.	April 7th.

Note : I am indebted to S. Hossack, Lighthouse Keeper, for special efforts to record Gannet returns before my arrival.

Pattern of re-colonisation. The first area to be re-colonised on the Bass each year was a band running at mid-cliff level around the Rock, though extending up into a pocket on the N. face and towards the top of the W. and S.W. faces. Later arrivals spread above and below this band, and the upper breeding limits on flatter ground were re-populated, by established birds, up to six weeks later than the first areas. Superimposed on this distribution were the effects of age and experience, old males returning first (see Table 6) and in several cases the pair

were first seen within 24 hours of each other (Austin 1947, Richdale 1944 and Serventy 1941, consider that Common Terns, Sooty Shearwaters Procellaria griseus and some petrels, respectively, return to their breeding grounds already paired, but do not give supporting details).

Newly-returned Gannets show great wariness and occasional 'panics' (though nothing like so frequently as terns, Cullen), and it may be that the areas first re-populated are the safest and provide easiest take-off. No early birds occupy sites far away from the cliff edge and most are actually on ledges. They are also probably the oldest-established areas on the Rock, although containing only the same proportion of old birds as any area colonised for more than a few Gannet generations. Coulson & White (1960) record that the Kittiwakes returning first belong to the densest colonies, and suggest a 'cumulative' effect of social stimulation carried over from year to year. Gannets, however, nest at a fairly uniform density except in fringe areas.

Return and weather. The date of return is largely independent of weather. For example, birds returned in the last quarter of January 1963 when the severe weather was at its worst. They remain on their sites for a spell, regardless of conditions, leave again, and gradually build up periods of attendance (see Appendix C).

Weather records for the Bass were examined in detail for the latter half of February and the whole of March 1962 for any correlation between weather and the number of Gannets on the Rock. It was clear that adverse conditions had little if any effect on the birds present at the time. Fluctuations in numbers could not be accounted for by temperature, wind direction, wind force or visibility (Snow 1960 correlated the return of Shags to Lundy with the mean temperature of the sea).

However it seemed possible that the effect of weather on fishing conditions could be influential. Thus strong winds and low temperatures tended to be followed by a decrease in numbers, even though these conditions no longer obtained (Table 5). It may be that as birds left the Colony during or after gale force winds they were forced to spend longer on fishing trips and the rate of departure from the Rock could then exceed that of arrival. However the decreases were often rather more dramatic than such a gradual process would suggest. The Colony density fluctuates widely, not only in January and February but up to the third week of April. As late as the second week of April 75% of areas occupied by established birds, mostly experienced breeders, may be suddenly depopulated. Such decreases were not correlated merely with the absence of good landing conditions. By contrast sudden increases occurred during icy gales with sleet and snow. Sometimes the emptying was due to the simultaneous departure of males who had attended their sites for two or three days without the female appearing.

TABLE 5. Weather and attendance in the early part of the season.

Gales	Date of large decrease and subsequent low population
February 15th./16th.	February 19th./21st.
February 26th./27th.	February 28th./March 7th.
March 8th.	March 12th./13th.
April 1st.	April 6th./9th.

Prolonged mild weather, however, does apparently have effect and, as already mentioned, Gannets remained on the Bass throughout the mild winter of 1934/5.

The effect of 'bad' weather on early Gannet attendance is clearly complicated by other, possibly more powerful, factors and it may safely be said that the most extreme

conditions cause little discomfort at the breeding station. Whether its effect on attendance is mediated through its influence on fishing conditions, or whether it is merely a relatively weak factor superimposed on physiological states (to which, of course, day length changes and temperature probably contribute) remains to be shown. It may be added that Guillemots, Kittiwakes and Fulmars appear far more susceptible to unpleasant conditions before laying and, unlike Gannets, vacate their ledges at such times.

Return and age. Colour ringing and site-mapping, begun in 1960, provided four categories of returning Gannets by 1963 ; experienced birds having bred at least two successive years; experienced birds having bred once only; birds having established sites for the first time early the previous year but not bred and birds newly established towards the end of the previous season.

Table 6 summarises the return data for these groups. Older birds return first and spend more time on the site, but are also absent from the colony for long periods during the first six to eight weeks. At this stage there is little chance of them losing their sites, since new males do not usually prospect for sites until April.

Departure. Seasonal departure, like arrival, is correlated with increased wariness and distrust of land, detectable by alarm postures and an increase in the frequency of rotary head shaking which rises with alarm.

The first signs of departure are seen in club birds, which begin to leave in August, and in non-breeding birds or failed breeders, which temporarily desert the Rock during unfavourable weather from early September onwards. Attendance records show that males establishing sites late in the season tend to spend longer on them than males establishing sites

TABLE 6. Correlation between the date of return and previous breeding experience.

Date of return	Status: Bred at least twice	Bred once	Established a full season	Established near end of previous season
Feb. 24th.	13	1		
" 25th.	19	3		
" 26th.	2	-		
" 27th,	11	-		
March 2nd.	8	-		
" 3rd.	7	-		
" 7th.	4	1		
" 8th.	16	-		
" 9th.	6	2		1
" 10th.	7	2		-
" 11th.	7	-		-
" 13th.	2	1		-
" 14th.	3	1		-
" 15th.	6	1		-
" 16th.	3	2	4	-
" 18th.	1	2	-	1
" 20th.	1	1	1	-
" 21st.		-	2	-
" 22nd.		2	-	-
" 23rd.			1	1
" 30th.			-	1
April 4th.			-	1
" 13th.			1	-
" 14th.			-	1
" 19th.			-	2
" 27th.			1	2
" 29th.				1
May 2nd.				6
" 3rd.				2
" 5th.				2
" 10th.				1
" 19th.				1
" 29th.				1
Totals	116	19	10	24

earlier in the season. Also a slackening of site attachment is apparent among breeders, and there is more wandering than formerly. Most chicks have fledged by mid-September and the empty spaces left by absent adults (non-breeders, etc.) encourages this. The pair bond also slackens and many females begin visiting nearby males.

In late September bad weather causes many birds to leave the Colony temporarily and by the beginning of October it begins to empty drastically, though by no means finally. Activity remains high in favourable periods until the end of October (Appendix D.). The latest dates on which 'several' birds were actually on the Rock fell in mid-November, but it may be entirely empty of adults at any time from the end of October. The mid-cliff band, which was the first to be colonised, is also the last to be deserted and males tend to remain longest.

Duration of stay at the breeding Colony. Gannets may be present at the breeding Colony from the end of January to November, though during February, parts of March and October, and November visits may be intermittent. This period is between a third and two-thirds longer than in other British colonial sea-birds (Shags excepted, since they often remain in the breeding area all the year). If measured in time actually spent at the breeding site the ratio is probably higher, since many of the early returners (Guillemot, Razorbill and Fulmar for example) desert the ledges in bad weather even as late as May. Gannets, having bred at least once, spend about four months on the site additional to the time required for incubation (44 days) and feeding the young (94 days). This gives the Gannet an even longer breeding cycle than the Emperor Penguin, despite the 55 - 66 day incubation period and five and a half month fledging period for the latter (Prevost 1953).

Fig. 3 shows the relationship between the duration of their stay at the Colony and the extent of the different phases in the breeding cycle over the Colony as a whole. Gathering of nest material continues for most of this long period, indicating the active interest displayed in the site throughout.

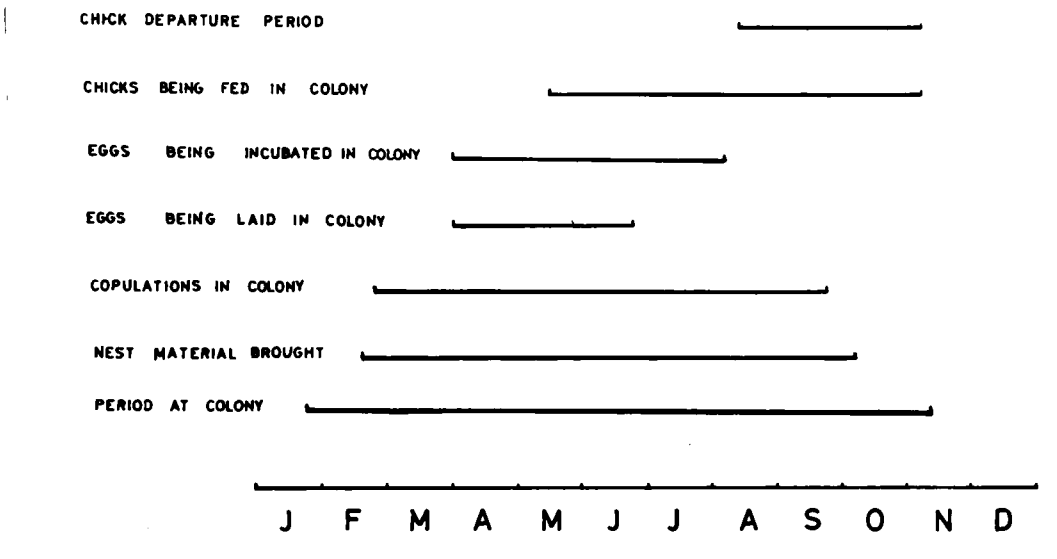


Figure 3. The seasonal extent of stages in the breeding cycle.

It is possible that Gannets (on the Bass) are now spending more of the year at the Colony than formerly. Older records, though vague, indicate a later return and earlier departure than at present. This trend, if present, could be related to the current expansion of the Bass Colony, early returning birds running less risk of losing their sites. It is also advantageous for lower status birds not to arrive too early or they would tend to occupy unattended sites and thus find themselves in severe fights when the rightful owners return. This in turn raises the question of why Gannets leave their nesting Colonies at all. The answer probably does not lie in the weather nor in short daylight hours in winter (since they return in January anyway). It may be that their winter food occurs too far from land to make fishing trips practicable particularly when there are no compelling reasons to make such journeys. When fish do approach land in winter Gannets appear

to have no hesitation in coming with them. In Lerwick harbour 1948 500+ Gannets fished for Coal-fish Gadus virens for several days (Kay 1948).

Adults apparently do not usually go very far south in winter, mainly dispersing into the North Sea and North Atlantic. However, one of my colour ringed adult males was recovered in Senegal (reported recovery date 22nd. April 1963) which seems to be the record for a southerly adult recovery. It is possible that fish are relatively scarce in winter in northern waters and would preclude Gannets from attending their sites in winter.

Fidelity to Site.

Site fidelity is a striking feature in the Gannet (site-establishment behaviour is treated separately in Chapter 8). In the early stages, even before the acquisition of nest material, males defend a very limited area, though this becomes more precisely demarcated later. By contrast S. dactylatra are much less precise in their early attachments, behaving rather like club Gannets. Guillemots, despite their often crowded conditions, also show relatively less precision and may shuffle inches with their egg to avoid an aggressive neighbour. In the absence of any nest material and under the crowded conditions normal in Guillemot colonies, the striking variation in egg colour and the strong preference shown by Guillemots for their own egg (Tschanz 1959) will have survival value. King Penguins also move sites quite considerably within the colony (Stonehouse 1960).

Table 7 shows the proportion of surviving colour ringed males returning to the same site in successive years. Since pairs generally remain constant it is usually not possible to differentiate between site and mate attraction in the female. However cases where the male disappeared during the winter showed that the female also has a strong tendency to

return to the site as such. Of 13 such instances, in ten the females acquired a new male on her old site; one moved to another site within a yard or two; one tried unsuccessfully to pair with a neighbouring male and one remained on the site but was displaced by a pair formed during her absence. Of 16 comparable instances in which males lost their female, 15 remained on the same site and acquired a new female, and one moved to a next-door female whose male had died.

TABLE 7. Site fidelity of male.

Males returning to the same nest :-

Year ringed	Number ringed	1st year after ringing	1st & 2nd years after ringing	1st, 2nd & 3rd years after ringing	Not known
1960	26	26 (26)	22 (23)	14 (16)	5
1961	26	25 (25)	22 (23)		
1962	11	5 (8)			
Totals	63	56 (59)	44 (46)	14 (16)	

Notes: (i) The figures in brackets represent the number of males surviving.

(ii) The number ringed in 1962 included a higher proportion of younger birds than in other years (see later).

(iii) A bird unfaithful in one year is not subsequently counted in these results.

Instances given later show that a female may continue to defend her old site even after joining another male on his. Females, therefore, clearly acquire a strong site attachment which fits with evidence concerning the probable importance of a process of site-attachment 'hardening' in the female in the pre-breeding phase (p. 186).

Birds of differing status show different degrees of site attachment, experienced breeders showing most, and males newly establishing sites late in the season least. Many such males fail to take up these sites the following year and

probably establish new ones (see Table 7). Failed breeders are more likely to change sites than are successful breeders. Thus 13% of failed breeders changed sites the following year (either one or both partners) whilst the mate was known to remain alive. Richdale also showed that in the Yellow-eyed Penguin failed breeders were much more ready to change the place of breeding than were successful breeders. He also found that females were more prone to change sites than were males. It would seem adaptive for individuals to return to the area in which they had already bred successfully, but to change it after a nesting failure.

Fidelity to Mate.

Pair-formation behaviour is treated separately in Chapter 10. Many long-lived birds apparently breed together in several successive years and possibly for life (e.g. Laysan Albatrosses Rice & Kenyon 1962, 94.7% retention of pair bond; eagles Brown 1955; Seton-Gordon 1955; Yellow-eyed Penguins Richdale, 60% of pairs remain intact from year to year; Herring Gulls Tinbergen 1953; corvids Lorenz 1931; Common Terns Austin 1947, 79.1%retention of pair bond; etc.).

Where permanent site attachment exists it is usually difficult to measure mate attachment independently of it. To use mate-fidelity as a blanket term which includes site-fidelity is misleading, though most authors apparently do not distinguish the two.

A figure for site/mate attachment can obviously be measured only for those years in which both partners are known to have survived. Table 8 gives the results of observations on 18 pairs for four years, 43 pairs for three years and 23 pairs for two years. It is in terms of infidelity rather than fidelity to allow distinction between the sexes in this respect.

TABLE 8. Site/mate fidelity in the Gannet.

No. of years pair known to survive	No. of pairs	Mate unfaithful in :- Second year Male	Second year Female	Third year Male	Third year Female	Fourth year Male	Fourth year Female
4	18	0	0	0	3	0	1
3	43	0	4	2	6	-	-
2	23	6	2	-	-	-	-

Total infidelities : male 8
female 16

Notes : (i) First year = year of ringing (in which no birds were unfaithful).
Second year = year after ringing; etc.

(ii) Birds unfaithful in e.g. 4th. year had been together three successive years, unfaithful 3rd. year together two successive years, etc.

Thus over the four-year period eight males left their mate and site of the previous year (irrespective of how many years after ringing this occurred) and 16 females did so. Looked at the other way round, out of four years in which both survived 14/18 (78%) of such pairs remained together the whole time, 1/18 (5%) remained together only three years in succession and 3/18 (17%) only two years. Equivalent figures for pairs known for only three and two years are readily derived from Table 8. Therefore males seem to have a stronger site/mate attachment than females.

However this difference has already been shown to exist in 'pure' site attachment. Can one further gain an idea of whether <u>any</u> of this site/mate figure is due to mate attraction, or whether it may all be accounted for in terms of site attraction?.

The 16 cases of female infidelity arose from a possible total of 163 'chances' to be unfaithful ((3 x 18) + (2 x 43) + (1 x 23) = 163) in the year(s) following ringing. Their actual score is therefore 10% and their site/mate fidelity 90%. Similarly males were unfaithful in 5% of the possible 'chances', giving site/mate fidelity of 95%.

The only figure for 'pure' site attachment in the female is 10/13 (77%) of cases in which she returned to the site even though the male had disappeared during the winter. The difference between the 90% site/mate figure and the 77% site attachment may represent the additional effect of the mate.

The male's 'pure' site attachment may be reckoned as all cases in which he returned (not merely those in which the female died or disappeared) since the male returns first in any case. This figure is 94% compared with the site/mate figure of 96%. Alternatively 15/16 (94%) males losing their mates stayed on their old sites.

It therefore seems that site attachment is very strong in both male and female; that mate attraction plays an additional part in the case of the female, but not in the male. This fits with the role of the male as the site-establishing sex and the female as responsive to the attraction (advertising display) of the male.

Age of First Breeding.

Delayed onset of maturity is common among long-lived birds (Chapter 7). Former estimations of the age at which Gannets achieve adult plumage varied from three years (Gurney 1913) to six years (Saunders 1885), and Booth (1881) showed that in captivity a Bass Gannet laid its first egg in its fifth year. My own series of Gannet plumage developments is given in Chapter 6 (Plate 6), and shows that adult plumage is usually reached in the fifth year, but it should be noted that this does not necessarily prove ability to breed. ~~On the other hand~~ By contrast, Herons Ardea cinerea may breed at one year although not acquiring adult plumage until two years (Lowe 1954) and several other species may also breed in immature plumage.

Gannets usually breed for the first time at five years (Table 9). The earliest reliable breeding records were of a four a year-olds, and the latest a six year-old bird. These

records refer to retrapped birds ringed as chicks and known to be breeding for the first time when re-caught. Additional less certain evidence comes from plumage characters. Since Gannets usually return to the same place having once nested, it was safe to assume that most of the birds in slightly immature plumage, breeding for the first time in the observation colony, had not previously bred elsewhere.

TABLE 9. Known age of first breeding.

Age	Male	Female
4 years	1	-
5 years	3	3
5/6 years	1	4

Both S. dactylatra and S. leucogaster gain adult plumage earlier than the Gannet - S. leucogaster at about 33 months - and therefore almost certainly breed at a much earlier age. Both are, of course, considerably smaller (S. leucogaster about 1,800gm. against about 3,500 for the Gannet). Many pairs with sites in the fringe of the observation colony were slightly immature, retaining one or two black secondaries and/or rectrices. The sex ratio of these birds was unequal with more females than males (Table 10). Therefore unless females achieve adult plumage later than males they must begin breeding earlier.

TABLE 10. Sex difference in immature site-holders and visitors.

	Male		Female	
	Very immature (c. 3yrs.)	Slightly immature (c. 4yrs.)	Very immature (c. 3yrs.)	Slightly immature (c. 4yrs.)
Owners	1	13	1	31
Visitors	2	13	10	47

In addition Table 10 shows the difference in the number of immature birds which temporarily occupied newly-established sites from which the owner was absent. Here again females predominate. The difference may be less than at first glance, however, since on balance females tend to wander more than males and are more likely to be counted twice or more.

Richdale shows that female Yellow-eyed Penguins breed at an earlier age than males (7 records of two-year-old males and 40 of two year-old females, 22 three year-old males and 55 females). Kluijver (1935) also shows earlier female breeding for the Starling Sturnus vulgaris. However immature feathers are probably not a reliable indication of age in the Gannet. The moult cycles leading to adult plumage are complicated, with two or even three cycles of feather replacement overlapping, and slight traces of immaturity may remain unchanged for two years or more. One male with several dark secondaries bred in 1961 for the first time and retained the same degree of immaturity throughout 1962 and 1963. Earlier stages are similarly difficult to assess. Known two year-olds were usually very dark above, with pale head and underparts. One colour ringed bird, however, was in typical third-year plumage in its second year. It may therefore be unwise always to assume that a slightly immature bird is in its fourth year. There is no evidence suggesting a possible sex-difference in juvenile mortality. Mortality among my colour ringed adults (see Table 28) also showed no sex-difference. As Wynne-Edwards (1962) pointed out there is nothing to suggest that females require a shorter pre-maturity period. As the heterogametic sex, however, they may conceivably be subject to differential mortality. The significance of delayed maturity will be considered together with other factors affecting recruitment rate in Chapter 7.

Success of First Breeding.

There is evidence for several wild birds that first-

time breeders have a lower breeding success than older birds - e.g. Coulson & White (1958) show this for the Kittiwake; Snow (1958) for the Blackbird Turdus merula; Austin (1947) for the Common Tern and Hornberger (1944, quoted by Wynne-Edwards 1962:531) showed that in the White Stork Ciconia ciconia the average number of young reared increased with the age of the parents - from 3 to 4 and 4 to 5 years - due to increased efficiency. Richdale provides figures for the Yellow-eyed Penguin suggesting that whereas first-time breeders at two years old are less efficient than experienced birds, those breeding for the first time at three years are not. This implies that age, rather than experience as such, may be responsible for lower success. Although Richdale does not suggest a possible explanation for his results, it is implicit in the equal success of first-time three year-old breeders and more experienced birds, that the former have responded adequately to the requirements of incubation and care of young. This fits with the widely accepted opinion (now becoming suspect) that many innate behaviour patterns such as nest building, incubation and care of young are perfect from their first appearance (Lehrman 1955 has shown that they are not in the Ring Dove Streptopelia risoria, but doves may not be representative of the generalisation. ~~this may be a special case~~). It therefore suggests inability of the two year-olds to find enough food for the young and seems to support Lack's (1954) suggestion that the gradual perfection of special feeding methods may require several years. However in accounting for the tendency for s sex-difference in age of first breeding, it seems improbable that a male should require longer than a female, or that either should require more than four years.

The relevant Gannet records (Table 11) are not explicable on the above lines. It is a striking fact, based on enough records to require consideration, that inexperienced birds have a significantly lower success, but this is due largely to inadequate incubation and care of the very young

chick, and not to inability to find enough food for it. Coulson & White (1958) found the same thing for Kittiwakes - "in several instances birds breeding for the first time failed to incubate their eggs satisfactorily and a number of others were deserted before the incubation period was completed. There were also three records of newly-hatched chicks dying because they were never fed and in each case the parents were breeding for the first time". The implications of these observations are not clear, since it is obvious that by failing to hatch its egg or rear the chick beyond a very young stage, the parents will deny themselves the very experience held to be useful (unless the 'experience' be just another year of self-support). Wynne-Edwards considers this kind of phenomenon an example of 'intrinsic' population control (i.e. imposed by the species on itself, and not by an unavoidable outside influence), but serious objections must be raised to this interpretation (see Chapter 7).

TABLE 11. Difference in breeding success (chicks fledged from eggs laid) of Gannets with differing degrees of experience.

	Number of years previously bred								
	None			Once		Twice	Three or more		
	1961	1962	1963	1962	1963	1963	1961	1962	1963
Chicks fledged	% 59	% 54	% 35	% 81	% 48	% 77	% 78	% 88	% 79
Chicks * died	11	14	13	4	9	8	12	1	1
Eggs infertile	15	14	9	11	0	8	6	6	7
Eggs lost	15	18	43	4	43	8	4	5	13
Total eggs laid	27	22	23	26	23	26	121	115	117

* 89% of first-time breeder chick deaths occurred at less than two weeks due to inadequate care by parents.

It may be seen from Table 11 that the breeding success of the most experienced birds was very similar from year to year. An unusually high number of eggs were lost in all categories in 1963, but the loss was proportionately higher in the less experienced birds. The latter also had a higher proportion of infertile eggs.

Richdale claims that one male Yellow-eyed Penguin first bred at ten years, of which eight were spent as an unmated adult.* Elsewhere, however, he says that this species takes five years to mature. His definition of 'maturity' is probably different in the two cases, but if a bird in full adult plumage and capable of breeding is taken to be mature then it seems, at least, safe to assume a good deal of intraspecific variability in the age at which first breeding occurs, and some difference in success between first breeders and more experienced birds. Whether this difference is due to age, experience or both remains to be settled.

THE EGG

Egg Characteristics.

393 eggs were weighed ranging from 81 - 130gm. (Fig. 4) mean 104.5gm. (variation constituting 47% of mean). This may be compared with an average weight of 84.5gm. for 77 Herring Gull eggs (variation 44%); 47.8gm. for 86 Shag eggs (variation 50%) and 105gm. for 12 Guillemot eggs (variation 31%). The eggs of S. dactylatra weigh on average 67.3gm. and S. leucogaster 51.9gm. (Stonehouse 1963). They constitute 4% of the adult weight in both these species, compared with 3.4% for the Gannet.

Egg shape was not systematically recorded but varies from bluntly obovate to narrow and pointed, most are a normal ovoid; from 65 - 89mm. long and about 50mm. broad at the widest point. The shell is unusually thick for the size of the egg, possibly to withstand pressure from incubation underfoot, against

* This case should be treated cautiously and not as any grounds for a generalisation.

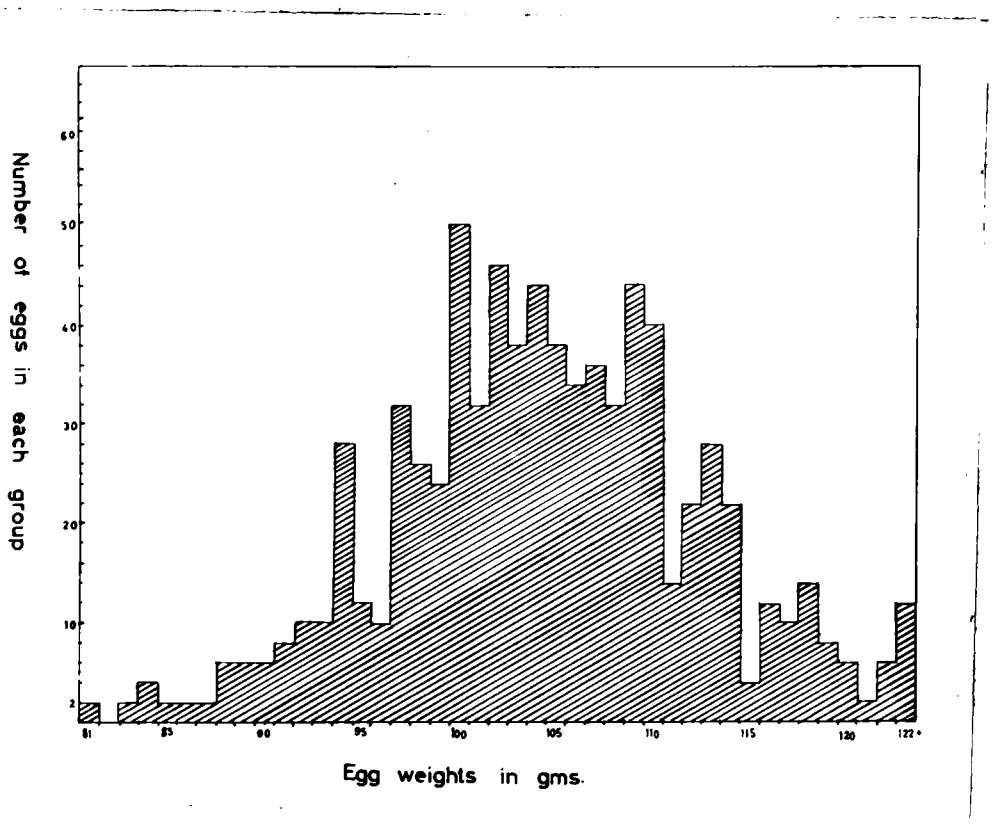


Figure 4. Distribution of egg weights in a sample of 393. (See also Fig. 10 for egg weights arranged in relation to time of laying)

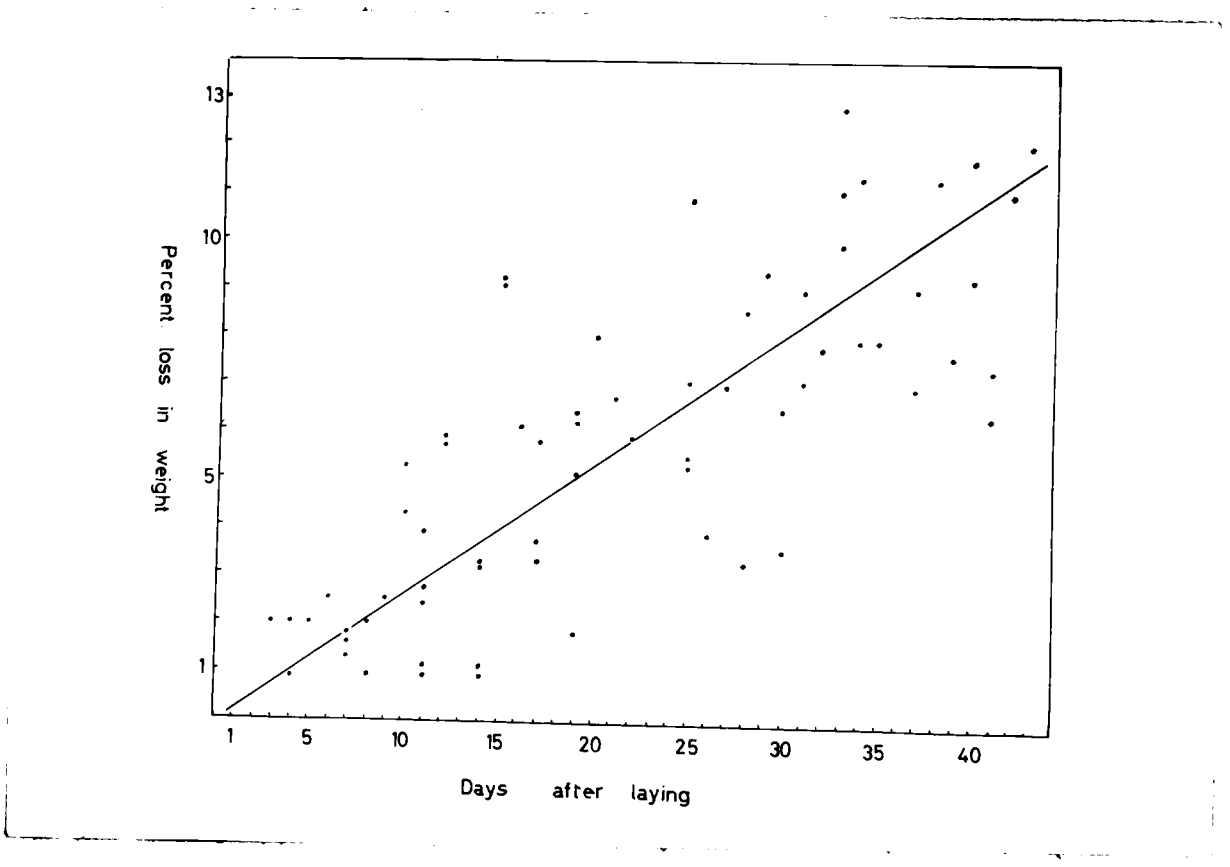


Figure 5. Loss in egg-weight during incubation.

a relatively unyielding nest surface.

The egg is pale blue and translucent when laid, quickly turning white with an outer chalky layer which chips readily, producing a roughened surface which may help to prevent the webs slipping during incubation (pot eggs substituted for experimental purposes shot out from beneath the webs on three occasions). It becomes stained, occasionally black and shiny due to the transference of mud from the webs and their polishing action when settling into position. During incubation a weight loss of 9 - 13% occurs (Fig. 5).

Clutch-size in Sulidae.

Although the Gannet rarely, if ever, exceeds a clutch-size of one the following members of the genus Sula lay more than one (Murphy) :- S. sula usually 1, but occasionally 2; S. leucogaster 1 - 3, usually 2; S. dactylatra 2; S. nebouxii 1 - 3; and S. variegata 1 - 4. Such wide variation in clutch-size between closely related species suggests some correlation with differences in their food supply. Murphy records that Pacific members of the three Sula spp. (sula, dactylatra, leucogaster) more often rear two chicks than do the Atlantic members, possibly due to the richer food supply of the Humboldt current, and Dorward summarises available evidence for the ability of any member of the Sulidae to raise more than one chick.

However, although the habit of laying two eggs has persisted even in those forms which seem rarely to rear two (as Dorward found for S. dactylatra and S. leucogaster on Ascension), it has never been found in the North Atlantic Gannet, which, as we shall see (Chapter 4), can rear two. It is hardly likely that laying two eggs would impose a significant physiological stress on the Gannet, since the relation of egg to bird weight is even less than in S. leucogaster for example, nor should the evolution of synchronous hatching of

the two eggs (see p. 68) pose any special problems. The single-egg clutch must therefore be explained on other grounds.

Replacement Laying.

Replacement laying is, of course, an ability found in most birds with the notable exception of the procellarii, Emperor Penguins (Prevost 1953) and probably a few large raptors (Wynne-Edwards 1962 for refs.) and it is therefore not surprising to find that the Gannet will lay at least one or two replacement eggs and possibly more. Douglas (1898 - reprint with no details of where published) speaking of Bass Gannets states without support that as many as 12 may be laid in a season, but this seems unlikely. Table 12 shows the time taken to re-lay and its relation to the degree of incubation of the eggs lost.

TABLE 12. Replacement egg laying.

Degree of incubation when lost (in days)	Date egg lost	Date re-laid	Interval in days	Status of female
New	7.5.61	20.5.61	13	1st. time breeder
"	23.4.62	7.5.62	14	Experienced
1	28.4.61	8.5.61	10	"
1	27.4.61	9.5.61	12	"
2	21.4.61	6.5.61	15	"
3	24.4.62	8.5.62	14	"
5*	8.5.62	20.5.62	12	"
6*	8.5.62	29.5.62	21	"
c.6	21.5.62	27.5.62	6†	1st time breeder
7	29.4.62	20.5.62	21	Experienced
7*	8.5.62	30.5.62	22	"
7*	8.5.62	27.5.62	19	"
8*	8.5.62	2.6.62	25	"
8*	8.5.62	28.5.62	20	"
8*	8.5.62	31.5.62	23	"
8*	8.5.62	30.5.62	22	"
9*	8.5.62	1.6.62	24	"
11*	8.5.62	31.5.62	23	"
11	13.5.62	7.6.62	25	"
15*	8.5.62	30.5.62	22	"
16*	8.5.62	30.5.62	22	"
16*	8.5.62	31.5.62	23	"
16*	8.5.62	30.5.62	22	"
16	6.5.62	28.5.62	22	"
17*	8.5.62	30.5.62	22	"
17*	8.5.62	9.6.62	32	"
18*	8.5.62	1.6.62	24	"
26	20.5.62	4.6.62	14	"

Notes : * First egg removed

† First egg not incubated after first few days.

The Gannets' ability to replace lost eggs is not altogether to be expected since there is little egg loss in colonies undisturbed by man (on the Bass 6% in 1961, 7% in 1962 and 20% in 1963). However, non-human predators may not always have been insignificant, though in view of the species' present habitat preference for isolated sea-stacks it would be necessary to postulate a historically earlier mainland breeding stock, when mammals such as the wolf or bear as well as man could have been predators (see Chapter 15 for discussion of cliff-nesting habit). Large gulls take Gannet eggs only after human disturbance or occasional aberrant behaviour in leaving the egg unattended. Replacement laying could possibly be a modified relic of a larger clutch (cf. boobies) which was itself perhaps an insurance against infertility (for one thing) - now very low in the Gannet, but apparently higher in S. dactylatra (Dorward). It is probably correlated with the Gannet's long breeding season which allows time for chicks to be reared from late eggs.

Whereas 26/34 experienced birds re-laid after losing their egg, only 2/16 first-time breeders did so, and neither of these had incubated their first egg. There is thus a marked difference between the two categories in this respect. First-time breeders lay later than experienced birds, however, and may have failed to re-lay because of the lateness of the season.

Eggs lost by experienced breeders up to 26 days after the beginning of incubation were replaced, but thereafter usually not. 7/8 experienced birds which lost their first egg and did not re-lay had incubated it 25 days or more.

A significantly lower proportion of re-lays (10/27 37%) than of 'first' eggs (152/192, 79%) gave rise to fledged young, mainly because a higher proportion of re-lays were infertile (37% against 10%). This, however, was not tested by examination for embryos, and the eggs may have been fertile but inadequately incubated. They were not chilled by human

disturbance. Unfortunately there is no information concerning the proportion of infertile eggs in those boobies laying more than one.

Incubation.

Incubation behaviour is discussed in Chapter 12. The incubation period is 42 - 46 days, mean 43.6 (Fig. 6) mode 44 (observations accurate to ± 24 hours). The incubation period in pairs with differing degrees of breeding experience showed no significant differences. Pairs provided with two eggs took 46 days to hatch them, probably due to the greater difficulty in covering them, though some boobies (S. variegata and occasionally S. leucogaster) hatch three eggs (Murphy).

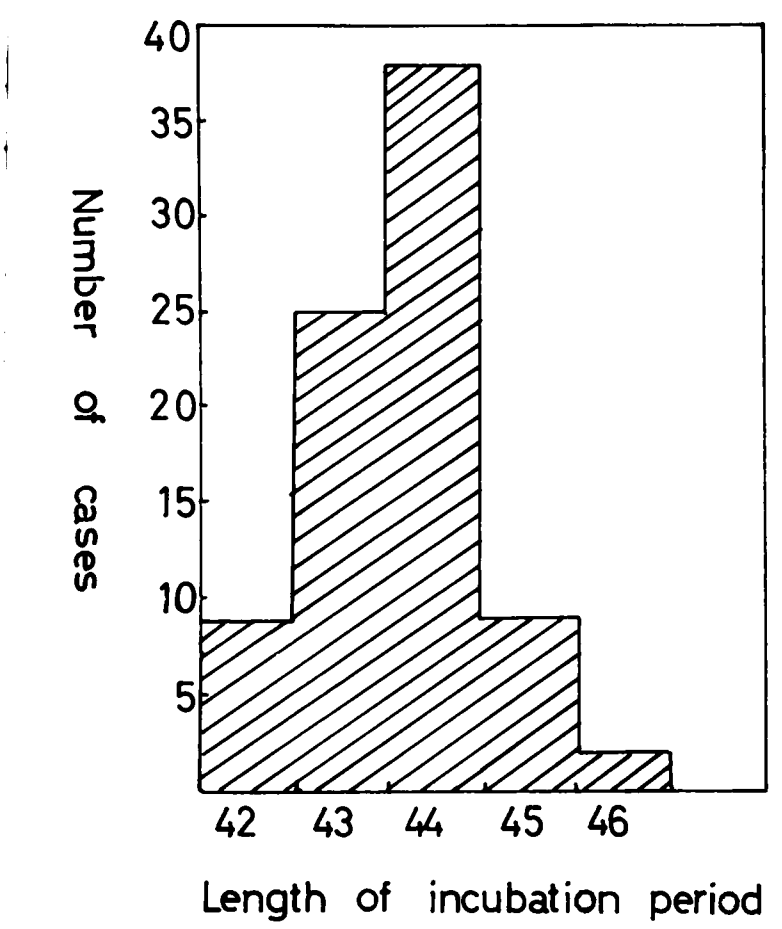


Figure 6.

Incubation period.

Hatching Success.

Figures from the observation colony averaged over three years show that Gannets hatched 82% of eggs laid (Table 13). The results were uncomplicated by any disturbance throughout laying and incubation. This very high figure may be compared with, for example, a substantial egg-loss in S. dactylatra (Dorward, no actual figures given); not more than

48% for the Yellow-billed Tropic Bird and 69% for the Red-billed Tropic Bird (Stonehouse 1962); 69 - 73% over four years for Shags (Snow 1960); 67% for the Madeiran Storm Petrel (Allan 1962); 58% for the Black Noddy (Ashmole 1962); 79% for the Yellow-eyed Penguin (Richdale) and 66% for Adelie Penguins (Taylor 1962). In many species, though not in the Gannet, egg-loss is due mainly to predation, though there may be considerable loss through desertion (e.g. S. variegata Vogt 1942; S. dactylatra Dorward).

TABLE 13. Hatching success.

Year	No. in sample	Eggs hatched %	Eggs infertile %	Eggs lost %
1961	148	87	7	6
1962	163	85	8	7
1963	189	74	7	20
Total	500	Av. 82	7.3	11

Of the 18% recorded egg-loss in the Gannet 7.3% were infertile (cf. 17.25% in the Yellow-eyed Penguin, Richdale) and the remainder were lost either by accident or aberrant behaviour of the adult, e.g. leaving the egg unattended. There was, however, a rather puzzling decrease in hatching success in 1963 when 27% were lost (see Table 13). Wodzicki & McMeckan (1947) suggest that at Cape Kidnappers in 1945-46 the Australasian Gannet had a very low breeding success (not more than 16%) mainly due to infertility of eggs, so it may be that some years are particularly prone to this interesting phenomenon. However, infertility was no higher among my birds in 1963 than in other years, and the lower success may have been due to exceptionally wet weather in late June. First and second time breeders tend to have small nests which often become very soggy. Also their eggs are late and were therefore exposed to this influence far more than those of

experienced birds.

Inexperienced pairs hatched 62.5% of eggs laid compared with 86% by birds breeding for at least the third time, and of this difference 18% was due to egg-loss and the remaining 5.5% to non-hatching, possibly resulting from ineffective incubation.

Egg-loss, recorded in three groups subject to different degrees of human disturbance (Nelson 1962) was shown to be directly related to the degree of disturbance due to exposed eggs taken by Herring Gulls or pulled out by neighbours stealing nest material.

The Onset and Synchronisation of Laying.

Onset of laying. Eggs laid within three weeks of the first egg in the Colony as a whole (an arbitrary definition for 'early') tend to occur (a) in the larger, denser masses (b) in large nests (c) within relatively short distances from the cliff edge (if on flattish ground) and (d) are significantly heavier than later eggs (see Fig. 7 for (a) and (b)).

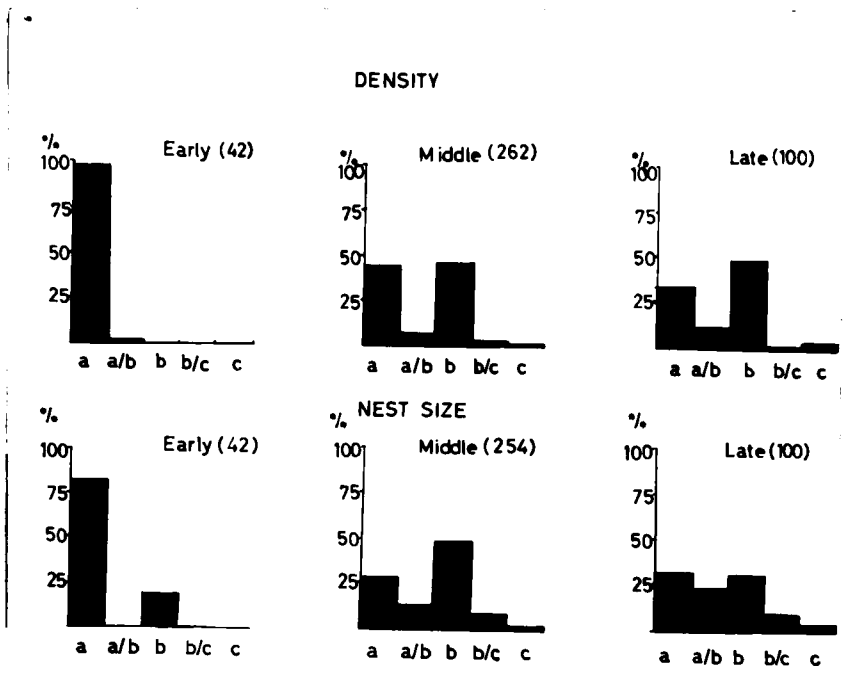


Figure 7.

Density, nest size and the time of laying.

Group size, density and age. Figure 7 shows that all early eggs were laid in denser groups and that later eggs were often in less dense ones. Also Table 14 shows that larger groups tend to start laying earlier than small ones (max. 13 days in 1962). This is probably not merely due to numerical superiority, since comparison of an isolated group with groups

of similar size from the centre of a larger one shows that the latter begin laying earlier (Fig. 8). This, together with the magnitude of the difference between colony 6 and the Green Circle suggests that increased social stimulation brings about earlier laying, first suggested by Fraser-Darling (1938) as one of the effects of colonial breeding and shown by Coulson & White (1959) for the Kittiwake.

TABLE 14. Dates of first eggs in groups of different size.

		1961		1962	
Area	No. of nests	Date of first egg	Date of median egg	Date of first egg	Date of median egg
Observation colony *	250	April 19	April 29	April 15	April 30
Green circle	150	-	-	April 6	April 28
North fog horn	135	March 31	-	April 8	May 1
Plateau & shovel	125	-	-	April 10	May 1
Colony 1	59	April 11	April 27	April 16	May 5
Colony 6	20	April 15	April 29	April 19	May 2

* See p. 54 for explanation of late laying dates.

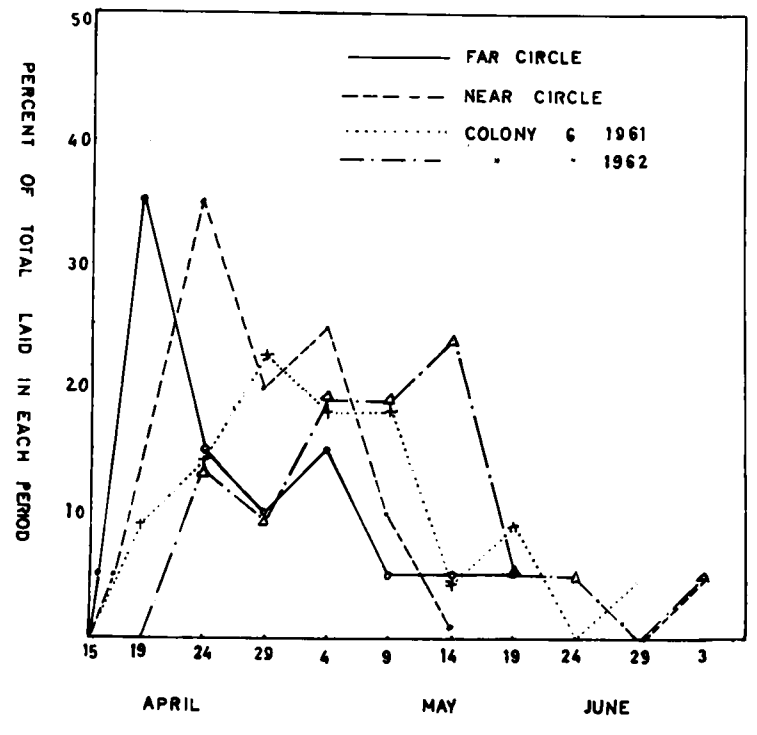


Figure 8.

Isolated and non-isolated groups (equal size) compared for onset and spread of laying.

The age composition of the groups concerned might also have contributed to this difference and, in fact, it will be shown later that in the Gannet, as in the Kittiwake (Coulson & White loc. cit.) and other birds (Lack 1954; Wynne-Edwards 1962 & refs.), older birds lay earlier than younger ones. However, in the groups under comparison in 1962 (a small isolated group and two comparably sized ones from the middle of a large group) it was known that over 80% of the birds in each were present in 1960 and 1961, so that the difference between them is unlikely to have been an age-effect, and was probably an effect of difference in social stimulation.

The effects of density are difficult to assess because on flattish ground it is much the same throughout the colony, and also an age-effect is involved when density is less. Of 408 inter-nest distances measured (from centre to centre) 72% measured between two feet and two feet six inches*. There is an important exception to this, since the fringe area of any expanding group contains more widely-spaced nests (Plate 3) mainly because these areas consist of either newly-established males and pairs, or pairs which have bred only once or twice, and new sites tend to occupy a greater area than old ones. Figure 9 shows inter-nest distances (arranged in relation to time of laying).

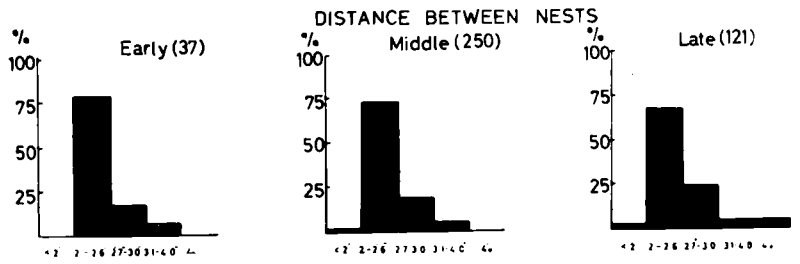


Figure 9.

* Taking $2\frac{1}{2}$ feet as the average inter-nest distance (r) gives a maximum density of 1.6 nests/sq. yd. or 2.0/sq. metre, if the nests are maximally packed like honeycomb cells and according to the formula $D = 1.15/r^2$. In fact the modal inter-nest distance may be between 2 and $2\frac{1}{2}$ feet - say $2\frac{1}{4}$ feet. The maximum density would then be 2.7 nests/sq. metre which fits very well with the figure of 2.5/sq. metre for S. capensis (Broekhuysen & Rudebeck 1951). It does not give the actual density of the Bass Gannets since the method of packing has not been certainly demonstrated, but the true figure is probably not much different from the theoretical maximum of 2 - 2.7 nests/sq. metre.

Plate 3. The observation colony fringe.

A.

Part of fringe of observation colony with most site owners present.

B.

Same area early in April with many site owners absent.

C.

Part of B. early in April. Pins mark sites established the previous season. Note ownership display by upper male.

D.

Group of newly-established sites late in the season (note moult-feathers lying about). Birds widely spaced and one in third year plumage.

Since Gannet colonies consolidate partly by a process of insertion - new nests being established between older ones - the newer areas do not achieve maximum density for several years. Insertion is also helped by the occasional demolition of nests belonging to late-returners, the space so created perhaps then accommodating two sites by slight alteration in disposition. On Plate 2 the blocked-in circles show the location of 18 nests inserted between 1961 and 1963 in this way, mainly in a group which had already existed for many years. The criterion for an inserted nest was that it should be established in such a position that the birds had no clear exit on any side.

There is usually an unbroken succession of owners at any particular nest, either because a lost partner is replaced (a dead male, parent of a chick, was replaced in 11 days in June 1961, though the chick died), or an empty nest is quickly taken over by a new male (a male left his former site to associate with a female, but retained an interest in the old nest and had to return to drive away four or five new males within a few hours, in May 1963). This succession means that usually an inserted site is not merely a replacement of a former nest which had been demolished and unoccupied for an interim period. Where nests are established on an appreciable depth of soil constant digging completely transforms the local topography, uncovering boulders, etc., and may create entirely new niches. It also produces a characteristic 'tiered' effect.

In view of the above it is difficult to separate the effects of density from those of age, and my results merely indicate that early eggs have a strong tendency to occur in the denser parts of the colony and are also correlated with the other foregoing features.

Nest size. Early eggs also tend to occur in large nests (Fig. 7), though it is not always safe to assume that

large nests represent long periods of accumulation. Very ancient-looking pedestals can form in a short time. However large nests have either accumulated over seasons of continuous occupation or because of consistent attendance and gathering of nest material - a characteristic of well-established pairs which may partly explain the correlation between nest size and early eggs.

Distance from cliff edge. It was thought there might be a correlation laying date and the ease with which birds could leave their nests, since birds first back to the Rock were those with sites relatively inaccessible to man and permitting easy take-off. Grades A. and C. were defined respectively, as those which could jump straight off the nest under any wind condition, and those with a flattish area to traverse on foot unless wind conditions were favourable, with grade B. as an intermediate category. No early eggs were laid in category C. nests. Since birds returning early tend to be older, this correlation is partly one of site (birds occupying 'safe' sites tending to return and therefore lay early) and partly one of age.

Egg weight. Figure 10 shows that earlier eggs tend to be heavier than later ones (difference significant at the 5% level). This is probably due to an age difference in the females concerned. It is well known that in birds older females tend to lay heavier eggs than young ones, so that this too fits with age of female as an important factor in determining the date of laying. As mentioned above, there is direct evidence for this in the Gannet, and Figure 11 shows that in the observation colony the first-time breeders laid significantly later than those breeding for at least the second time and that this trend continues for at least another year.

Although all the features so far mentioned as characterising early laying birds fit the interpretation that these are older and earlier to return (the return being also

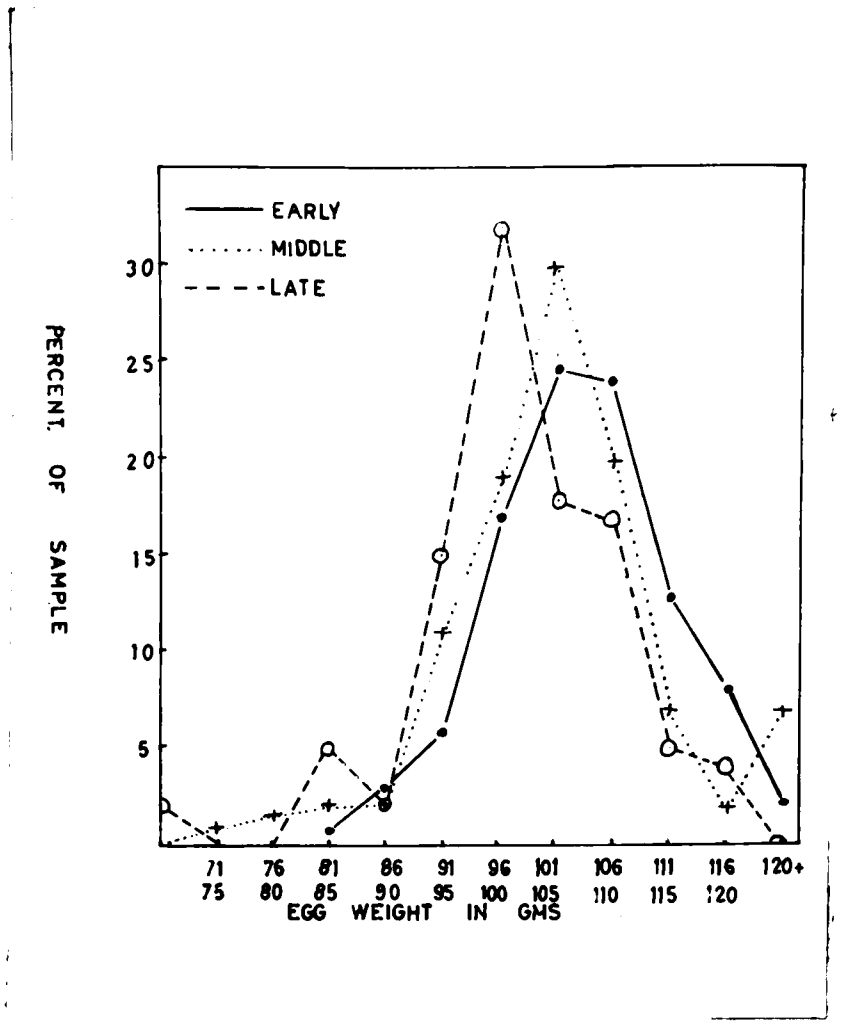


Figure 10. Egg weights in relation to time of laying (early, middle, late).

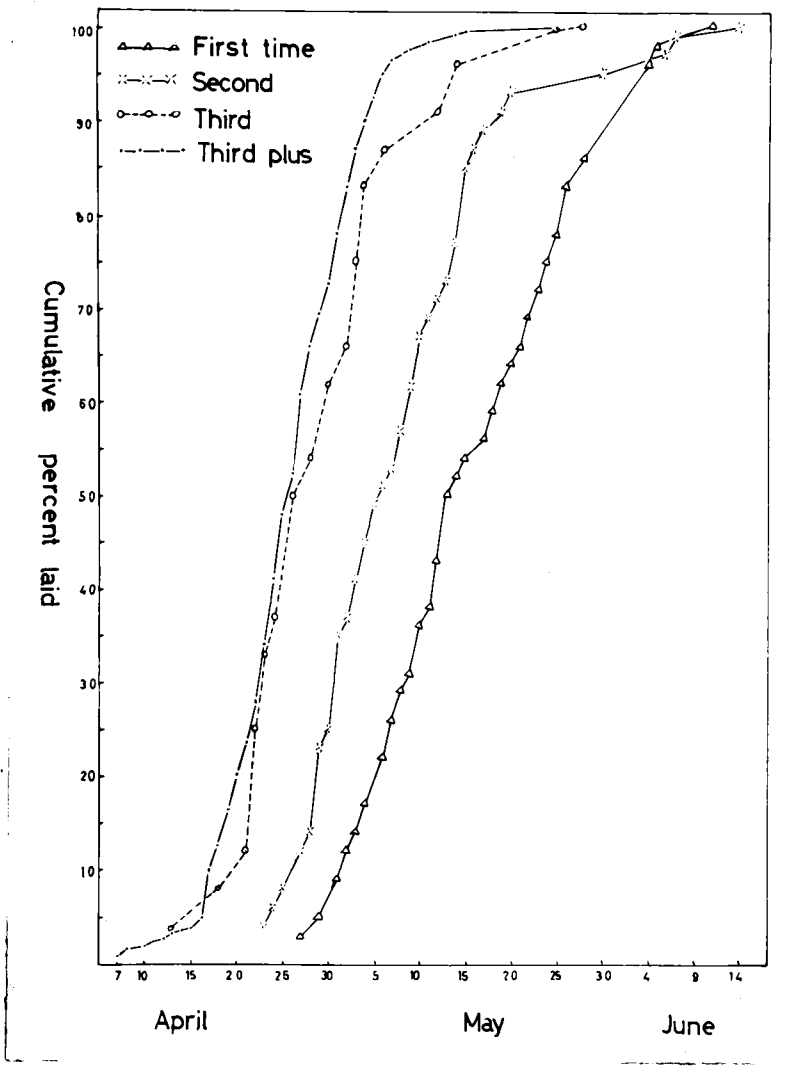


Figure 11. Differences in rate of laying between birds breeding for the first, second, third and more than third time.

influenced by other factors such as experience in breeding) there is no fixed interval between the date of return and the date of laying. Late-comers returning to sites newly-established the previous year may precede laying by less than a third the time spent at the Colony by early birds (cf. Coulson & White 1956, on the effect of latitude on this phenomenon in the Kittiwake; Colonies at higher latitudes compress the breeding cycle). Also the laying date is determined mainly by the female (cf. Starling, Kluijver 1951; Yellow-eyed Penguin, Richdale; Shag, Snow 1960), so that if an old male in a dense part of the colony acquires a young female, their egg will be relatively late. This may be partly due to acquiring her later than an established female would have returned. Of 11 such cases, the date of egg laying varied between May 1st. and June 2nd.; thus the median laying date for the group as a whole was earlier than the first date for such pairs. However it is noteworthy that, whereas pairs in which both members are new to the colony remain on their sites a season before breeding, newcomers, even bearing traces of immature plumage, may breed in their first season in the colony if partnering an experienced bird. Further, newcomers may breed in their first year at the colony when partnering adults which, though established for part of the preceding season, have not bred. The implications of this will be discussed under 'recruitment rate' (Chapter 7).

The replacement factor, by which bereaved males or females remain on the site and often acquire a young partner, means, of course, that even the densest and oldest parts of the colony with the largest nests will contain some five year-old birds breeding for the first time. This will blur the correlation between these factors and an early date of laying, but it remains justifiable to conclude that the early-laying birds are generally the oldest females.

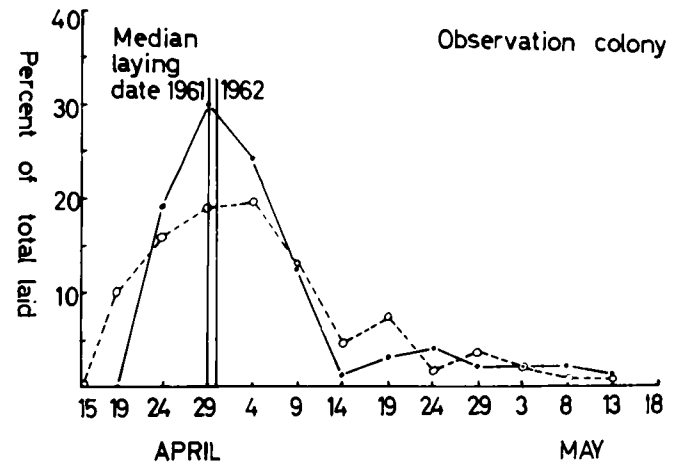
Rate of laying. The rate of laying was analysed in seven different areas, varying in geographical aspect, size and position relative to the cliff edge. In five the rate of laying was graphed for 1961 and 1962, and in the remaining two for 1962 only (Fig. 12).

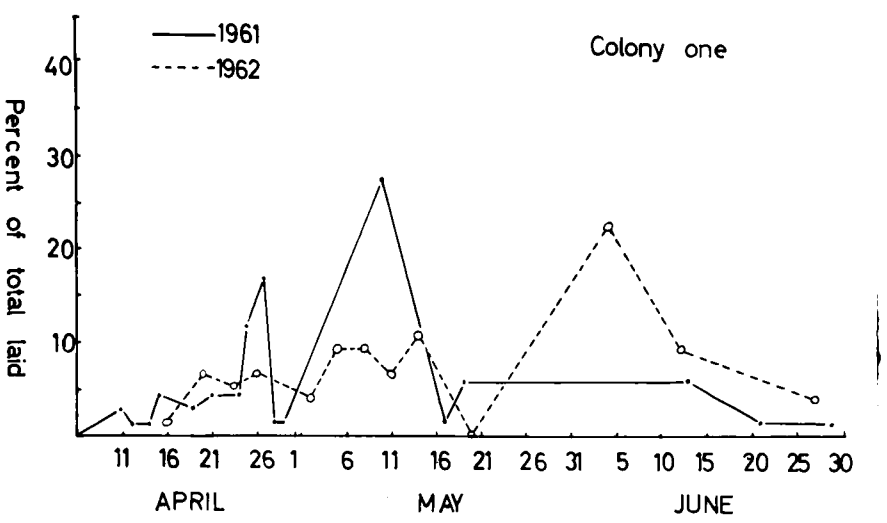
In all areas except the observation colony the rate of laying was obtained by marking all new eggs at three-day intervals, weather permitting. In the observation colony it was recorded during daily observations from the hide, and throughout the pre-egg laying and egg laying periods there was no human disturbance. Most studies inevitably cause some disturbance, thereby introducing a complicating factor, but this possibility can fortunately be excluded from the observation colony results.

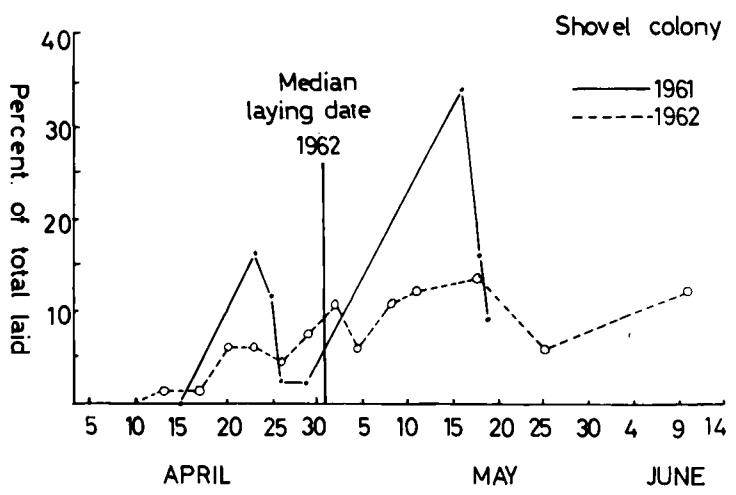
The main peak of laying tends to be preceded by a smaller one and followed by a long tail, with a small hump comprising birds laying late, or replacement-laying, and with each peak separated by troughs of varying depths. In two cases (North fog horn 1961 and Green circle 1962) the main peak is slightly obscured by secondary ones - artefacts resulting from gaps between visits. In the Green circle 87% of the late hump represents replacement-laying and the remainder probably represents eggs from first-time breeders. The wide spread of laying and the small annual variation in median laying dates are noteworthy points.

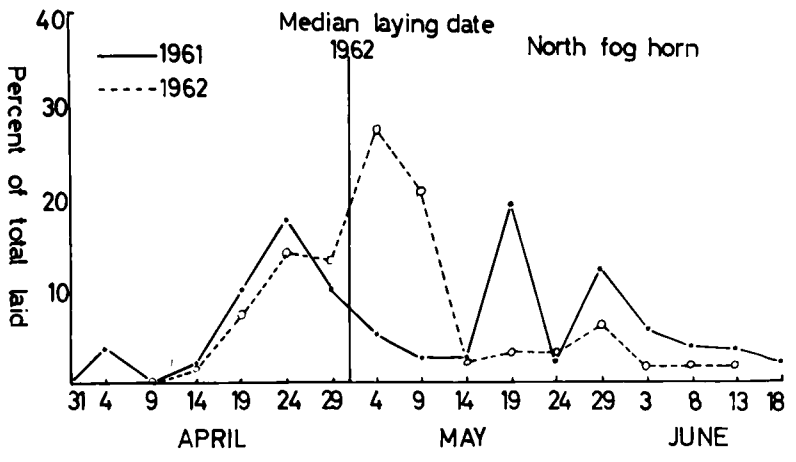
Differences in laying between the same groups in different years. The onset of laying may vary according to weather by one to two weeks in successive years on the Rock as a whole and within a small group. The median laying date, however, falls within a much narrower range from year to year, despite difference in weather (see Table 14).

The observation colony, for which the most detailed









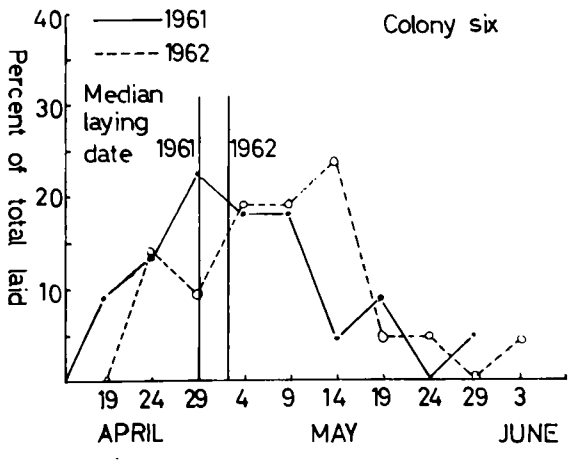
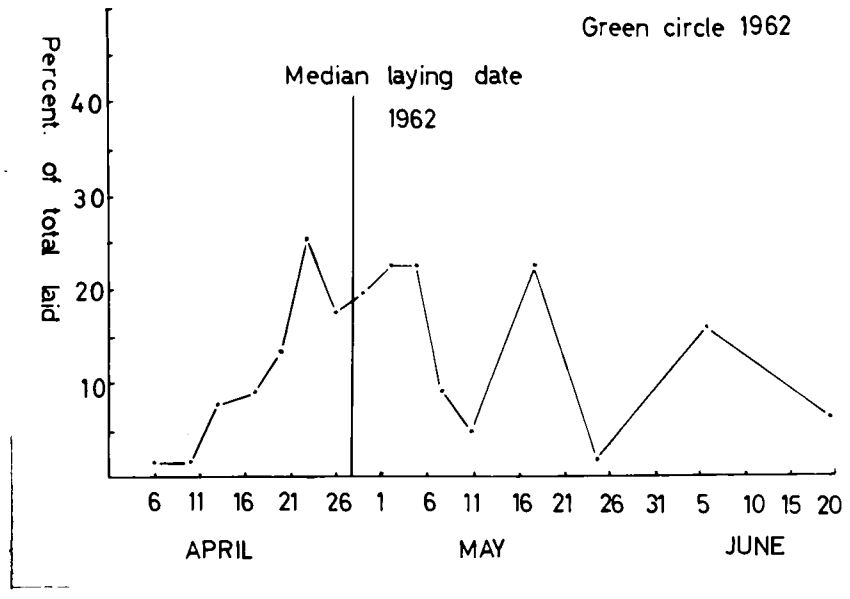


Figure 12. Rate of laying in seven different groups in 1961, 1962 or both (see also Table 14). Median laying dates are calculated only for those groups with sufficient details (usually 1962).



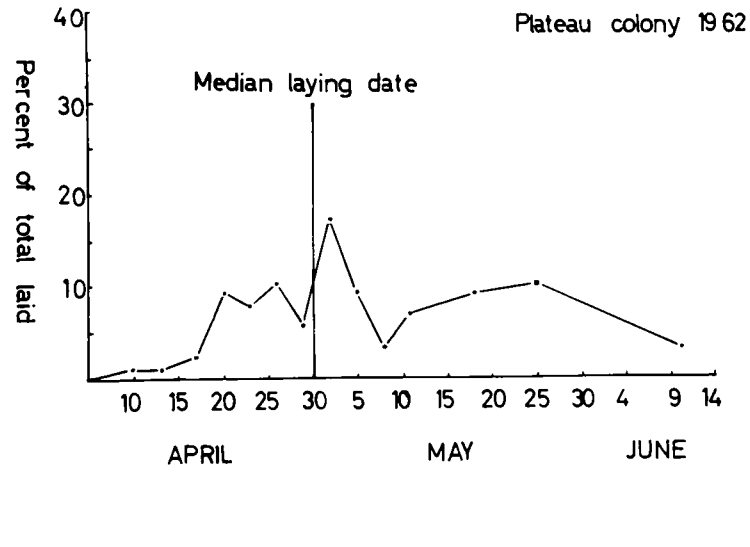


Figure 12. continued.

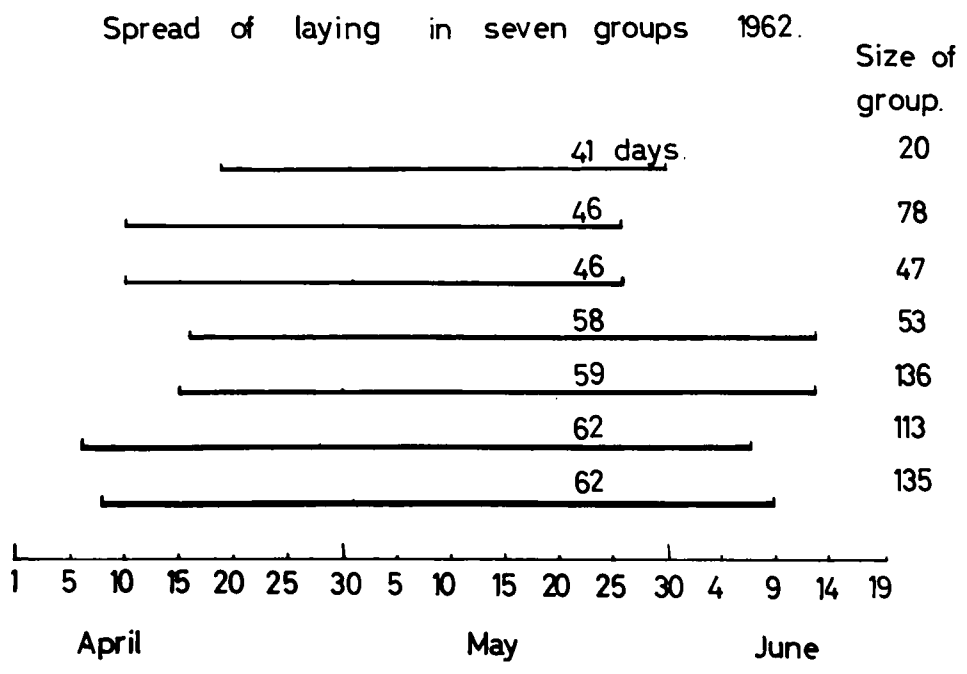


Figure 13. Spread of laying (1962) in the seven groups shown in Figure 12.

figures are available, showed successively earlier first laying dates in the three years. This was not due merely to one or two early laying birds. Table 15 shows that, whereas in 1961 only 14.7% of the total eggs laid in the group (excluding replacements) had been produced by April 23rd., the figure was 23.1 in 1962 and 35.2 in 1963.

TABLE 15. Onset and rate of laying in the observation colony over three years.

		Percentage of total eggs laid by following dates :-				
	Total eggs	April			May	
Year	laid	18th.	23rd.	28th.	3rd.	8th.
1961	116	0	14.7	49.1	73.3	87.0
1962	134	6.7	23.1	41.0	64.2	76.8
1963	173	15.6	35.2	58.3	77.4	84.9

This gradual precession of laying was not shown for the Rock as a whole, where the onset of laying was later for 1962 than for 1961. It was evidently due, in the observation colony, to recovery from the effects of severe disturbance which had retarded the onset of laying in previous years.

Spread of laying. Another regular feature of laying in the Gannet is its notably wide spread (Fig. 13 schematises this for several different groups). Both this and the relatively constant median laying date from year to year are presumably adaptive but would seem to have opposite effects to some extent (see below).

Effect of social stimulation. Differences in the spread of laying between an isolated group of 20 nests and two groups of twenty from the middle of a larger group were analysed. Laying in the former was spread over a longer period (Fig. 8) possibly due to the greater social stimulation received by the less isolated groups. The isolated group tended to return later than the non-isolated, and throughout the season was subjected to many fewer arrivals and departures of

nearby birds, with the attendant disturbances and outbursts of display. The ownership display (Table *) was significantly less frequent in the isolated group. There is good evidence for believing that stimulation of this kind affects the physiological condition of those receiving it (Emlen and Lorenz 1942).

Discussion of laying spread. With a laying spread over the entire Colony of some three months the Gannet probably exceeds that of any other single-brooded British bird.

Richdale has provided direct evidence for the genetical basis of time of laying, so that where close synchronisation occurs it presumably has survival value. Darling (1938) suggested that close synchronisation reduced predation. In some species where a steady (i.e. non density-dependent) toll is taken by predators the total effect may be lessened by synchronised breeding. Also very early or late young may survive less well than intermediate ones due to inadequate feeding(Ashmole, 1962 showed that in the Black Noddy probably no young survived from late eggs). In the Gannet there was no difference in survival to fledging between young from early and late eggs of experienced breeders except for extremely late chicks from eggs laid after mid-June.

If the wide laying spread (Fig. 13) is not disadvantageous, neither does it possess obvious advantages. A constant mean laying date leads to the heaviest demand on food falling over the same period each year - i.e. when most of the young require maximum food - thus concentrating food-exploitation in a particular yearly period. Laying over a long period, on the other hand, results in a spread ~~the~~ load on food resources. If it was really important either that the load should be spread (e.g. if seasonally unpredictable and critical food shortages occurred) or that concentrated seasonal demand should be synchronised with supply, then (since the Gannet cannot reduce clutch-size) one might have expected a much higher percentage of eggs to be spread over the period of laying (rather than a consp-

* omitted.

icuous mode) or a reduced spread respectively. The effect of food-shortage on some sea-bird populations is catastrophic (Wideawakes Sterna fuscata had a breeding success of about 2% on Ascension (1958), much of the mortality due to starvation, Stonehouse 1960). In the Yellow-eyed Penguin "food-shortage is an ever-present threat" (Richdale), though despite this they invariably lay two eggs and can normally rear two chicks.

In fact, the strong evidence for believing that in the Gannet only the very late chicks suffer from food-shortage (and then probably due to the adults' waning tendency to care for the chick and strengthening urge to leave the Rock rather than its ability to find food for it) seems to support the idea that it usually has a dependable food supply throughout most of its remarkably long breeding season.

The tropical Sulidae, on the other hand, apparently have a more wide-spread laying season and, in fact, seem to suffer from just such critical shortages (Murphy; Vogt 1942; Dorward).* This, together with their variable and larger clutch-size, one chick of which usually dies, suggests that the boobies are adapted to a fluctuating environment (in terms of food), whilst the north temperate Gannet inhabits a more stable zone. In fact one of Dorward's main conclusions is that breeding in S. dactylatra (and probably S. leucogaster) is largely determined, in many of its aspects, by food-shortage. However, the seasonal limits imposed by the north temperate climate and food have contracted the Gannet's laying to within certain wide limits, although the factors responsible for precisely defining them are unknown.

It is possible that spreading the load on a roughly constant food supply is adaptive by minimising temporary depletion. Although young Gannets (like many other single young of sea-birds with long fledging periods) are well able to withstand periods of food-shortage, it may be advantageous

* There is not enough evidence to show regular food-shortage.

in critical years to have an adaptation of the above kind. Only a long-term study will show whether such years occur.

Summary.

First annual arrival at the breeding Colony is not much influenced by weather. A certain pattern of re-colonisation is followed, dictated by topography, age of birds, etc.. The seasonal stay at the Colony is eight to nine months and departure in October/November follows, in reverse, the same pattern as arrival in spring.

Gannets are largely faithful to the same site in successive years, males showing a stronger site attachment than females. They also mainly form permanent pairs, but females are slightly more prone to change mates than are males, probably due to the males' greater site attachment. An attempt to distinguish mate and site attachment is made.

They breed when four/five years old; more females than males are immature when first forming a permanent pair bond. First-time breeders are less efficient than more experienced birds, and success improves even after the first attempt. Failure is not due to inability to feed young.

Characteristics of the egg are described and clutch-size in the Sulidae discussed. The incubation period is 43.6 days. Average hatching success over 3 years was 82% (500 eggs).

Early eggs are laid in larger, denser groups; in large nests; relatively near to the cliff edge (if on flatter ground) and are significantly heavier than the mean weight. These factors are partly correlated with the age of the female.

The rate of laying is given for 7 groups. Annual differences in the same group are also described.

The significance of the spread of laying is discussed. It seems that Gannets have a dependable long-term food supply, so that close synchronisation of laying is not required. Nevertheless the mean laying date is remarkably constant from year to year.

- 4 -

THE BREEDING CYCLE (PART 2)

Feeding and Growth of Chicks.

This subject will be discussed first in relation to the feeding of the normal single chick and then with respect to twinning experiments. Feeding behaviour is also included in this chapter.

No attempt was made to collect a representative selection of food samples, but it was clear from chance regurgitations that, for the years of this study, Mackerel Scomber scomber formed by far the most important prey species, although Herring Clupea harengus, Cod Gadus morrhua, Saithe, Sand eels Ammodytes spp. and once a Goby Gobius sp. were also recorded. Ammodytes seemed more frequent in the disgorgings seen early in the year (23 in one disgorging) before Mackerel are locally abundant.

Feeding of single chicks. Gannets feed their young by regurgitation, the chick inserting its bill between the adult's mandibles and then pushing its head far into the parent's gullet (Plate 4). Food is transferred in large gobbets which make a conspicuous bulge as they travel up the adult's throat and down the chick's. Spilled food is usually eaten by the adults, even to tiny fragments on bare back-bones. In contrast, fish regurgitated by frightened adults is not normally eaten. Armstrong (1942) gives a photograph of a Gannet clearly eating spilled fish and calls it displacement nest eating. When the chick is tiny the adult gently engulfs it with widely parted mandibles. The chick must then grope about inside and frequently emerges with food piled on top of its head. At this stage the adult produces a semi-digested mess rather than large pieces and apparently feeds the chick without recieving a specific begging stimulus. Feeding sometimes occurs even before the chick is free from the shell. A considerable amount of food is taken

Plate 4A.

Adult about to feed 10-day chick.

4B.

Note adult bending without active begging from chick.

4C.

Adult about to regurgitate to chick begging at high intensity.

Plate 4D.

High-intensity food begging. Adult 'receptive'.

4E.

Entry. Note bulge in adult's neck.

4F.

Note large bulge and stretched inter-ramal skin.

4G.

Note hinging of lower mandible.

at a relatively early age. A ten day-old chick was given at least three successful feeds in four minutes, involving six entries into the female's bill, and from regurgitations of handled chicks it is also evident that a considerable amount is taken.

From the age of about a month chicks are quick to pester a newly-arrived parent. The chick usually faces the adult and touches the tip of its beak (see Plate 4) in a series of rapid, small-amplitude side to side movements. In low intensity begging short bouts of this activity are punctuated with long quiet spells. When the chicks become larger they importune more vigorously. At the highest intensity of food-begging (from five weeks onward) they retract their necks and with bill pointing upwards (but not touching the adult's) perform a regular swaying head movement (cf. threat behaviour in S. leucogaster, p. 143) accompanied by throat pulsations (the 'gular fluttering' common to Pelecaniformes) and a rhythmic yapping noise, like a puppy. Usually, however, begging is merely a matter of following the adult's bill-tip with its own, making quick stabbing and caressing movements (cf. mutual fencing p. 176).

The adult takes evasive action if unwilling to respond to begging; otherwise it remains motionless, bill slightly inclined upwards and allows the chick to pester. A motionless adult stimulates the chick to intensify its efforts and is the adult's highest form of 'co-operation'. All these forms of begging have a marked effect on the adult and at times cause violent regurgitating movements even when there is no food to be passed.

Rather surprisingly, adults are capable of producing food even after a long spell on the nest and several prior feeds. This was sometimes shown by the visible signs of food-passing (chick gulping, food spilling, etc.). On several occasions the adult which had been on duty fed the chick even

though its mate had just arrived from a fishing trip.

Hundreds of feedings were seen during the normal periods of observation, but to study more systematically fluctuations in feeding rate with time of day and age of chick all visits and feeds were recorded from 27 nests with chicks, chosen to cover a wide age-range, throughout daylight (totalling about 40 hours) on the 14th. and 15th. of July 1962. Table 16 sets out the feeding frequencies during this period. The large number between 04.00 and 08.00 G.M.T. is due to the return of adults after a night at sea. The next increase (14.00 - 18.00 G.M.T.) represents the return of adults relieved in the early morning. Table 17 shows the number of feeds given to chicks of different ages throughout the 40 hours. The number of 'bouts' is more constant over the age range studied than the number of actual feeds. A bout of feeding is here the collective terms for a series of successive entries. Between them, twins are fed about twice as often as singles.

TABLE 16. The number of chick feeding bouts falling into each two-hour period (daylight) from a 48 hour watch.

G.M.T.	Number of feeding bouts Day 1	Day 2	Total
02.00*- 04.00	4	1	5
04.01 - 06.00	8	9	17
06.01 - 08.00	7	15	22
08.01 - 10.00	8	5	13
10.01 - 12.00	10	5	15
12.01 - 14.00	11	6	17
14.01 - 16.00	12	9	21
16.01 - 18.00	16	8	24
18.01 - 20.00	11	9	20
20.01 - 22.00	3	6	9
Totals	90	73	163

* First feed 02.45

TABLE 17. The number of chick feeds (arranged according to age of chick) during a 48 hour watch.

Age of chick in days	No. of feeding bouts	No. of entries Fed	No. of entries Prob. fed	Age of chick in days	No. of feeding bouts	No. of entries Fed	No. of entries Prob. fed
1	7	15	- (4)	29	6	16	5
1	6	8	-	31	5	13	7
2	7	6	1	35	5	24	1
4	4	4	2	35	5	11	1
4	5	8	-	Twins 35/37	8	22	3
17	3	10	-	37	5	12	3
23	5	19	2	37	5	12	3
24	4	9	3	40	4	9	-
25	4	17	-	42	4	6	1
25	4	14	4	42	4	15	2
26	6	10	5	42	3	10	-
Twins 26/27*	9	37	8	43	6	15	3
Twins 27/28*	6	26	11	43	4	16	16
28'	7	20	2				

* One twin subsequently died.

' Formerly twins, one now displaced and no longer fed.

The figures in brackets represents unsuccessful entries.

Table 17 shows that chicks are fed several times each day - none of the chicks in 27 nests were unfed on either day. By contrast Richdale showed that Yellow-eyed Penguins were fed three times every two days (but data from only one nest) and that nestling Sooty Shearwaters aged 36 - 44 days may be unfed for eight consecutive nights; on average throughout their dependent phase chicks may be fed for only 52.8 % of nights (Richdale 1945). Many species are, of course, well adapted to withstand these long periods of food shortage. Rice & Kenyon (1962) showed that Laysan Albatross young could survive four to six weeks without food, and young Gannets can

certainly survive at least a fortnight and probably much more (Booth 1881-87). Even a small chick (12 days) survived a further 12 days when one parent died and the other stayed on guard.

Time, effort and fishing. The 48-hour check on 27 nests revealed that during the period with chicks the sexes spend an equal amount of time on duty and that their fishing trips usually take 7 - 13 hours (Table 18). Trips less than 3 or more than 24 hours are comparatively rare. The accuracy, to within 3 or 4 hours, of the long periods was checked by extra observations before and after the 48-hour watch. The concentration in the 7 - 13 hour range might suggest a tendency to visit a specific area (or areas). Alternatively they may merely hunt wherever they strike prey on the outward journey and rest on the sea for any remaining time. Their fishing range is probably at least 100 miles, and may be much more. The Bass gannetry is the only one on the east coast of Britain (excluding the tiny group at Bempton) and adults fishing south of the Farnes and north of Aberdeen, both regular fishing grounds, are likely to be Bass birds. Barlee (1956) timed Gannets flying round the Bass and estimated that a speed of 34 - 40 m.p.h. was leisurely flight, and 50 m.p.h. could be achieved. A ten-hour absence with three hours fishing, one hour resting and the remainder flying gives a conservative estimate (at 40 m.p.h.) of 240 miles covered - i.e. just over a 100 miles fishing range. The maximum figure could well be a range of over 400 miles, which obviously represents an astonishing food gathering area.

A considerable amount of daylight (15% of the watch) was spent by the adults together on the site (Table 19). This applied even in the case of pairs with chicks six weeks old or more, at which stage food intake is approaching its maximum. Indeed, parents with chicks between 1 - 17 days spent only 0 - 3 hours together at the nest whereas parents with chicks aged

TABLE 18. Length of fishing trips during the chick rearing period, timed over 48-hour check on 27 nests.

Hours absent	Number of cases
1 - 4	10
4 - 7	11
7 - 10	28
10 - 13	31
13 - 16	6
16 - 19	1
19 - 21	3
26	1

TABLE 19. Time spent together at the nest, by pairs with chicks, during a continuous 48-hour period.

	Number of cases			
No. of hours pair present	Age of chick in days 1 - 4	15 - 24	25 - 34	35 - 44
0 - 3	4	2	1	2 (1)
3 - 6	0	1	1	1
6 - 9	0	0	2 (1*)	2
9 - 12	0	0	1	3
Overnight	1	0	3 (1*)	3

Notes : (i) Mean number of hours pairs present in daylight = 6; or 15%.

(ii) Figures in brackets represent nests with twins.

(iii) * Nests in which one twin subsequently died.

26-43 days (including one set of twins) spent 9-12 hours together.It should be added that time spent resting on the site, though apparently 'wasteful', may be a necessary recuperation. Nevertheless birds sometimes remain on the nest with their mate after a prior spell of duty and not merely after return from a fishing trip. Further evidence that Gannets have some 'spare' time and are not forced to work to the limit of their capacity to feed a single chick is that after relief the male and, less often, the female collect nest material which seems to have little importance for the nest structure at this stage (out of 37 male absences of less than one hour 36 were for the gathering of nest material).

Unlike many species (including some Sulidae, Verner 1961) Gannets do not feed their young after these have left the nest. Since much of the high post-fledging mortality is probably due to starvation (many of the recoveries are emaciated) which may well be due to the juvenile's imperfectly developed hunting behaviour (newly-independent Tawny Owls, Strix aluco, suffer heavy mortality, Southern 1959) it might seem advantageous for the Gannet to evolve post-fledging feeding . The young could then acquire the presumably difficult art of plunge-diving under less critical conditions. Strong selection pressure must therefore be acting against the evolution of this habit (see Chapter 5, Discussion).

Growth of single and twinned young. An account of behaviour involved in care of young is given in Chapter 13. Only feeding and growth are considered here. A more detailed introduction and discussion are given because of the wider interest of this section.

Introduction. Clutch-size in birds is generally considered to correspond to the number which, on average, leads to the greatest production of offspring surviving to breeding age and with unimpaired breeding powers. Several

selection pressures could be involved in fixing this number, and it is due mainly to Lack's work on passerines that clutch-size is now accepted as being adjusted to the largest number of young the parents can feed adequately (1954 & refs.). Thus he shows that the number of young which fledge may be lower for larger clutch-sizes, or, if bigger clutches produce more fledged young, that these sometimes have a lower post-fledging survival which probably (but not certainly) offsets the higher productivity. Some cases do not apparently uphold this general statement (Lack 1949 & 1950), but he explains these as adaptations to particular conditions. There is no reason to suppose that this theory should not apply to the Gannet which normally rears one chick, particularly since Lack (discussing the Procellarii) suggests that a single-egg clutch and a long nestling period are adaptations to a limited or erratic food supply. It should be said, however, that if they are shown to be capable of rearing two young to fledging, Lack's general theory is not thereby disproved. A disproof would require that more young per pair of adults survived to the breeding stage as a result of rearing twins. In addition it would be necessary to know that this advantage was not offset in some way (e.g. by reduced longevity or productiveness of the parents) and that critical counter-pressure was not applied to the twinned Gannet chicks in particularly unfavourable years, before accepted interpretations cpuld be queried. These points will be discussed later.

The main aim of this part of the study was to show whether, and if so how successfully, Gannets on the Bass could rear twins, as a first step towards elucidating the wider problem. The idea of following the growth and fledging of artificially twinned chicks stemmed from the chance observation that very occasionally two chicks appeared in the same nest (but may have been the product of eggs from two females). The normal growth-curve of the chick will also be discussed. For

comparison with the Gannet twins a growth-curve for Shag chicks, based on broods of two, is discussed.

Food and the young. Even though the breeding season in many species is closely correlated with the seasonal abundance of food (Lack 1954 & refs.) there is much evidence that the young of very many species, including widely different groups from passerines to sea-birds, suffer severely from shortage of food. In these circumstances the clutch-size is not low enough to provide a wide 'safety margin'. The amount of food supplied to the young usually depends on the collecting abilities of both parents working simultaneously. The Gannet, however, does not exploit its food-gathering potential in this way, and the chick, unlike for example that of S. sula (Verner 1961), S. leucogaster and S. dactylatra (Dorward), the Red and Yellow-billed Tropic Birds (Stonehouse 1962), is attended unremittingly throughout the entire fledging period. This considerably reduces the time the adults spend fishing, since the pair are virtually never absent simultaneously, though there is no need for chicks to be protected from extremes of weather after the first three weeks. One good reason for this prolonged guard stage is the tendency of other adults to attack unattended chicks, even though these do not trespass. Other Sulidae are apparently less aggressive than the Gannet and both adults ~~may be~~ are released for fishing. S. sula nests in trees, so that nests are probably less dense than in Gannet colonies and aggression between neighbours less important in preserving boundaries. S. leucogaster and probably S. dactylatra also apparently (from Dorward) nest less densely than Gannets (though dactylatra is described as "dense") and certainly seem to fight less severely.

Throughout the breeding season Gannets spend some daylight hours at the nest together. Though this reaches a sharp peak prior to egg laying, when more than half the day is spent at the nest together, during the growth period of the

chick pairs spent on average 15% of daylight hours at the nest together during a 48-hout watch. Two pairs with twins of about 27 days spent 18% together as a pair showing that even twins did not eliminate this habit. A third pair, with twins of 35 and 37 days, spent only 1% of daylight together as a pair and it may be significant that only this pair (out of these three) successfully reared both twins.

The above contributes strongly to the impression that the adults are not fishing to the limit of their powers, even during the phase of maximum chick-growth, and it seems that Gannets with single chicks are rarely hard pressed to find sufficient food. In fact, during three seasons I never had reason to suspect that a normal single Gannet chick died from starvation, an occurrence which could hardly have been overlooked in the observation colony.

This situation deserves emphasis and may be contrasted with Vogt's (1942) account of S. variegata on Lobos de Tierra, where all the nests were abandonned, due in his opinion to lack of food, Dorward's detailed account of starvation of chicks in S. dactylatra and S. leucogaster (he also mentions other recorded instances of chick starvation among boobies), Budd's (1961) statement that under-nutrition is the major cause of chick mortality at several Emperor Penguin rookeries, and Ashmole's (1962) account of the serious food-shortage among Black Noddies on Ascension (see also p. 56). These examples merely cover a range of sea-birds; they could be paralleled among other groups.

Despite the rarity of starvation in the young Gannet at the nest the weight increase of the young, which reach 150% adult weight (cf. S. leucogaster chicks whose maximum weight is less than the adult maximum), do*es* suggest that two such dependents might outrun the parents' resources, and there seemed good reason to ~~actually~~ test their ability to feed two chicks.

In 1962 eggs and chicks, of known age, were donated to appropriate 'host' nests to produce two-egg clutches, in some cases with the two eggs of the same age, whether fresh or part incubated, in other cases with the eggs differing in age by one, two or three days. In further the cases the birds were allowed to hatch their own eggs before a chick was added.

The data for the growth of single young, obtained in 1960, 61 and 62, came from the same group of nests as that for the twinned young, thus excluding the possibility of either category being biased by the age-composition of the adults comprising the group, or other 'local' effects. Small young were weighed to 1gm. on a spring balance calibrated from 0 - 150gm..

Although aware that certain variables could conceivably affect the growth of the young, I assumed for simplicity that, at any particular age, the weight increases reflected the amount of food taken by the chicks, and that the twins were not differentially affected by any other factor. For example, twins were not noticeably more active than singles, and did not spend all their time fighting each other, both of which might have reduced their weight gains.

Normal growth of single Gannet chick. Figure 16. shows the average growth rate of 47 single chicks (from 1 - 35 days) based on 383 weighings. The chick weighs more than the adult from the age of six to seven weeks, achieving a maximum weight of some 4,250gm. against an adult weight of some 3,000 to 3,400gm..

From hatching to the age of three weeks its weight increases 20 times. When it fledges its weight is 65 - 70 times heavier than at hatching. The hatching weight of the chick is, of course, influenced by the size of the egg, which in the Gannet is about 3.5% of the adult's weight.

Starvation period. The history of the widely held view that the young of Gannets, penguins, petrels and some

auks are subjected to a period of starvation before fledging, is reviewed by Richdale (1954). It has now been disproved for several albatrosses, and is certainly untrue for Bass Gannets, despite many traditional claims to the contrary in the literature. Young Gannets were fed right up to the day and occassionally the hour of leaving. Although the chick loses some weight before it fledges at 13 weeks, it usually still weighs more than the adult.

Comparative growth-rates, singles and twins. Provided the twins were of the same age (in one case they differed by two days) they grew up together at about the same rate, but lagged slightly behind singles throughout their period of growth and probably fledged at a slightly lower weight than singles. Precise differences for fledging weights could not be obtained due to practical difficulties, but on the only figures available (at 72 days two twins averaged 3,500gm. against two singles 3,930gm.; at 74 days two twins averaged 3,900gm. and two singles at 78 days averaged 3,800) it seems unlikely that the final difference would be very great. In view of the marked recuperative powers of birds with long growth periods, it is even less likely that this small difference could be important. Twins fledged at an average age of 94 (89-103) days against 90 (84-97) days for singles, a statistically significant difference ($P = <.001$).

When twins differed in age by a day or more the younger was deprived of food and eventually, by active persecution from the older, killed or evicted from the nest. This is precisely what happens in S. leucogaster and S. dactylatra (Dorward), which normally lay two eggs but rear one chick.

It was therefore well within the Gannet's ability to rear two chicks in 1962. One cannot as yet fully exclude the possibility that twins can be reared only in certain years, and that in others both may die, thus providing overall a selection pressure against twins, but it must be pointed out

Plate 5. Twinning experiments.

A.

'Twins' about two weeks old. Note barer head of near chick, possibly due to attack from sibling.

B.

Twins about one month old. Note equal growth.

C.

An experimental group showing five pairs of twins between eight and eleven weeks.

that such years would have to occur on average every two or three years to counteract the 80% advantage of years such as 1962, which, in fact, is unlikely to have been better than average for fishing, since the weather was poor with much wind. High wind is assumed to make fishing more difficult, if it affects it at all. Heavy mist may be more harmful, but rarely persists long enough to have a marked effect.

Before discussing the implications of the results, growth-curves will be discussed in more detail.

1. Mean growth rates. It was not possible at the time of weighing to know when a chick had last been fed, also growth was occasionally interrupted, for unknown reasons, by relatively short periods during which the chicks lost weight, probably between well-spaced feeds. These factors could clearly affect unequally the means for the two categories (Fig. 14) on a given day, which would account for much of the fluctuations in weights gains. The experiment was planned to ensure that twins hatched at intervals throughout the normal spread of hatching, so that there was no question of all the twins growing up during the same part of the season, and thus (possibly)being more affected by seasonal food differences than singles. Nevertheless the twins occasionally fell a long way behind the singles, and fluctuations in food supply would be expected to hit them the hardest. As an extreme example, at the age of 24 days the average weight of singles was 1,481gm. and of twins 950gm., less than 60% of the singles' weight. On the other hand, over the entire growth range, twins averaged 90% of the weight of singles, so that extreme weight losses by twins were rare and in any case largely recovered again. Also, the weight fluctuations never approached the magnitude recorded for the Yellow-billed Tropic Bird by Stonehouse (1962), which at 40 days varied by about 190gm.; 39% of the maximum weight ever achieved by the chicks.

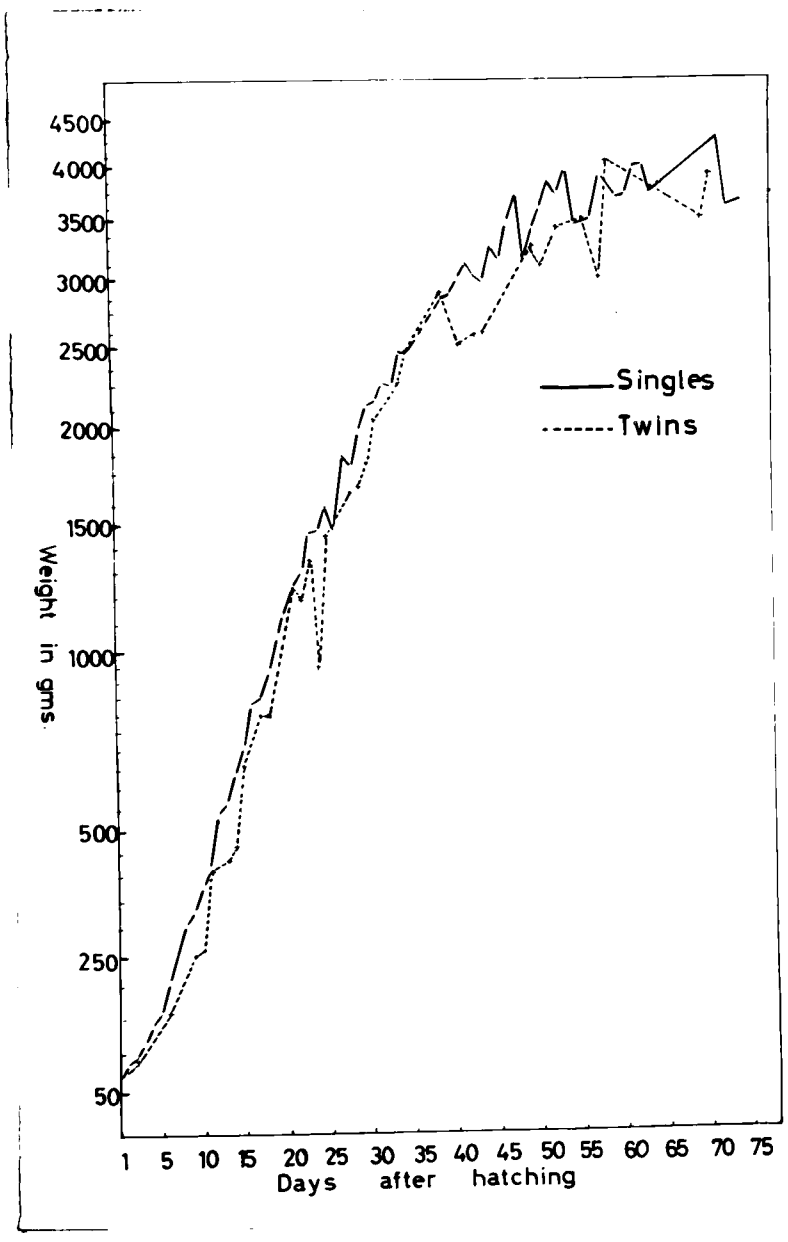


Figure 14. Mean growth rates for single chicks (47 individuals) and 'twins' (21 pairs).

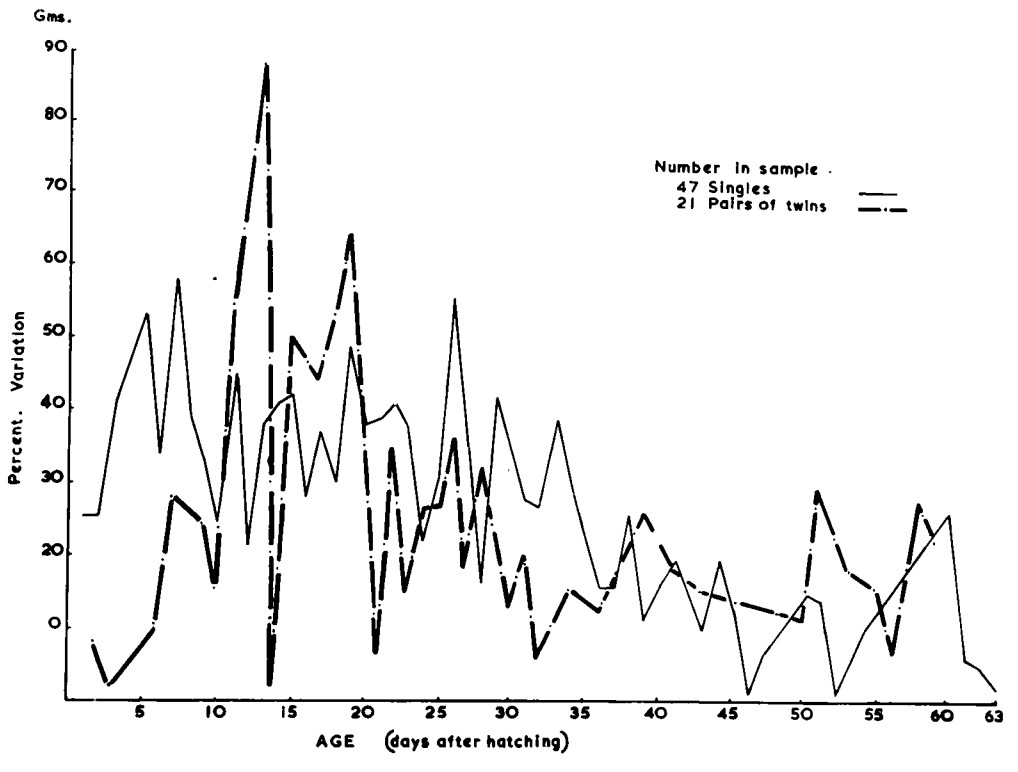


Figure 15. Comparison between singles and twins in total variation in weight, (difference between greatest and least weights expressed as a percentage of the mean).

To equal it the Gannet would have to vary by 1,800gm. at 40 days and, in fact, varied by about 500gm. and this despite the much smaller size of the Tropic Bird.

A difference appears on the first day after hatching (see later) and remains practically throughout the period of growth, but the greatest fluctuations in both singles and twins occur when chicks approach their maximum weight. Variations in food intake at this time of intensive feather growth and high metabolic requirements will quickly be reflected in the weights of the chicks. However, the differences in weight between well-grown singles and twins is much less surprising than those between very tiny chicks of the two categories (see Fig. 14).

The total variation (Fig. 15) at any age, obtained by expressing the differences between the greatest and least weights as a percentage of the mean (the number of individuals providing the data varied from day to day) shows that on the whole single chick weights varied more widely than twins', though there are several ages for which this does not hold. These exceptions are not thought to have any particular significance and may be expected when daily weights are involved rather than grouped ones, for reasons already mentioned.

When the heaviest and lightest individuals (involving different birds) of the two groups are plotted on the same graphs (Figs. 16 and 17) one finds greater and earlier fluctuations in the lightest (for both singles and twins) than in the heaviest. Lightest singles and lightest twins showed weight decreases from one day to the next, at a very much earlier age than did heaviest singles and twins and on more occasions (Table 20). This suggests that in the parental response to the light chicks is for some reason inadequate, quite independent of the effect of an extra chick. It is possible that one partner was inexperienced or that the chicks were unable to buffer fluctuations in food supply to them.

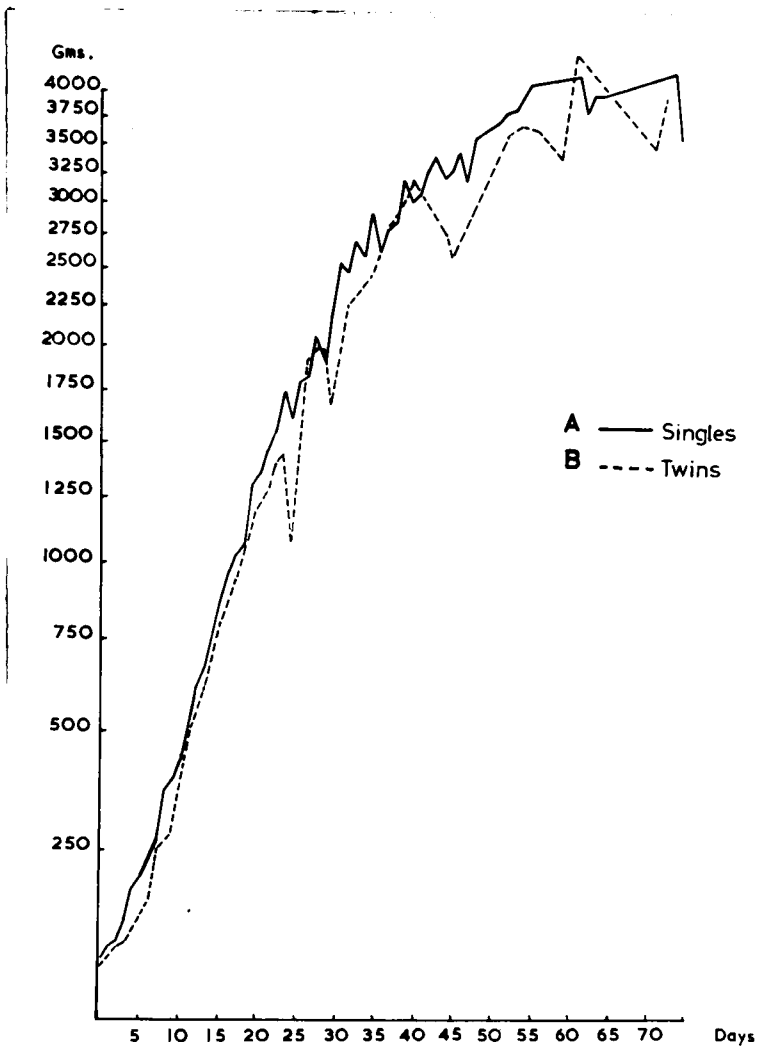


Figure 16. Growth of 'heaviest' singles compared with heaviest twins, (i.e. maximum recorded weight for any individual at that age).

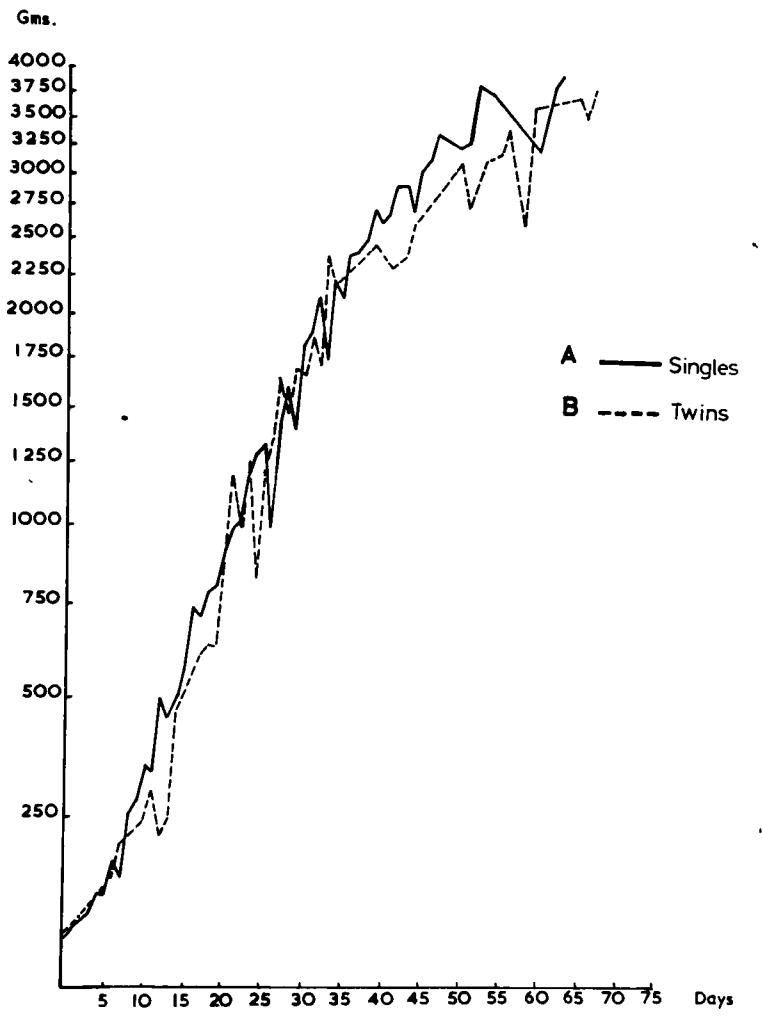


Figure 17. Growth of 'lightest' singles compared with lightest twins, (i.e. least recorded weight for any individual at that age).

The age (less than a week) at which decreases may occur in single chicks precludes lack of food available to the parents as a possible reason.

TABLE 20. Age, in days, at which a decrease in weight occurred between one weighing and the next (individual cases).

Lightest single	5,7,11,13,17,26,29,33,35.
Lightestst win	12,19,22,24,28,30,32,34.
Heaviest single	24,28,31,33,35.
Heaviest twin	24,29.

2. Variation in single chicks. Figure 18 shows the range of individual weights of single chicks from 1 - 35 days old.

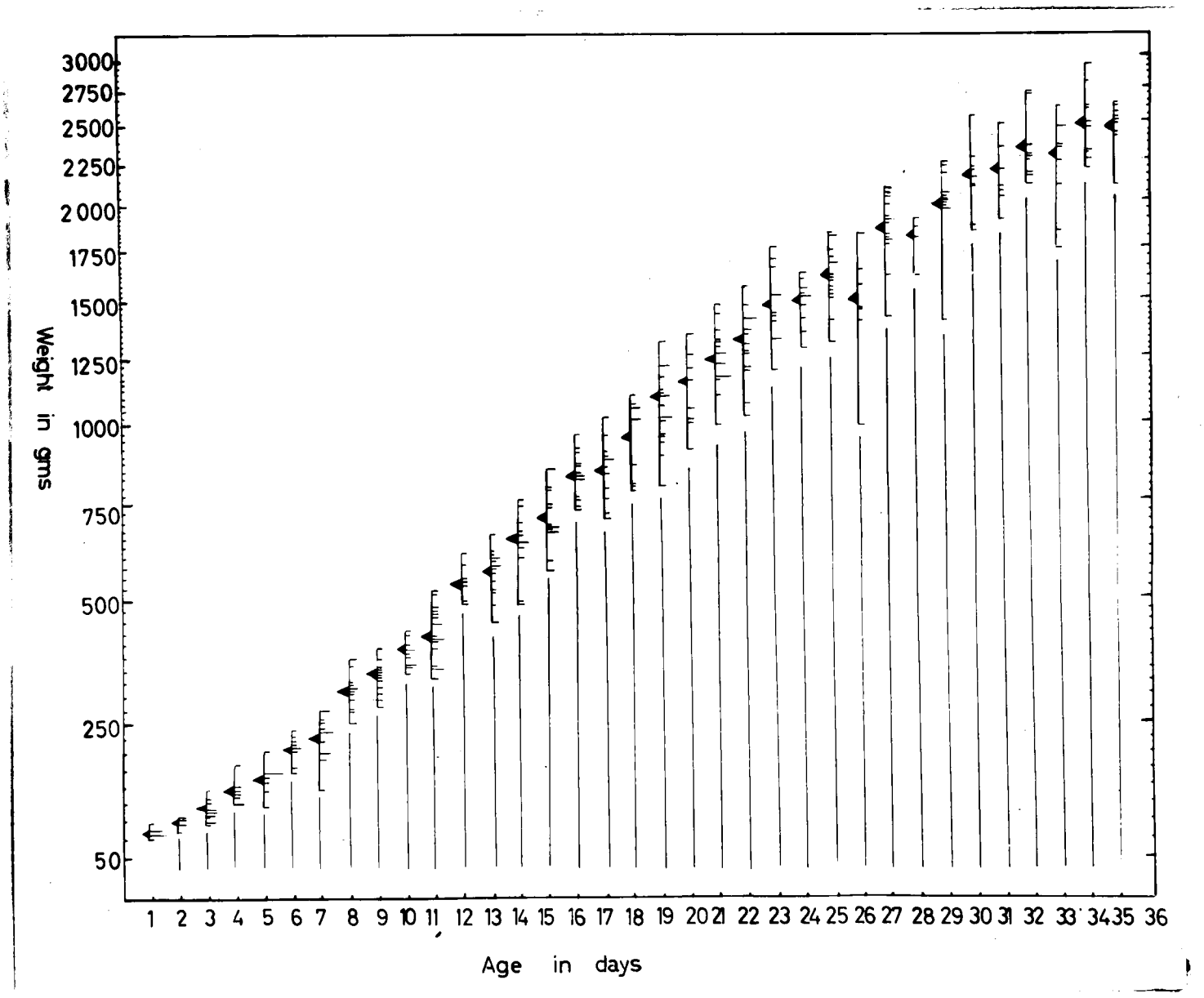


Figure 18. Weight of Gannet chicks 1-35 days. Weights are given on the vertical axis, and the vertical lines show the weight range for any age. The length of the small lines at right-angles to them shows the number of individuals at that age with that weight, the shortest corresponding to one individual. The mean weights are shown by solid triangles on the left side of the vertical lines.

The variation in normal, single chick growth is clearly considerable. It could be due to physiological differences between individuals or to inefficient feeding by their parents, in turn possibly the result of inexperience or a generally poor food supply in the year(s) in question. To answer such questions it would be necessary to know how many times each pair involved had bred, and to have the growth-rates of a large sample of chicks in each year. So far as the present study is concerned, it may be said that much individual variation reflects merely a temporary retarding of growth, which quickly accelerates again. It is sometimes found that a particular chick jumps from a far-below average weight to above average in one or two weeks. This probably indicates that, like many other species with long fledging periods and a potentially erratic food supply, the Gannet chick is adapted to withstand lean periods and fatten up in good ones. It also suggests (as previously mentioned) that relatively minor differences in fledging weights between singles and twins will be unimportant.

3. Shag growth-curves from nests with two chicks. These provide many useful points of comparison. My data, from 14 nests containing two Shag chicks, show that the younger lags behind the older throughout its growth (Fig. 19). The difference between the two is similar to the difference between twinned and single Gannet chicks. Of course, the comparison is only valid up to a point, since the two Shag chicks were differently aged members of the same brood, whereas the twinned Gannets (of the same age) have been compared with singles from other nests; but parallels may still be drawn. Just as the single Gannet chick shows an early advantage in weight over a twin of the same age, so does the older of two Shag chicks. This weight difference persists up to about six weeks, and probably to fledging age.

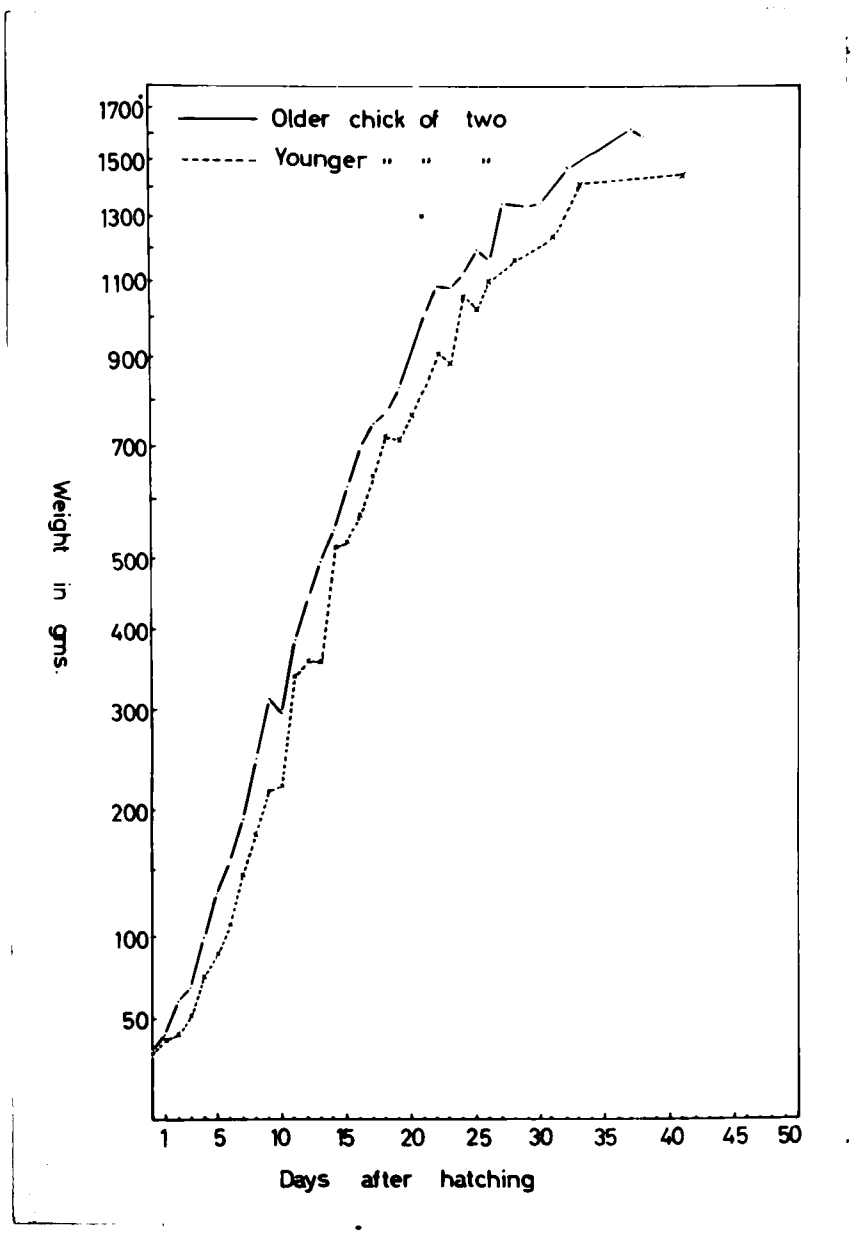


Figure 19. Mean growth rates of Shag chicks from broods of two (14 broods).

Snow (1960) gives a mean growth-curve, based on several years, with which my figures closely agree. Her figure for the growth of three chicks from a single brood, however, shows chicks 1 and 2 crossing and re-crossing on the way up, whereas my records for 14 Shag broods of two show that, even without the competition of a third mouth, chick 2 did not catch up in this way. Moreover, her chicks 1 and 2 were both above average weight. This clearly demonstrates that the parent Shags were responding adequately (to say the least) to chicks 1 and 2, in the presence of chick 3. Yet (in my cases) where there were only two Shag chicks, the younger fell behind and weighed less at a given age than the other did at that age. The importance of this (see later) is that these differences occur early, when the chicks are consuming relatively tiny amounts of food.

Feeding behaviour in relation to weight gain. Two things call for an explanation. One is that, given a small initial difference due to asynchronous hatching, the younger Gannet chick falls progressively further behind the other; and the second that, even though twin Gannets of the same age grow equally as well as each other, they nevertheless grow slightly less well than singles; and in both cases this occurs at a time when the actual amount of food consumed is extremely small. The latter qualification is very important, since it immediately invalidates the plausible assumption that when chick growth is retarded it must be because the parents are unable to gather sufficient food for them.

In the Gannet, the chick is usually fed in bouts consisting of one to seven entries into the adult's bill. The precise number depends on several factors such as the age of the chick, the length of time elapsed since the adult's return to the nest and the proportion of entries which are successful.

During the first few days the chicks are completely

hidden under the adult and it is therefore impossible to see whether the adult feeds them as a response to some external stimulus such as chick movement, or whether feeding occurs 'spontaneously', i.e. independently of external stimuli. Both factors may, of course, be involved in eliciting the adult's behaviour. In the case of Gannets with twins I have observed that after feeding one chick the adult goes through a refractory period during which, though ample pre-digested food is present in the gullet, it does not respond to the second chick. I have no evidence concerning the cause of refractoriness but it seems reasonable to suppose that the adult's ability to give repeated feeds may be temporarily exhaustible, independent of the amount of food available in its gullet. This refractoriness may well be relatively more important in regulating its readiness to feed a very young and inactive chick than an older one whose pestering provides a potent new stimulus tending to overcome the refractoriness. It is helpful in this case to distinguish between stimuli which release a response and those which orientate it.

Thus it becomes easier to understand the observations from which we started. If, in the early stages, the adult's feeding of the chick occurs to some extent endogenously, but is also directed by some form of stimulus (e.g. movement) from the chick, one would expect that the older and more active of the twins would get, on balance, progressively more food than the smaller. If very young chicks do not beg in proportion to their hunger, it is hardly surprising that the amount of food provided by the adults is adjusted to a single chick and

not to twins. The adult's feeding mechanism, including the refractoriness, will thus control the amount of food the chicks get and this will be shared either fairly evenly, if the chicks are matched for age, or unevenly if they are not. Either way the mean growth rate of twins will lag behind that of singles. Once the chicks begin actively to solicit for food, however, the adult response may be expected to be controlled more fully and the amount of food regurgitated to be more or less proportional to this activity so long as food-gathering ability permits. The data suggests that something of this sort is happening. Thus, after the initial lag the mean curves run roughly parallel for five to six weeks , which implies that during this period, at any given weight the twins are receiving as much food as the singles did at that weight, but are behind in time (i.e. they should have reached this weight earlier). If this were not so one would expect the curves to diverge progressively as the chicks grow, which they do not, at least during the first six weeks. The inference is that the adult's response is being regulated adequately by the chicks' begging (Table 21).

TABLE 21. Frequency with which twin and single chicks were fed during a 48 hour watch.

Age in days.	Average number of separate feeds:	
	per pair of twins	per single.
25 - 29	41 (2)	19 (5)
35 - 37	25 (1)	17 (4)

Notes:

(i) Figures in brackets refer to number of nests involved

(ii) The above age-ranges have no special significance. The only twins in the group of 27 nests watched for feeding frequency fell within these ranges.

Finally, it was only during the phase of maximum or near-maximum growth of the twins that the adults began to show detectable signs of the burden imposed by their response to twins. At this time they began to spend less time together at the nest, and sometimes (a rare thing under normal circumstances) left it entirely unattended. Also from about eight weeks onwards, twinned young pestered the adults more intensively than did singles, often eliciting futile regurgitation movements. Thus, even though the mean curves do not, in themselves, show a convincing late-stage divergence between twins and singles, the evidence fits with the expectation that, at this period of maximum demand by the young, the adults are attempting to respond fully. If they do not quite succeed, it is because they <u>are</u>, at this time, limited by their food-gathering powers, and not by any characteristic of the food-giving response mechanism of the adult that caused the early divergence immediately after hatching.

In the 14 Shag's nests with two young, my data showed that the younger of the two, judged by weight gain, suffered some degree of food shortage, again, it must be emphasised, at a time very early in growth when the actual amount of food consumed was extremely small. It may be concluded from Snow's (1960) observation on the three Shag chicks, where the two older chicks grew as fast or faster from the start than average chicks, that there is clearly no mechanism by which the parent Shags are limited to providing a fixed quota of feeds for the brood as a whole at an early age, unless the parents of her brood were very atypical food-donors (fishing ability and food abundance are irrelevant here). Otherwise, of course, three small chicks would inevitably grow less well than two. Shags are therefore adapted to rearing two or more young. However the asynchronous hatching and the slower growth of the second young of Shag broods indicates a 'built-in' safeguard against the possibility of endangering the whole

brood, similar (but less extreme) to that which operates in several raptors (Lack 1954:40). This ensures that during food-shortage one suffers instead of the whole brood. Nevertheless until such a time the younger is allowed to exist, apparently without active persecution from the others.

The situation thus differs markedly from that in the Gannet or S. dactylatra and S. leucogaster (Dorward) where, when there is a size difference between chicks, the smaller (artificially produced in the Gannet, but naturally in the boobies) gets less and less food and is eventually killed by the larger. This effective mechanism for killing off one of the chicks is perhaps not surprising in the Gannet, with a normal clutch of one, but may be, at first glance, surprising in the boobies, which lay two or more eggs. Dorward, on the other hand, took exactly the opposite view, and concluded (it seems wrongly) that in a species laying only one egg the chick would have no need to establish supremacy and would therefore lack the necessary behaviour patterns. Dorward found that in S. dactylatra it effectively ensured that only the larger survived. Unfortunately there is not enough data to show how often, if at all, boobies manage to rear two. If they never, or hardly ever do, it suggests that the habit is perhaps a relic from the days when it was (perhaps irregularly) advantageous. It is, in the boobies at any rate, a specially evolved response.

Fledging Success of Singles and Twins.

The fledging success (expressed as a percentage of eggs hatched) was 70% of all twins from nests which at one period, however short, held two chicks. If, however, those nests are excluded in which the twins differed in age by one or more days, the fledging figure for twins is 83% (Table 22). It is this figure of 83% which should be compared with the fledging success for singles (94% for 1962) in the observation colony, since one from a pair of unequally aged young usually

died. Thus even with a slightly higher mortality, more young (on the above figures about 80% more) per pair of adults are raised from twinned nests than from singles. This is in striking contrast to the Laysan Albatross which Rice & Kenyon (1962) show could not feed two chicks on Midway in 1959: from 18 artificially twinned nests only five young survived, and two of these were so emaciated that they had little chance of fledging,confirming in the strongest possible way that the Laysan Albatross was rigidly limited to one chick, first because it could not hatch two eggs and secondly because it could not feed two chicks.

TABLE 22. Fledging success of twins.

Twinned as :-	Age difference (in days)	No. in sample	Fledging success: Both	One	Neither
Eggs	0	4 (2)	2	1 (1)	1 (1)
	1	5	-	4	1
	2	5 (2)	1	4 (2)	-
	3	3 (1)	-	3 (1)	-
Chicks	0	13	9	3	1

Note : Figures in brackets represent nests in which only one of the eggs hatched.

Discussion.

In considering the question whether, without any significant change in habits (e.g. of site attendance), Gannets could rear two young with overall reproductive advantage to the pairs doing so, it has been shown that during a year when weather seemed to be if anything unfavourable, a high proportion of the Gannets tested were indeed able to feed two young up to fledging stage. However, although the twins finally averaged slightly less (probably not more than 5% and perhaps not at all) than the singles in weight, the possibility, though

unlikely, of lower post-fledging survival cannot be entirely ruled out. The only direct evidence on this question comes from Richdale, who found that in the Yellow-eyed Penguin of 100 fledglings from two-chick families and 19 from single-chick families 39% and 37% respectively were subsequently recovered as juveniles or older birds. Hence twins and singles survived about as well.

It could be suggested that the high fledging success of twin Gannets was partly due to the fact that my experimental nests were all on fairly flat areas and that the fledging figure would have been lower for cliff sites, possibly because a higher proportion of twins would fall off. If Gannets were originally purely cliff nesters (see Chapter 15) could not this have been decisive in limiting them to a brood of one ?. However, even on cliff sites the nests are very often large and would be fully capable of holding twins and many cliff ledges would allow a little overspill. Gannets usually avoid very small ledges, whilst, in any case, a large proportion of the gannets of all three 'species' today utilise flat areas, where conditions exactly comparable to the experimental ones occur.

Finally, one must consider the possible deleterious effects on the adults of rearing twins. If their chances of rearing further chicks were, in the long term, diminished to any great extent, then this might be sufficiently important to eliminate the habit of rearing twins. However, the Gannet is an extremely powerful bird and obviously has enormous fishing powers, so that it seems improbable (though possible) that it would suffer significant physiological stress from the extra burden. Further it is relatively free from food shortage during the winter months and could reasonably be expected to recuperate easily during the period when it has no young to feed, from September to May. Baldwin, Prentiss & Kendeigh (1938) state that large birds,especially, show great individual

daily and seasonal variation in weight, and a temporary loss inflicted on the Gannet, it is suggested, would not be deleterious. Rice & Kenyon (1962) show that Laysan Albatrosses may lose up to 22.1% of their weight in one incubation spell. Gannets do not feed their young once these have left the nest, whereas S. sula, for example, does (Verner 1961), but this need not imply that the Gannet lacks post-fledging feeding because of any strain this might impose on the adults.

The whole question, in birds, of the possible effects on parents of rearing more than the usual number of young seems worth more systematic investigation than it has had. In long-lived sea-birds, especially, these effects could be of importance. One could investigate the problem in the Gannet by weighing the parents of singles and of twins after the young have fledged, and comparing them with the April/May weights*.

If Gannets could, in fact, produce more young per breeding pair, as my experiments suggest, and the above possible disadvantages could be ruled out, it could still be suggested that the present conditions did not obtain when the Gannet's single-egg clutch was evolved, and that clutch-size has not since changed. It must be emphasised that there is no certain case of a Gannet producing two eggs close together, but if two-egg clutches occur naturally and with sufficient frequency, the fact that these have not been favoured certainly requires an explanation.

The second general question to be considered is whether the Gannet, by some apparently simple change in social behaviour, could facilitate the adequate feeding of twins. From the evidence given, it appears that in the later stages of growth twins begin to strain the food-gathering powers of the adults. It is obvious that by guarding the chicks and

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* This has been started in 1963, but the results will not be ready for inclusion in this account.

nest-site less, the parents would, as some boobies have done, greatly increased their food-gathering power. Several advantages would seem to accrue from this, such as increased time for the adults' own needs as well as for feeding the chicks. In unfavourable years this might well eliminate the possibility of catastrophic selection against twins. In fact, they show enormous site-tenacity and associated aggression in defence of their sites, guard their chicks vigilantly and even attack unoffending chicks of absent neighbours, thus actively discouraging such absence. This strongly developed aggression may be essential for successful site-establishment and site-maintenance and thereby provide a strong selection pressure in favour of aggression, and both strong site-attachment and the tendency to attack neighbours' chicks could act to prevent adults from leaving site and chick unattended. If this is so it is a nice example of balance between different adaptive interests.

With an increase in site-tenacity (and aggression, since aggression is confined to the site), there would be an even stronger tendency to remain on the site which would possibly reduce the time spent gathering food for the young. There seems no obvious need for this and it would tend to prejudice survival even of the single young in years when food is short. With a decrease, sites would be more readily usurped in the earlier stages, with an attendant increase in fighting. Since males hold a site for a year or more before breeding, retain it permanently, defend it vigorously and spend a great deal of time on it (up to five days uninterruptedly at one stage) it may be assumed that the site is sufficiently important to warrant such aggression, despite the disadvantages - hence the balance.

It is interesting to note that despite an apparently less productive environment (see Murphy regarding richness of food supply in different areas), and possible drastic food

shortage which sometimes occurs even before there are chicks to be fed (Dorward considered food shortage the possible cause of egg-desertion in S. dactylatra on Ascension), most boobies lay more than one egg. As already mentioned, they frequently leave their large young unattended and in connection with this show markedly less aggression and site-tenacity than Gannets (though this has not been critically examined).

Finally, clutch-size in the Gannet cannot be invoked as a flexible population control mechanism since it does not vary. Also, of course, there is no generally acceptable proposal for an evolutionary process which could favour less productive individuals, since reproductive rate is produced by natural selection and is not adjusted to mortality rate (Lack 1954). Therefore if laying two eggs resulted in more chicks surviving to breeding per pair of adults (and was heritable) one would expect it to spread through the population until it reached a balanced polymorphism commensurate with its advantages (compare clutch-size in the Swift Apus apus Lack (1951) and in the Starling Lack 1948). In fact, a larger clutch seems not to occur at all. A single-egg clutch could, of course, evolve as a density-dependent response to food competition, if those laying more than one nevertheless reared less than one chick. This, however, presupposes food competition as a direct limiting factor (see Chapter 7). Group selection as proposed by Wynne-Edwards (1962) would predict that, even if the habit of laying two did lead to more young surviving (as it apparently does), it would not necessarily spread if it would be against the long-term interests (in terms of exploitation of the local food) of the species. Logically, of course, there inevitably comes a point at which an increasing population must over-exploit the local food, but if such over-exploitation has its own preventative mechanisms, these reside, in the Gannet, in variables such as the size of the non-breeding population, deferred maturity, etc. (Ch.7) and not variable clutch-size.

- 5 -

THE BREEDING CYCLE (PART 3)

Chick Plumage.

When hatched the chick is blackish, sparsely covered with the first generation of white neossoptiles whose distribution is shown in Figure 20. The eyes are closed until the second or third day. The skin is loose, particularly in the gular area.

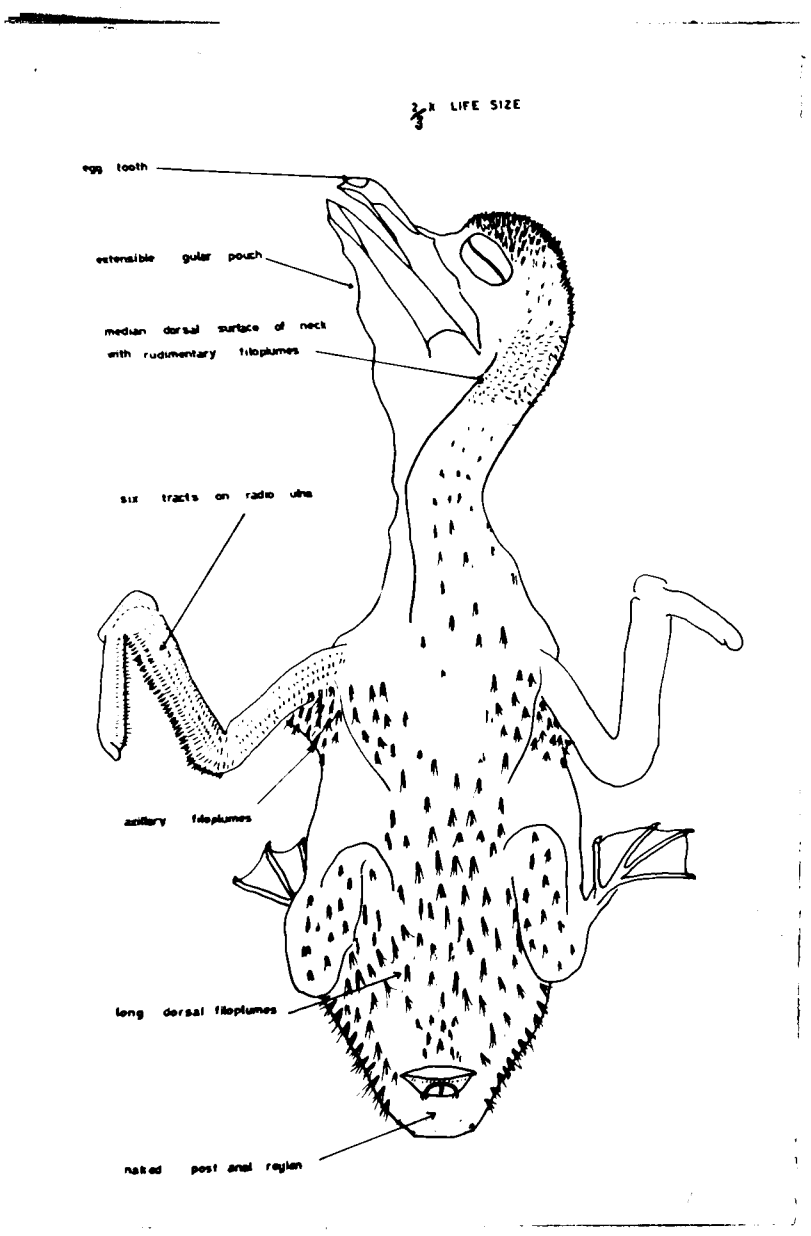

Figure 20.

Pterylosis in two-day old Gannet chick.

Longer white down forms a thick, woolly covering from about two weeks and may clothe even the forehead and crown though these areas sometimes remain naked as though the down has been rubbed off by pushing its head into the adult's mouth. The long down consists of plumules each bearing up to sixty separate branches 80-90mm. long, stemming from a rachis, about 3mm. above the growing point. Each branch is densely covered with fine, hair-like processes. The plumule structure is light and fine and the whole

covering very thick. When dry it must form an admirable insulating layer, but, as previously remarked, it becomes inefficient when thoroughly soaked. It forms the only protection until about five weeks, when the liberated tips of the newly-erupting primaries and rectrices begin to show black. The down is not literally replaced by the growing teleoptiles and persists to a very variable extent (Table 23) during development of the true feathers. A summarised form of plumage development, based on a large number of chicks, is given in Table 23 (see also Plates 4, 5, 20 & 21).

TABLE 23. Chick plumage development (in days)

	Primaries & rectrices erupt and show black	Much down. Back, forehead & tail clearing	Some down on nape, flanks & back	Wisps on nape and flanks	Clear
Earliest at this stage	34	54	67	72	76
Latest at this stage	43	74	80	93	93+

The loss of down may be extremely rapid and a bird with a considerable amount on its head may be clear half a day later. Adults often help by preening the head. I have only a single record of a juvenile leaving the nest whilst retaining some down on the head (at 93 days).

Juvenile Gannets vary considerably in plumage, which is normally black above, finely speckled with white, and slaty-grey below, also finely spotted with white and lighter in overall tone. The spots are not uniform in size or density. Along the leading edge of the wing from the carpal joint to the elbow they are fine and densely distributed, whilst on the wing coverts, scapulae and mid-back regions they are larger and fewer. On the head, chin, throat and lores they are extremely fine and densely packed, becoming larger and fewer on the upper breast and underparts.

There is individual variation in the size and density of spots, and also in their whiteness and the shade of the background. Some chicks are almost coal-black, with very inconspicuous white spots, whilst others are a beautiful silvery grey, and extremely pale beneath. The plumage, incidentally, seems to bleach and become browner between fledging and first moult of the flight feathers.

Function of dark plumage. The function of dark plumage in the young Gannet is puzzling. Plunge-diving birds are predominantly pale beneath, and it has been suggested by Phillips (1962) that this is highly adaptive in rendering the bird less conspicuous to fish. He has demonstrated this advantage experimentally. It therefore becomes pertinent to wonder why, with a high juvenile mortality, most of which occurs in the first month of independence, the young Gannet should be handicapped by a dark ventral surface. Circumstantial evidence indicates that young Gannets often die of starvation at this stage, so that any plumage advantage would be strongly favoured. Yet at this critical stage they lack a plumage adaptation which would seem beneficial, and which does in fact appear later. The ventral surface is the very first area to become pale, and does so quickly. This is a striking feature of first-year plumage, which may otherwise retain juvenile characteristics for over a year after fledging. A further possible disadvantage is that, according to an experiment by Probine & Wodzicki (1955), the Gannet's juvenile plumage is less efficient than the adult's in preventing heat loss.

The dark plumage must, therefore, serve a function important enough to override its post-fledging disadvantages, and I tentatively suggest that it has to do with reducing aggression in the parents. Aggression in the Gannet will be repeatedly stressed when describing behaviour and it will be shown that, under some circumstances, chicks release strong

attack (sometimes even from their own parents). It may be significant that, although the downy stage is white (at that stage the young are of course completely different from adults in size and shape and also stand and sit in quite different postures, see Plate 4) the black plumage is acquired from the very time the chicks become like adults in size, shape and stance (see Plate 21). There are several ways in which Gannet aggression has probably affected, indirectly, systems apparently unconnected with it. Chick plumage may be one example.

A very interesting point is that juvenile S. serrator (judged from colour photographs) seem to be markedly and consistently paler on the ventral surface. One would expect that the juvenile plumage would tend as far in this direction as other pressures allow. This kind of difference between related forms is worth attention.

Fledging.

Existing accounts of this interesting and important phase of the Gannet's life-history are fragmentary and inaccurate, since occasional visits to the breeding colony have naturally failed to produce much evidence on the subject.

This section provides an account of the general aspects of fledging based on thrice daily observations of about 200 nests throughout the fledging periods in 1961 and 1962 (see Chapter 13 for behaviour). About 50 departures were witnessed and many more were known to have occurred within narrow time limits fixed by successive visits.

Fledging periods. Table 24 gives 111 fledging periods accurate to ± 12 hours, and 31 accurate to ± two days. These are fully representative of undisturbed conditions. Fledging occurs between the 84th. and 97th. day, at a mean age of 90 days, significantly longer than previous estimates of two months feeding followed by ten days starvation, in the wild (e.g. Gurney 1913), though in agree-

ment with Booth's (1881) figure of 13 weeks in captivity. As mentioned previously, the starvation period, sometimes referred to as an adaptation enabling young to descend safely to the sea, does not in my experience, occur.

TABLE 24. Fledging periods of single and twin chicks.

	Number of cases		
No. of days	Singles ± 12 hours	± 2 days	Twins ± 12 hours
103	-	-	1
98	-	-	2
97	1	-	5
96	2	1	1
95	3	1	1
94	6	-	2
93	13	2	3
92	7	2	3
91	13	-	2
90	15	3	2
89	19	1	2
88	13	3	
87	6	6	
86	4	7	
85	6	3	
84	3	1	
83		1	
Averages	90	-	94

The cause of variation in the fledging period of single chicks is not known. It is probably not the experience of the adults (and hence possibly their ability to feed the chick) since the fledging periods of chicks from parents breeding for the first time did not differ significantly from those of more experienced pairs (mean fledging period of 50 experienced birds 90.1 days, range 85-97; mean fledging period of 23 first-time breeders 90.1, range 83-96). Nor did it seem to depend on the chick's difficulty in reaching a point (usually the cliff edge) from which to fly, since there was no significant difference in mean fledging period between chicks from nests near the cliff edge and those from nests near the inland fringe (cliff edge 16 cases, mean 88.8, range 84-95; inland fringe 20 cases, mean 88.9, range 83-96). Obviously the external situation is of little importance in

deterring the juvenile.

Experiments were described earlier in which 32 nests were given an extra egg or chick to test the Gannet's ability to feed two chicks. 83% of these twins fledged successfully, but took a significantly longer time to do so (see Table 24), probably because twins lag slightly behind singles in growth. This indicates that slight food shortage retards fledging and suggests that if the fledging period is normal feeding has been adequate - a useful guide in estimating the ability of inexperienced adults to feed their chick, as mentioned above.

Fledging success. 89% of all eggs hatched gave fledged young in 1961, 94% in 1962 and 94% in 1963* (average 92.3% based on about 500 nests) where fledging is defined as irrevocably leaving the nest when fully grown. In comparison with evidence already quoted for other Sulidae this figure is extremely high. It is also consistently high in different years, despite considerable variations in the weather. This makes it unlikely that success in the year of the twinning experiment was unusually high. Gannet success may be compared with the following figures for other colonial sea-birds, in order of success : 88% for 179 pairs of Kittiwakes over three years (Cullen); 83.2% over four years for Shags (Snow 1960); 79% for Yellow-eyed Penguins over 16 seasons (Richdale); 75% for Adelie Penguins 1959/60, Cape Royds, was considered an exceptionally good year (Taylor 1962); 45% or less for Razorbills, but only on 50 eggs (Keighley & Lockley 1948); c. 36% for Herring Gulls (from several sources listed in Cullen loc.cit.). For the Laysan Albatross, Rice & Kenyon (1962) give figures of 73 chicks fledging from 419 nests (17%) but it is not clear whether some of the failed breeders suffered experimental interference. Snow's Shag results are

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* In order to include this year's figures, success for 1963 is calculated from young slightly less than fully grown, but chick loss at this stage is negligible (figures calculated 15th. August 1963).

compared in detail since they represent the only series of comparable figures for another member of the Pelecaniformes (Table 25).

TABLE 25. Comparison between Gannets and Shags* in fledging success.

Year	No. of nests		% hatched of laid		% fledged of hatched		% fledged of laid	
G.	S.	G.	S.	G.	S.	G.	S.	G.	S.
'61	'54	145	49	87	69	89	90	77	62.5
'62	'55	159	83	85	69	94	93	77	63.8
'63	'56	186	78	74	71	94	67	69	47.2
-	'57		84		73		95		70.3

* The Shag figures are from Snow (1960).

Causes of chick loss. Starvation was not known to be a cause of chick mortality but the following factors were of some importance :-

Weather. High wind, prolonged rain and low temperature caused death in at least six cases of 3 - 5 week-old chicks. These are too large to be adequately brooded, yet lack the protection of true feathers and are unable to resist extreme soaking and chilling, though generally hardy enough. Wodzicki (1953) says 10% of Cape Kidnappers Gannets may die in bad weather, and it is conceivable that in certain years particularly unfavourable conditions could destroy a large proportion of chicks if they were all at a vulnerable age. By late August conditions on the exposed Rocks used by Gannets can be extraordinarily harsh. Two to three-day northerly gales with heavy rain turn even the well-feathered chicks into miserable caricatures, and would kill large numbers of young if these were still downy. This must certainly limit the total extent of the breeding season and may also favour a wide spread of laying, so that unseasonably severe weather

does not find all chicks vulnerable.

Attack by neighbours. Five deaths were recorded due to attack by neighbours on unattended chicks (caused in some cases by the death of one parent), However, chicks are attended so consistently that adult attacks can constitute only an insignificant mortality factor under present conditions, though as stressed in Chapter 4, they may be important in preventing both parents gathering food at once.

Falling. Several chicks were probably knocked off their nest by adults departing in unfavourable wind conditions and three were known to fall off during wing exercising. No nests were known to come away from the cliff face, as sometimes happens in Kittiwakes (Cullen estimated that falling was equally as important as food shortage in Kittiwake chick mortality).

Inadequate parental care. A minor source of chick loss occurred as a result of inadequate attention to new chicks especially by inexperienced adults (e.g. two inexperienced birds either incubated the chick underfoot or trod on it whilst shifting position, etc.).

Fledging. The extremely low mortality during the actual descent to the sea may be roughly estimated in two ways. First by recording the number of fatal crashes actually observed as a proportion of the number of departures witnessed (2/50 or 4%). These were the direct result of severe handling by neighbouring adults, before the chicks struggled clear, causing them to fall over a 300' sheer drop whilst facing in to the cliff. They were than unable to right themselves and obtain the necessary lift by facing into the wind (or in the absence of updraughts, using their forward and downward momentum to generate lift). As a result they were killed by the fall. Nevertheless they are extraordinarily robust and can withstand great falls which would almost certainly kill most heavy birds.

Secondly the number of injured or unsuccessful birds may be counted on suitable areas at the base of a cliff section and the number of nests from which these young came roughly estimated, although this is only an order of magnitude indication. Several would probably get away eventually, and only injured or very 'fouled' birds (in positions where excreta falls on them) should be counted. By this method 10-20 young were seen below a sheer section of the N.W. face, which held a nesting mass of some 1,000 - 1,500 pairs in 1961 and 1962. It may be concluded that mortality due to fledging in the Gannet is certainly not more than 1 - 4% on the highest estimate. Mortality due to the attacks by adults on fledged chicks (p.225) could not be estimated but is likely to be completely insignificant compared with the main mortality factors.

The Fact that very Few young Gannets die as a result of activity involved in fledging is ...../
~~The young Gannet's low mortality due to fledging is~~ noteworthy when compared with certain other cliff nesting sea-birds, e.g. Guillemots whose chicks are reported to suffer a 25% mortality through failure to make a safe descent and departure (Perry 1948). Gull predation causes some loss of newly-descended chicks - a factor which does not significantly affect the young Gannet.

Season. Fledging continues from August to November (Fig. 21). The implication of the long laying period have been discussed (p. 55). So far as post-fledging mortality is concerned, the majority of ringing recoveries from the Bass occur in September and October (Table 26). This may indicate higher mortality among later fledging juveniles; if the critical transition period between utilisation of reserve fat and learning to fish should fall among equinoctial gales higher than average mortality would probably follow. Earlier breeding would in this case be favoured and it may be assumed either that birds breeding later than the optimum survival date requires are constrained to do so for physio-

logical or behavioural reasons, or that a wide spread of laying dates confers other advantages (e.g. less seasonally concentrated food exploitation). However many variables could affect the picture given by ringing returns and I have not yet undertaken a detailed analysis.

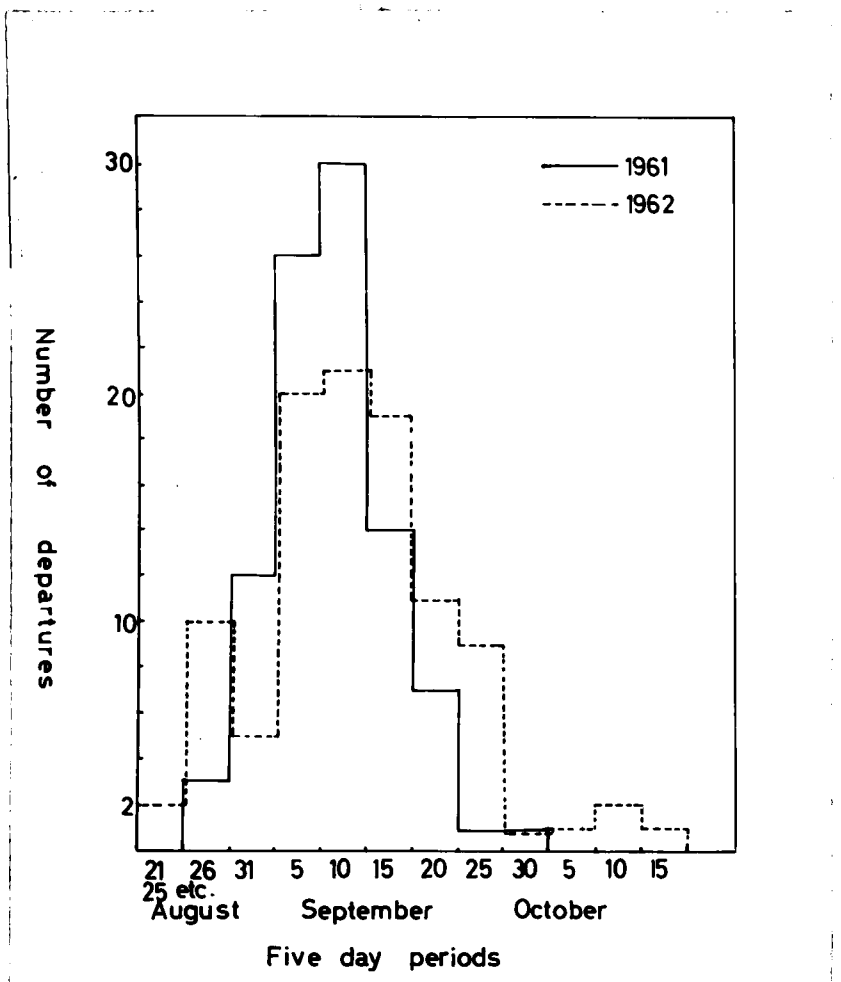


Figure 21.

Proportions of young fledging in different months.

TABLE 26. Months of recovery of Bass-ringed young Gannets (in year of ringing).

July				August				September				October			
1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1	0	2	2	2	17	8	5	10	9	18	16	16	13	14	13

November				December				January			
1	2	3	4	1	2	3	4	1	2	3	4
9	4	2	2	2	2	4	4	0	1	0	0

Total recoveries 176.

Notes : (i) Recoveries up to and including 1959 from all sources; 1960-63 personal.

(ii) Excluding all birds killed.

(iii) The high figure in the second quarter of August includes 5 birds recovered near the Bass as a result of ringing too late in the season.

A small proportion of late chicks are abandonned. Beyond mid-October Gannets become strongly disinclined to remain on their sites. On the 16th. October 1960 there 80 - 90 chicks remaining on the Rock and on 10th. October 1961 60 - 70. My latest record was for a chick due to fledge in mid-December 1960, though it apparently died before then (per Lighthouse Keeper).

Time of day. Table 27 shows that departure times are spread over much of the day, though there are significantly fewer in the last third. There was no marked tendency for a pre-dusk exodus, comparable to that in the Guillemots, in which most of the chicks appear to leave around dusk (pers. obs.), which fits with the view that it is an anti-predator device in the Guillemots, for which the Gannets have no need.

TABLE 27. Time of chick departures.

G.M.T.	06.00-09.00	09.00-15.00	15.00-21.00
No. of cases	66	86	16

Departure scatter also suggests that the adult persecution on the water is not very important, since a dusk departure would reduce this. However, other factors may well favour departure in full daylight.

Direction. The direction of the initial flight merely reflects the direction faced by that part of the colony from which the chick flew and the wind direction at the time. East-facing chicks flew roughly S.E., E. or N.E. and west-facing S.W., W. or N.W.. Even the birds facing W. - S.W. initially flew roughly towards Edinburgh, i.e. away from the open sea. The flight often curved widely and several birds ended by flying at an acute angle to their original line of flight.

The initial flight, therefore, was not markedly orientated geographically, but this orientation must, of course, occur soon after the Gannets begin swimming away from the Rock. From ringing recoveries it is known that many then head north, round the north of Scotland and down the western sea-board of Europe; others swim south from the Bass.

Weather. This has no pronounced effect on departure, apart from gale-force winds which inhibit it. Ordinary strong winds do not affect it, nor does calm settled weather. Visibility is relatively unimportant and young birds were seen to leave in very misty, overcast weather with visibility limited to a few hundred yards. They may also leave in heavy rain. Rough water does not appear to affect them, since they are, of course, truly oceanic birds, unlike Shags and Cormorants which eventually become water-logged. Probably there are optimum conditions which stimulate leaving, but they are certainly not obvious and departures are not significantly held up in their absence.

Discussion.

The absence of post-fledging feeding in the Gannet must increase chick mortality during the transitional period between living on fat reserves and acquiring skill at fishing. Post-fledging feeding could take the form of accompanying the chick, as in Guillemots, or periodically feeding it near the nest after its initial flight, as for example in Shags and Cormorants (the latter have a six-week period of post-fledging feeding, Kortlandt 1942), Red-footed Boobies (Verner 1961) and Kittiwakes. The former would be impracticable for a widely-foraging plunge-diver with the apparently limited degree of chick recognition shown by Gannets (see Chapter 13). Terns are specialised plunge-divers and continue to feed their young, but they show strong chick recognition. Also, the young Gannet's inability to fly for some weeks after leaving the nest would have to be modified, presumably by less

deposition of fat. Gannets need to forage widely for fish (probably much further than a tern or auk) and unless the juvenile could accompany the parent impossible difficulties of re-location would arise. The first flight would have to be accompanied by one or both parents. Presumably both would need the mechanism to respond to the departure, unless the chick delayed its leaving until the responsive parent was present. In either case a greater readiness, than at present, to leave the site would be required from at least one parent. Site-attachment is so strong that Gannets remain on the nest some two to two and a half months after the chick fledges. Whilst it may or may not be true that this site-attachment is advantageous to the birds at this point in the breeding cycle there is no doubt that at other times strong site-attachment is of the greatest importance. If, therefore, post-fledging feeding involved a lower overall site-attachment it could be disadvantageous. If only one adult accompanied the chick a one-sided strain would be imposed on that parent. The physiological strain which would result from both parents feeding a chick after fledging seems unlikely to be important.

The return of a fledged juvenile to the nest (as in Kittiwakes, for example) also presents many difficulties. Prey is often not available in the immediate vicinity of the Colony, so that the juvenile would have to intersperse wide 'learning' forays with intermittent returns. Locating the right nest would also be a problem - even adults sometimes mistake their own nest. Further the southward migration would be delayed. Fat deposition would also need modifying to allow the newly-fledged juvenile to rise from the water.

Even this sketchy survey of the problems associated, in the Gannet, with possible post-fledging feeding shows how fallacious it can be to make inter-specific comparisons of this kind. The Gannet has allied an unusually high breeding success to a system of stored food for the young. Other

species with lower breeding success in one phase reduce: losses in another. Only by disrupting a harmonious system of physiological and behavioural balance could Gannets achieve what at first glance may seem the easy and advantageous habit of post-fledging feeding of the young.

- 6 -

IMMATURE BIRDS

Plumage stages.

Between leaving the nest as a juvenile and reaching adult plumage in the fourth or fifth year, Gannets pass through a series of intermediate plumages (Plate 6). A long series of variations on each intermediate phase was collected during this study but will not (for reasons of space) be detailed here. Very few immature individuals were handled and the following account is based on sight records.

During their first year, counting from the August or September in which they fledge, young Gannets may retain practically the full juvenile plumage. By at least the August after fledging when they are about one year old (i.e. in first summer plumage in Witherby's terminology, The Handbook of British Birds 1949) I saw individuals completely brown except for a variable amount of whitish ventral surface. Head, neck and upperparts were indistinguishable from the juvenile stage except that the dark-grey/black had given way to a slightly browner tinge, possibly due to fading of the melanin. Some individuals, probably starting within three weeks of fledging, progressively lose many or all dark feathers on the head, neck and underparts, usually with a paling of the breast, belly and often the forehead, leaving a brownish thigh patch, chin, throat and pectoral band (see Plate 6A). A few individuals even become noticeably paler on the dorsal surface (6B.). It is very interesting in view of the findings of Phillips (1962) that the areas which pale first are precisely those his theory would predict (see p. 85).

The second year plumage increases the amount of variability already found in the first - a phenomenon probably associated with the pattern of moult in Sulidae in which two or more cycles of feather replacement may be in

A. First-year plumage. Note white throat, underparts and upper tail coverts. Plumage browner than full juvenile.

B. Back beginning to show whiter in first-year bird. Adult lines appearing on bill.

C. Early second-year plumage. Head whitening, conspicuous shoulder patches.

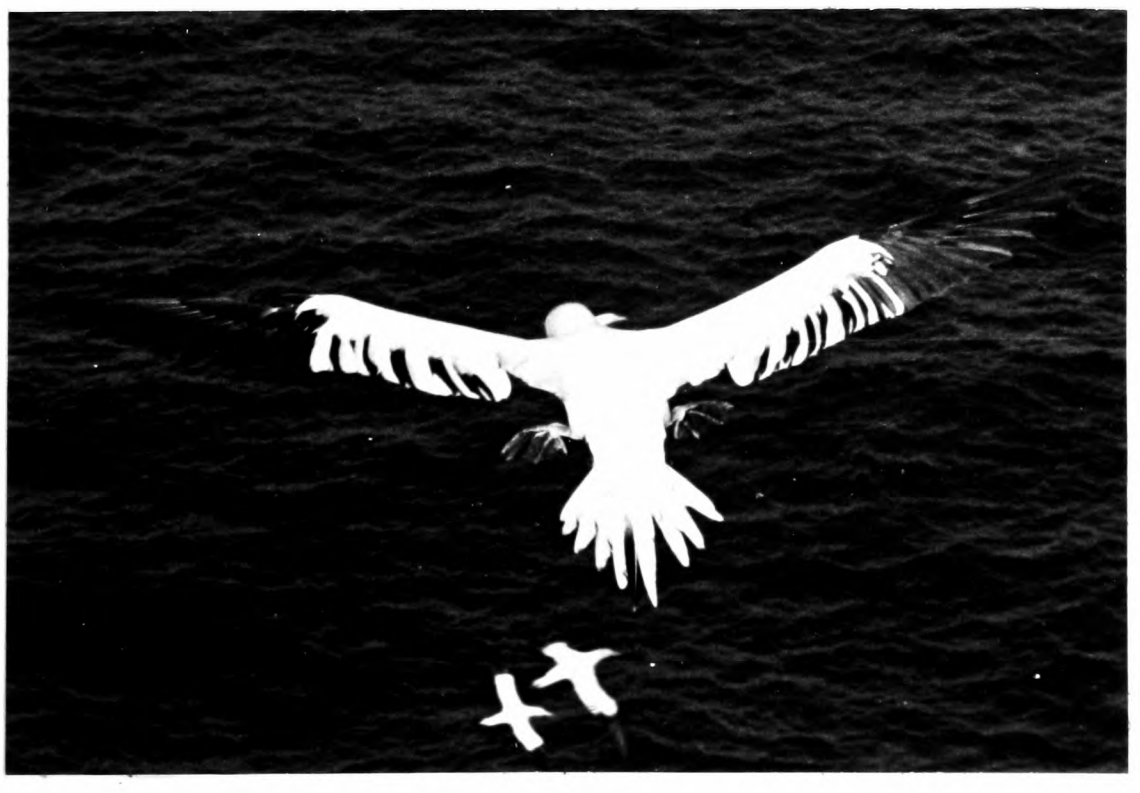
D. Second-year plumage becoming paler. Dark thigh patch persists. Head may be yellow by now.

E. Late second-year plumage. White spreading from leading edge. Head completely clear, bill as adult.

F. Later second-year plumage. Tail covert patch extending leaving typical brown ovoid on lower back.

G. Typical third-year plumage. Tail becoming white from the outer edges.

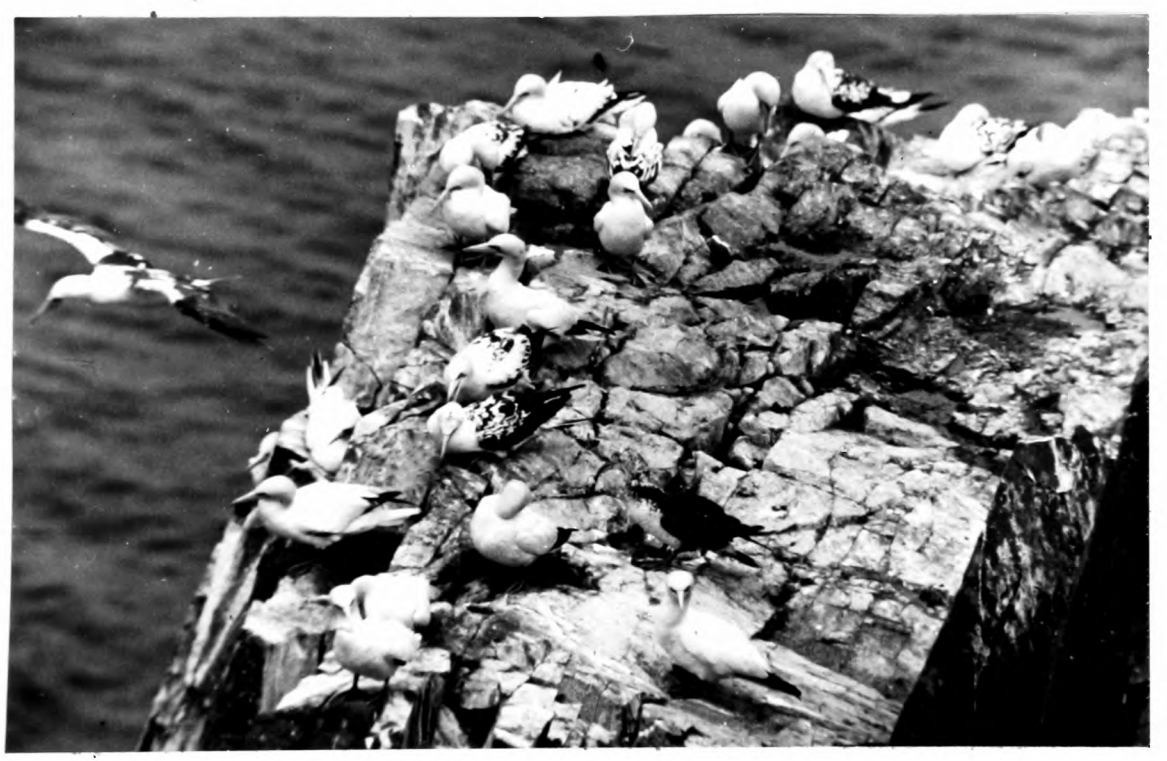
H. Late third-year plumage. Variable number of dark secondaries and mantle feathers. Some dark tail feathers.



I. Some birds retain this amount of immaturity in their fourth year.

J. Typical fourth-year immature plumage. Variable number of dark secondaries and/or tail feathers. May breed in this plumage.

K. Adult.



L. Group of one to four year-old immatures and three or four site-establishing adults. Note three year-old male biting two year-old female, and first-year bird with very dark head, to right.

progress simultaneously (see Dorward). The most juvenile form of two-year-old (6C) has a conspicuous paling of the upper and median wing coverts, showing as a white shoulder patch and leading edge. The V-shaped upper tail covert patch (always pale even in a juvenile) extends in area. Several birds retain brown speckles on the thighs and on the nape and sides of the neck (which is also the area to which the neossoptiles cling most tenaciously). The dorsal plumage may remain entirely dark brown except for the shoulder patch. Despite the retention of brown on the head these birds may nevertheless show some yellow and the blue adult bill-colour, together with conspicuous web lines - factors possibly associated with the considerable amount of precocious sexual activity shown by immature Gannets. Other two year-olds may be completely white on head and underparts, with many white feathers encroaching onto the secondary coverts, scapulars and mid-back feathers (6E,F), though primaries and secondaries remain black/brown.

The third-year plumage is the first to show adult flight feathers (secondaries and rectrices) intermixed with dark ones (6G). The whole dorsal surface becomes boldly patterned black and white, very variable in extent (6H). The head may be white or yellow - possibly white-headed birds are females. Certainly the paler of two immature birds forming a temporary pair in the clubs is usually a female. Three year-old females sometimes form more permanent associations with four or five year-old fringe males, but I have never known one breed. A chick colour ringed in 1960 and seen in 1963 still retained many black secondaries and tail feathers, and three black scapular feathers symetrically disposed on each wing.

The fourth year or sub-adult plumage (6I &J) may show several dark secondaries and/or one or more dark rectrices (usually central), or may be almost adult. Gannets

may breed in this plumage and may in fact retain some of it in their fifth year.

Moult apparently proceeds symetrically (though not necessarily by a complete annual cycle of feather replacement- some feathers being two or more years old, others a year or less). Thus a four year-old male caught on the 28th. May 1962 had an equal distribution of black and white-flanged black secondaries in each wing and also numbers 1, 2, 11 & 12 rectrices new and the remainder old and all broken.

Adult moult will not be discussed in detail here. It begins in the first week of May (Cormorants begin in June, Kortlandt 1942) with body feathers, but some birds do not shed flight feathers until late summer. The shedding is gradual and the final few centimetres of the tail feathers are usually broken off long before the feathers are moulted. Occasionally the barbs are entirely abraded and the spine-like rachis alone remains. The old feathers are also easily recognisable by the yellowish tinge on the shafts. Some worn plumage may persist during the chick feeding period, when maximally efficient flight is particularly valuable, but usually many new feathers are in place by the time of main chick growth.

Behaviour of Immature Birds.

The migration of juvenile Gannets is well known and will not be discussed here.

Return. Some return to the Rock in their first year, more in their second year and most immature birds around the Colony are in their third, fourth, or fifth years. Many, if not most, Gannets are probably three years old by the time they first return, but the return of much younger birds (especially one year-olds) is a phenomenon which has been previously little recorded. The annual return continues the trend already discussed for adults (i.e. oldest returning first) and the sub-adults begin to appear about the

third week in February, three to four year-olds arrive about late March to early April, two year-olds may appear in the second week of April, but are usually later, and first year birds are not common until May or later. There is considerable variation from year to year in the return dates of the different categories, and exceptionally even a first year bird may be in home waters by January. Nevertheless the main influx of immatures usually occurs between the fourth week of April and the first few days of May - just when an influx of site-prospecting males becomes apparent. Although the immatures begin to leave the Rock in August there are still many present as late as mid-September in favourable weather.

The proportions of the different categories of immatures in the clubs are shown in Table 28.

TABLE 28. Proportions of immature and adult birds in clubs, from 18 counts between April 25th. and October 10th. 1962 (3,435 birds counted).

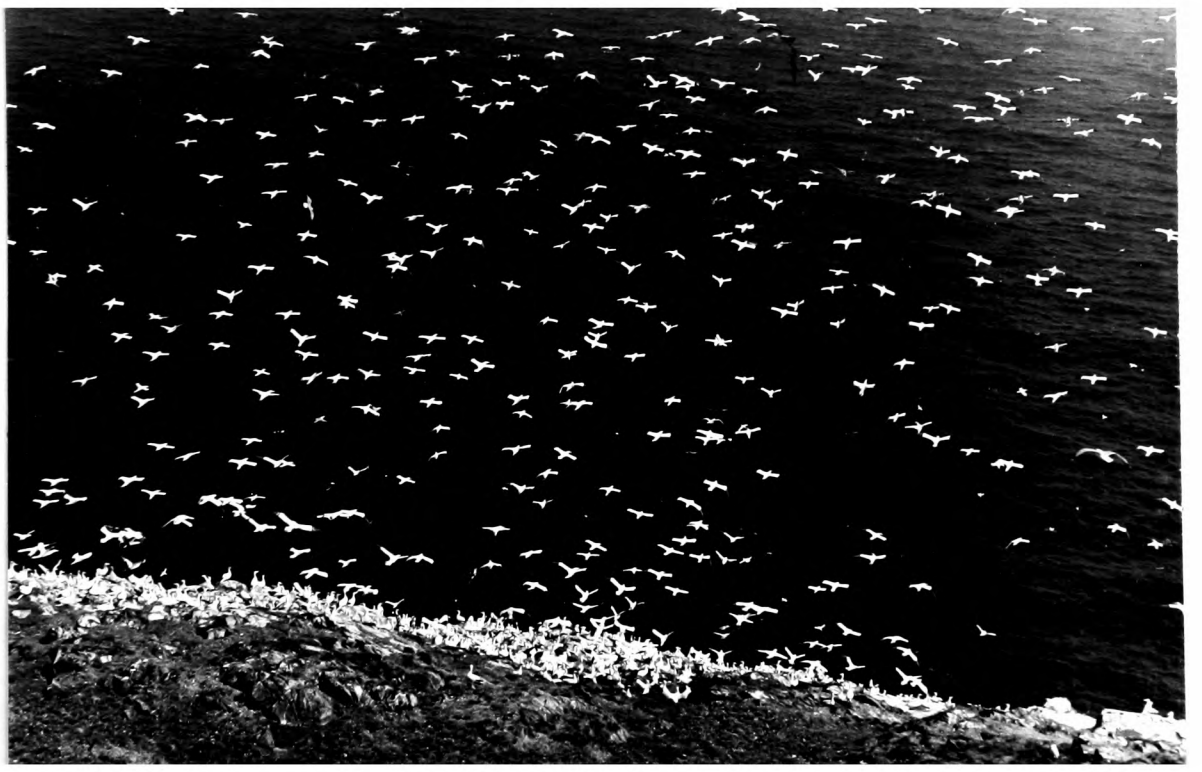
	Age in years					
	1	2	2-	3-	4 (sub-adult)	5 and 5+ (adult)
Overall percent	1	5	19	33	16	26
				49		

These counts were made by disturbing a mass of club birds (Plate 7) and then taking a random sample of as many as possible before they completely dispersed. Because speed was essential to count 100, 200 or 300 birds from the 1,000 or more in flight, the precise details of plumage stages could not be taken into account, and 2+ refers to birds which may well have been early three year-olds or in the late stages of second year plumage. Similarly 3- refers to birds which may have been fourth year. Together with sub-adults, this category constitutes about half of all

Plate 7. Club birds.

A.

Gathering of 'club' birds on north side of Bass.



B.

Club birds 'panicking'. They are much more wary than breeding birds.

club birds. The high proportion of adults should be noted. Early in the season adults may comprise more than half of such gatherings.

Behaviour in clubs. See Chapter 15.

Club Birds as Potential Breeders.

There can be no doubt, from observations recorded elsewhere in this account, that the four year-olds and adults represent a reserve of potential breeders. It is virtually certain that suitable nest sites exist on the Bass and in the immediate neighbourhood (e.g. the Isle of May, which once held a small Colony). It may therefore be that these reserves represent a density dependent regulating factor, i.e. the higher the number of breeding pairs in the Colony and the fewer the recruits added to it from the non-breeding population.

The mechanism by which their breeding is inhibited remains problematical. It could conceivably be a direct action of food in a given area around the Colony. This, as Ashmole (in press) points out, would require actual food-competition to be taking place. If it is not food acting directly, the restrictive mechanism can only be a social one in Wynne-Edwards' (1962) sense (and this interpretation is fraught with difficulties) or a physiological one which is not affected by the numbers and/or density of the population of which the birds form a part.

- 7 -

RECRUITMENT AND MORTALITY

Factors Influencing Recruitment.

Introduction. In this chapter I want to draw together evidence, already presented in part, bearing on the Gannet's reproductive rate.

Birth and death rates are the two chief variables controlling bird populations, though immigration and emigration may also play a part in a particular area. Lack (1947) has argued that it is erroneous to assume (as has frequently been done) that variation in reproductive rate is responsible for population stability. Instead reproductive rate is relatively inflexible and is fixed by the maximum number of fully 'fit' individuals which the parents can produce. It may thus be density dependent, since available food will be influenced by the number of birds competing for it. The number of young reared will eventually (other things being equal) introduce food-competition among adults and independent young, and it is this competition which Lack holds to be an important factor controlling mortality. Other density-dependent factors such as disease and predation may, of course, be linked with this competition, and aggravated by food shortage, but are probably much less important.

This view has been widely accepted, but an alternative has been developed by Wynne-Edwards (1962), whose view, like Lack's, is based on ultimate importance of food as a regulating factor, but proposes that reproductive rate can be varied, as it were 'deliberately', to avoid reaching the stage of direct competition for, or over-exploitation of, food resources. The mechanisms by which reproductive rate can be varied and to which he draws attention when discussing sea-bird populations (Wynne-Edwards 1955, 1962) include "social" regulation, which may involve mortality inflicted by the species on itself, and also various restric-

tions on breeding output.

I will discuss clutch-size, replacement laying, deferred maturity and non-breeding years in the Gannet. Despite its north temperate habitat conclusions about the factors and mechanisms controlling its breeding rates should be, in many respects, applicable to sea-bird colonies in other latitudes, including the tropics. As Ashmole (in press*) has pointed out, abundant food in a breeding area will affect the density of species within that area, but, given low mortality independent of density, and the absence of other limiting factors, will not affect clutch-size, etc. since (according to him) numbers will simply increase until competition for food around the breeding colonies prevents adults from raising more than one chick.

The number of young surviving to breeding from any pair of adults represents that pair's contribution to the next generation and through this to posterity, assuming the fertility and viability of the successive generations remains unchanged. In the Gannet this contribution is affected by the following factors, presumably susceptible to change by natural selection.

Clutch-size. Gannets invariably lay one egg. This could, theoretically, be due to inability to lay more, incubate more, or brood and feed more than one chick.

Gannets can produce at least two re-lays and since the egg is relatively small (3.5% adult weight) there is no reason to think that laying two would impose a significant physiological strain. Further, although there is no evidence whether or not a second oocyte is formed within a day or two of the first (probably necessary to produce synchronous hatching), this must occur in those boobies laying more than

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* All references to Ashmole in this chapter refer to this paper, unless otherwise mentioned. Similarly, references to Wynne-Edwards relate to his 1962 views.

one egg (S. variegata commonly lays three, Murphy) and presumably no physiological difficulty need prevent it in the Gannet. They can also successfully incubate two and are, as shown, capable of feeding two chicks. Some implications of this notable situation were discussed during the account of twinning and it is simply suggested here that (i) the twins would be likely to survive as well (or nearly as well) as singles, (ii) there is no reason to suspect that they would have a lower reproductive capacity and (iii) the subsequent breeding capacity of pairs laying two eggs and rearing twins would probably not be impaired as a result.

If Gannets were normally working near the limits of their food gathering capacity one would not, of course, have expected such an adequate response to an extra chick. This, therefore, runs counter to Ashmole's expectations on this point, since he requires breeding success to rise until compatition for food around the breeding colony (i.e. within the foraging area of breeding birds) reduces their success. However, Ashmole has carefully restricted his propositions to stable populations, and the North Atlantic Gannet may still be recovering from former exploitation and hence be below its food level. As mentioned already, the situation cannot be explained by supposing that if all members of the breeding group attempted to rear twins the extra competition would result in total failure, since in that case (and assuming the recurrence within the species of individuals with two-egg clutches) one would expect a new stability to be achieved in which some pairs attempted to rear two and others only one. The advantages of each would presumably be equal and result in a balanced 'dimorphism' of this kind, common enough in small-clutch species like the Arctic Tern, Kittiwake, some penguins, etc..

Thus, so far as clutch-size is concerned, there is a good case for believing that Gannet pairs laying two eggs

would be at a selective advantage over their fellows laying one. Since Gannets do not lay two, either one of the above suppositions must be mistaken, or the present conditions did not exist when the Gannet evolved its single-egg clutch (and, as pointed out by Wynne-Edwards, a single-egg clutch has been derived from a larger one), or laying one favours the group as a unit even at the expense of individual pairs, as proposed in Wynne-Edwards' 'group-selection' hypothesis. Nothing further can be said about the first propositions except to point put the inherent contradictions involved in the facts (a) that natural selection <u>has</u> resulted in a single-egg clutch for the Gannet, and could only have done so if such clutches produced more descendants than larger clutches and (b) the suggestions (i), (ii) and (iii) on the previous page. The third proposition will be discussed when other relevant points have been made.

<u>Replacement laying</u>. The absence of replacement laying is usually correlated with other characteristics of low reproductive rates. The fact that it nevertheless occurs in the Gannet has already been discussed (p. 43). It is unlikely to be important in regulating reproductive rate except after massive egg-loss - itself a highly unlikely event. The occurrence of replacement laying probably reflects the remarkably long annual potential breeding period available to the Gannet - as Richdale points out, some species like Procellarii would have no chance of successfully rearing young from replacement eggs, so the effort would be wasted.

The low tendency of first-time breeders, compared with experienced birds, to replace lost eggs may be partly due to the fact that they lay their first egg later and would thus be particularly late with their replacements. Since the tendency to replace wanes as the season advances, they are usually too late to attempt it. Nevertheless, I

have two records of first-time breeders re-laying almost immediately after egg-loss and (since the first egg had not been incubated) successfully rearing young.

Deferred maturity. From ringed recoveries and plumage characteristics it seems that Gannets breed for the first time between four and six years, but usually at five (see Table 9). This long pre-maturity is comparable to Royal Albatross, male 9 and 11 years, female 8 or 9 years (Richdale 1952); Yellow-eyed Penguin, female 2 to 3 years (mainly in 3rd. year), male 2 to 4- years (Richdale says "dispersed up to the 10th. year," 1957 ; 107); Short-tailed Shearwater Puffinus tenuirostris, 6 years (Serventy 1956); Cormorant 1-5 years (Kortlandt 1942); Golden Eagle Aquila chrysaetos $3\frac{1}{2}$-$4\frac{1}{2}$ years to adult plumage (Jollie 1947); White Stork 3-4 years (Lange 1940 in Wynne-Edwards 1962); Common Tern 3 years (Austin 1945).

However, Gannets are physiologically capable of establishing sites, forming pairs and producing viable eggs at an earlier age than they do. Males usually establish a site some time in their 4th. or 5th. year, and hold it for a season or more before breeding on it. This long pre-breeding period, during which they may form a stable partnership, is not, apparently, the result of inadequate territorial or sexual behaviour. Such pairs copulate, build nests and can produce eggs (when partnering, as replacements, established birds, four year-olds or either sex will breed sucessfully without such a pre-breeding season). In fact some pairs do breed in the year of site and pair establishment, though it is possible that these are all five year-old birds. It may be that, usually, part of a season is required by new pairs to fully establish their place in the colony and their attachment to the site and each other. Even slight aberrations in the rhythm of attendance and change-over could readily lead to egg or chick loss, as I saw from triangular associations in the observation colony. For example, one

male stayed away 90 hours and the female left the egg unattended (and therefore lost it) after a 51-hour spell of duty. It may also be suggested that this pre-breeding period allows them to learn the main fishing areas of the Colony. This, however, would be a more likely function of the two, three or four years spent by immature birds in the clubs. By the time they reach breeding age they should be fully acquainted with the fishing grounds.

If there is a reserve of potential four year-old breeders, it may then be suspected that site-shortage could account for their exclusion. It will be shown, when discussing site-establishment, that this is not so. The fact, alone, that the observation colony increased in the way shown (Plate 2) between 1960 and 1963 conclusively demonstrates that it is not necessary for new birds to find a site actually within an established group, though there is a strong tendency to do so if possible. Wynne-Edwards' contention that birds already breeding can in some way control the admission of new ones is thus apparently inapplicable in this case.

Since so few four year-olds breed it may be wondered whether their success would be very low and perhaps more than cancelled by the stress involved on the young parents. In the Gannet overall breeding success is certainly lower for first-time breeders than for experienced birds (p. 40). However, this is so when most of the birds concerned are breeding in their fifth year; birds breeding for the first time, whatever age, would probably have a lower success and there is no reason to suppose that this is the result of age rather than inexperience as such. This seems particularly probable in the Gannet where the lower success is largely due to inadequate incubation or care of the tiny chick, and not to inability to find sufficient food for it later in growth. The fact that chicks from first-time

breeders fledge at exactly the same age as those from experienced birds should be emphasised since it is concrete evidence to range alongside the suggestion (Ashmole) that young birds could have virtually no chance of breeding successfully even if they tried, due to inadequate development of their food gathering capacity (Lack 1954 suggested that specialised hunters such as the Gannet may require the full pre-maturity period to perfect their abilities). If food around the breeding Colony were really in short supply, as Ashmole suggests, and slight variations in efficiency so decisive, one would hardly expect a first-time breeder to cope so adequately, since, as already indicated, the fledging periods of the chicks suggest that these were fed equally as well as those of experienced birds. Also the very adaptations of long fledging period, resistance to starvation and quick recuperation would tend to mitigate slight imperfections in the capacity of these first-time breeders and hence increase their success.

Finally, the possible effects of early breeding on subsequent breeding capacity, by increased mortality, stress, etc., would seem too slight to offset the advantage gained. The advantage of breeding one year earlier than average would, of course, be considerably less than of laying one egg more (which produced an 80% advantage in 1962). Nevertheless, it is another factor potentially affecting recruitment rate, and it is not easy to account for the fact that Gannets normally breed for the first time at five years, when they can do so earlier.

Non-breeding. Non-breeding among adults could occur either as non-breeding years scattered regularly or irregularly between normal breeding years, or as a reserve of fully-adult non-breeders within the Colony.

Stonehouse (1960) showed that the King Penguin has a 15-month breeding cycle, making every third year a

non-breeding year. He considers this inevitable and not a restrictive measure in Wynne-Edwards' sense. The Royal Albatross (Richdale 1952) breeds only every second year, if successful.

Marshall (1952) lists previous references for non-breeding years among arctic bird populations. Here the phenomenon seems not to be a regular part of the birds' reproductive activity, regardless of weather, but rather a response to the absence of certain environmental conditions acting on the female gonads. These external stimuli could, theoretically, be of many different kinds, but the importance of non-breeding for this discussion is that it appears not to occur as a restrictive practice brought about independently of direct environmental control. It seems, therefore, not to be a mechanism which Wynne-Edwards would call intrinsic or socially induced. It has never been demonstrated for any British sea-bird, though suspected for the Fulmar (Fisher 1952; Wynne-Edwards).

Non-breeding years can be virtually excluded as a possible control mechanism in the Gannet, since my results show that practically all birds having bred attempt to do so each year thereafter*, though it remains possible that in certain years a higher proportion do not attempt to breed. Southern (1959) shows that Tawny Owl populations may not attempt to breed in bad mouse years. This, however, is a typical density-dependent response brought about by direct food competition.

Of 48 pairs of Gannets followed for four successive years, only 17% actually reared a chick in each of these, although in 27% of the 48 nests (involving at least one of the original pair) chicks were reared in all four years.

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* Although no pairs were followed for more than four seasons the large number of nests in the group and the very high proportion nesting each year show that non-breeding years must be rare.

Similar figures for 98 pairs followed for three successive years were 41% (same pairs) and 50% (same nests). In effect therefore, through some agency or other, most pairs are spared the necessity of rearing a chick every year for several years. Although this loss is accidental and could hardly be susceptible to natural selection, it could act as a buffer by making 'deliberate' non-breeding years unnecessary.

Finally, the reserve of non-breeding adults must be considered. Among the immature birds in the clubs there are many birds in adult plumage (Table 28). These birds have attracted many people's attention at various gannetries (Martin, 1703, quoted by Boyd 1961 and referring to St. Kilda, called them "a barren tribe of Solan Geese that never mix among the rest that build and hatch") and two suggestions have been made about their status. Gurney (1913) records them from the Bass (frequenting the same slope shown in Plate 7) and quotes the opinion of his informant that they were non-breeding birds. Wynne-Edwards, considering the problem in 1936, decided that they were off-duty birds. Later (1955, 1962) he recognised them as a further possible population control mechanism - allowing the breeding stock to be augmented as conditions required. Before this interpretation can even be considered it is necessary to decide whether these birds are in fact off-duty or genuine non-breeders. Warham (1958), in a small colony of Australasian Gannets, stated that his unemployed birds, though few, were definitely not off-duty breeders. However, it is clear from his account that he did not distinguish between newly-established site owners and genuine non-breeding club birds. The former are non-breeding in the sense of not having egg or chick, but I distinguish these from non-breeders proper (i.e. without a definitive site). Since there have been no other field observations to support either suggestion the following are recorded :-

1. Their behaviour suggests adult non-breeders. They establish temporary sites wherever they settle for a few hours and show incipient sexual behaviour, including copulation even when this has largely ceased (at least for a period) among breeders. Also the whole bearing of the males resembles newly-established rather than older birds. Thus, whereas breeding males are usually, at this stage, hostile to females other than their mate, these birds accept, and usually advertise to, wandering females.

2. In view of the strong site attachment of established Gannets it seems at least improbable that they would spend spare time at the Colony but away from their nests. For example, on first return, long before breeding begins, established birds go straight to their nests with no prior congretations outside the breeding limits. In the pre-laying period particularly, the pair spend much time together on the site and even when feeding the chick spend some time there as a pair. Also, having lost its egg, a pair immediately spends more time together at the site - as though any sudden access of spare time is spent there (though this might be an adaptation to facilitate copulation and re-laying). During incubation less time is spent as a pair, possibly because the size of the nest leaves little room for both an incubating and a standing bird. Why should a breeding male return to the Rock and yet ignore his site, which is obviously so important to him, and stand about with a crowd of immature birds ?. It should be added that none of the colour ringed breeding adults was seen in these clubs. Kittiwakes (Cullen) on the other hand, may be seen to fly direct from their nests to a 'club' and they too are strongly territorial, so that this point in my argument is far from conclusive though in the gulls there is increasing evidence that the club is a place with less danger from predators (N. Tinbergen pers. comm.).

3. The known spells of duty, length of fishing trips, time spent gathering nest material and time spent together on the site suggest little spare time for congregating with immatures, particularly since Gannets also spend some time bathing and resting on the sea. Even very approximate estimates of this kind can at least indivate that there are no considerable blocks of time unaccounted for in the normal routine.

4. The numbers of adults involved in the non-breeding population show that they could only represent a small proportion of off-duty breeders from the Rock as a whole, so that even if some off-duty birds do join the non-breeders, the habit could not be usual.

5. Unemployed adults are extremely wary, leaving the Rock at the slightest alarm, while nesting birds become very bold. It could be that away from the site they become much more wary, as in groups gathering nest material, but it seems unlikely that they would virtually ignore a ship's hooter, for example, when on the nest and be so alarmed by it when they are a hundred yards away. Nor can this be explained in terms of communicated 'panic' initiated by the immatures, since the adults are often among the first to leave from these 'unemployed' groups.

Among the reasons which could be suggested for believing them to be unemployed off-duty breeders perhaps the best is a rather wide fluctuation in numbers from time to time, with an increase about the period when most breeding birds are laying. However, much of this variation is caused by the habit of resting on the sea around the Rock at certain times and the number of immatures and non-breeders are tending to build up anyway by the end of April, since these birds return later than the breeders and gradually increase in numbers. Also, towards the end of the season, the numbers of non-breeders drop long before the breeding population

begins to leave the Rock.

An a priori reason which might well have led to other interpretations is the apparent improbability that a reserve of potential breeding power such as this should exist in a situation which emphatically does not suggest site-shortage. Nevertheless it is normally possible for birds to replace lost partners - a fact long known to naturalists and gamekeepers, and underlined by the experiment of Stewart & Aldrich (1951) which demonstrated an unexpectedly large reserve of potential breeders. In the Gannet this situation is made more obvious by their habit of congregating with immatures at the breeding station.

Whilst the situation remains to some extent unresolved, it is suggested that in the phenomenon of adult-plumaged non-breeders the Gannet shows another mechanism with potential effects in regulating the output of a population.

To suppose this to be another example of breeding being inhibited in a density-dependent manner by direct competition for food around the Colony, so that these birds are inhibited from even attempting to breed, does not explain how it comes about that each year some new adults enter the colony. These have, presumably, been subject to the same degree of food competition. It could, however, be suggested that they are the more efficient members of the reserve population and hence effectively less inhibited by food competition. Certainly, there is no evidence that any form of social behaviour by established birds prevents them from establishing fringe sites if they want to.

In summary, Gannets lay one egg, but can hatch two and feed two chicks. They usually breed at five years but can do so at four. They usually hold a site for a year before breeding but can breed without doing so. If the Bass situation is representative each Gannet population appears to

show a reserve of potential adult non-breeders.

At first glance the conclusion would appear to be that the breeding output of any Gannet Colony is somehow being affected apart from the limitations imposed by natural selection on the breeding rates of the pairs concerned.

Wynne-Edwards suggests this for many species, but the evidence for the Gannet is more cogent than for many of the more superficially studied. However there are still large gaps in the relevant information for the Gannet. These must be filled before excluding alternative explanations, in line with the more familiar theories of natural selection, which have proved so helpful in understanding much about reproductive rates in animals.

Ashmole's plausible argument for direct food competition in the feeding area of the Colony, whilst intended to apply primarily to tropical sea-birds, is also extended by him to cover other latitudes. It does not seem to fit the evidence from twinning experiments and first-time breeders given here. If one assumes that the Atlantic Gannet population is not stable in Ashmole's sense, and still below its food level, then there ought not to be a reserve of non-breeders, etc.. If, on the other hand, it is at the point of competition, then the above results would not have been expected. It so happens that the position in the Bass gannetry is less complicated than in many other Colonies, since the Bass is the only significant breeding station on the east coast of Britain. Its feeding area thus probably does not overlap much with those of other Colonies. These populations, therefore, cannot be competing with it, as they would do if overlap occurred.

Before Wynne-Edwards' alternative explanation postulating 'intrinsic' regulation of the output of a particular group or Colony to fit the local food resources and prevent over-fishing (i.e. competition) could be accepted it

would be necessary to overcome the objections to group selection as envisaged by him. Also, there is no evidence suggesting how regulation of breeding effort could be brought about socially. Yet it certainly appears from the information given here that, despite a favourable food level and available nest-sites, a number of potentially 'capable' breeders do not attempt to breed. This is exactly the kind of evidence which appears to support Wynne-Edwards' views, as also is the apparently well-developed tendency towards inbreeding. It is also true, however, that alternative suggestions can still be reasonably put forward to account for such facts, and some of these have been mentioned in this chapter. They have the merit of fitting in with much evidence supporting the more widely-held view of natural selection. It is therefore premature to attempt a firm conclusion from the facts given here, at least in terms of the correctness of Wynne-Edwards' views, and more fitting, at this stage, simply to record ~~the~~ Some evidence as apparently in keeping with them.

Mortality.

Adult mortality. Gannets are long-lived birds, as one would expect from their size, low clutch-size, extended pre-maturity period and long fledging period - all factors which restrict breeding rate. The Cormorant, comparable in size, breeds slightly earlier in life (usually at three years; Kortlandt 1942) and has an annual adult mortality provisionally estimated by him at 9% for males and 11% for females, with an average life expectancy of about 10 years. Other available figures for mortality in sea-birds include 12% for the Kittiwake (Coulson & White 1959); 14% for the Shag (Coulson & White 1957) though Snow (1960) calculates 7% for mortality of colour ringed adults in a sample of 28 birds and 10-14% adult male mortality derived from re-use of nest sites. These serve for comparison with Gannet adult mortality set out in Tables 29 and 30. These are based on

colour ringed birds, and since Gannets return annually to the same area (usually the same nest) and do not have years in which they stay away from the colony, the figures should be accurate within the limits of the sample. Over three years the annual mortality rate averaged 6% with a slight sex difference (though on these

figures not significant) in favour of females (4.7 female and 7.6 male).

TABLE 29. Annual adult mortality of birds ringed as breeding adults.

	No. alive in summer of year		No. surviving to next summer		Maximum % mortality		
Year	Male	Female	Male	Female	Male	Female	Total
1960	27	31	27	30	0	3	2
1961	46	50	43	49	7	2	4
1962	46	47	40	43	13	8	11
			Average		7.6	4.7	6.1

TABLE 30. Progressive adult mortality of colour ringed birds.

		Birds dead by :-					
		1961		1962		1963	
		No.	%	No.	%	No.	%
Ringed 1960	58	1	2	4	7	6	10
Ringed 1961	41	-	-	1	2	4	12

Causes of mortality. The death of most adult Gannets, it seems, is due to accident or man. Some die by fighting, becoming jammed in crevices, breaking a wing in falling, etc.. Many are drowned in nets or shot. I know of no record of epizootic disease among Gannets, though a salmonella infection has been isolated from two wild adult females, and the same virus Salmonella typhimurium has been isolated from processed Herring meal (Macdonald 1962).

The Gannet's size (which immures it from predation, man apart), remote breeding places and oceanic habits partly account for this very low adult mortality. However there is a high mortality among immature birds.

Adult expectation of life. The annual adult mortality may be expressed as the average expectation of life, using the formula $\frac{2 - m}{2m}$ where m = % annual mortality.

This gives a figure of 16.2 years for the Gannet (cf. near one extreme 0.89 years for the Blue Tit Parus caerulus with an annual mortality of 72%, Gibb 1961 and at the other, 36 years for the Royal Albatross with an annual mortality of 3% Richdale 1952).

Pre-breeding mortality. The major part of the pre-breeding mortality doubtless occurs in the first year (see for example, Boyd 1962, for waders). It may be calculated from the known adult mortality and breeding success, assuming a stable population. With a life expectancy of 16.2 years from about the second or third year onwards, and a breeding success of about 75% each pair rears on average 16.2 x 0.75 = 12.1 chicks. Only two are required to replace the parents, therefore, 83% must die.

The Bass Colony is, however, expanding. Fisher & Venables (1938) suggest that the increase in certain British gannetries (e.g. from about 2,000 to 5,500 pairs on Grassholm between 1924 and 1933) could be accounted for by a 10% annual increment and a 30% survival to maturity. It seems unlikely that such a high survival occurs and more probable that the Grassholm increase (and possibly increases at other Colonies) was partly due to immigration.

The Bass increase between 1949 and 1962 was from about 5,000 to 7,700 - i.e. 2,700 pairs, or 54% of the 1949 total in 13 years. The mortality over the five or so non-breeding years must therefore have been less than the 83% calculated for a stable population. In fact if the estimated increase is correct (corresponding to a 'compound interest' increase of 3 to 4% per year) and assuming no immigration or emigration, the mortality over the immature years would be reduced to 79-80%.

BEHAVIOUR

INTRODUCTION

This behaviour study aims to provide detailed descriptions of the Gannet's main behaviour patterns and to give quantitative information on many of their aspects. This kind of fact is still required as the raw material for comparative studies and also to test certain generalisations, sometimes made on a too-narrow basis; "generalisations which precede comparison can never be more than guesses" (Hinde 1959a: 566). In addition, the causation and function of some of the behaviour described here is also analysed.

Changes in responsiveness to a constant external stimulus are a familiar feature of animal behaviour. It is also noticeable that certain groups of activities (e.g. different forms of aggressive behaviour) tend to fluctuate broadly together, implying some dependence on common causal factors. The terms 'motivation', 'drive' etc. have been used to describe such facts and although these concepts have a number of shortcomings (see Hinde 1956b), when critically analysed, some conceptual framework of this kind is necessary for the preliminary stages of the analysis of behaviour, such as the present study of the Gannet. The term 'motivation' is used here to denote the result of the interaction between internal and external factors which together affect the liklihood of occurrence of given behaviour (this definition is modified from Thorpe's (1951) definition of drive). In a number of studies the motivation of many display postures has been broken down into two or three main components which fluctuate together with the readiness of the animal to flee, attack and behave sexually and it has been shown that changes in these components may alter the form of the display or cause one display to be replaced

by another (Tinbergen 1954, 1959; Moynihan 1955a.b.c., 1958; Hinde 1955/6; Marler 1956; Morris 1956; Manley 1961). This three component (FAM) system has been found useful by a number of observers and appears, for the Gannet, to be a helpful working hypothesis. Some workers, however, (e.g. Andrew 1961, 1963) find it inadequate, partly because some displays seem to include components difficult to fit into this limited framework.

The components mentioned above were sometimes called 'drives', a term which has been used in at least three ways by ethologists and which carried associations with certain motivation models. Hinde introduced the less ambiguous word 'tendency' which was free from these associations and used it, for instance, where causal factors for two or more incompatible types of behaviour were present together - e.g. "in the courtship behaviour of the male Chaffinch (Fringilla coelebs) the bird is principally under the influence of conflicting tendencies to flee from and behave sexually towards the mate" (Hinde 1954 : 207) and again " a courting bird has three incompatible tendencies; to attack, flee from and behave sexually towards its mate. The nature of the behaviour shown at any stage in the courtship depends on the strengths and relative strengths of these conflicting tendencies" (Hinde and Tinbergen 1958 : 256). Tinbergen (1959) analysing the displays of gulls also used 'tendency' to refer to the motivational components leading to aggressive, sexual and fleeing behaviour respectively, and, where used in the present account, it is in this way. It will be clear that this assumes to some extent the idea that a tendency is 'unitary' (e.g. that the various aggressive actions, biting threatenting, etc., share common causal factors and fluctuate together). However, Hinde has shown that this is not necessarily true, at least for the nest-building behaviour of the canary (Hinde 1958) where the short-term fluctuations of different components are partly

independent. Nevertheless, field observations of Gannet behaviour do suggest a certain 'unitariness' about the different behaviour systems.

A development of the earlier use of tendency, as for example in Stokes (1962) refers strictly to numerical relationships between observable behaviour components without direct reference to hypothetical internal factors. However, he too points out that tendency "presumably reflect(s) underlying causal factors both internal and external in nature" (1962 : 211). As already mentioned, however, fear, aggression and sexual tendency are used in the earlier sense in the present study.

The last paragraphs have discussed the factors which predispose animals to behave in certain ways - the causal network of behaviour. But the behaviour itself has effects, usually many, for which it is a cause. The point in a series of linked events which may be taken as the function of that series depends on one's viewpoint. It is here taken as that effect (or those effects) lying in the main stream of consequences leading from the behaviour and having survival value.

The identification of functions is complicated by a network of interacting effects, comparable to the web of causal factors mentioned earlier. It is only by a due appreciation of these interactions that the real significance of behaviour can be judged. Thus territorial spacing-out depends on balanced attack/escape systems (see Tinbergen 19[illegible] and any evaluation of aggression must embrace its relations with other systems (this subject will be discussed in more detail at appropriate points in the account).

Ritualisation refers to the various kinds of evolutionary changes in behaviour which enhance its effectiveness as a signal (see, for example, Tinbergen 1952, 1962). As Blest (1961), in his critical review of the concept, points out different authors have used different criteria, sometimes

inconsistently, in deciding whether to call a particular piece of behaviour 'ritualised'. However, most would consider behaviour to be ritualised if it is seen to function as a signal and can be plausibly derived from some less conspicuous non-signal behaviour. Even if the signal function has not been actually demonstrated the term has been widely used in the past for more or less bizarre actions without any apparent direct biological function, occurring in situations where signalling behaviour would seem beneficial. Some Gannet behaviour is ritualised according to the stricter definition, but as the evidence for a signal function is sometimes only circumstantial, it has been found more useful in the present study to employ the broader criterion.

Ritualised behaviour may be derived from various sources. Daanje (1950) shows that locomotory intention movements may acquire signal function, and Tinbergen (1952) discusses also the ritualisation of displacement activities. Since then, several other sources have been added (e.g. redirection activity, autonomic responses, protective movements). These may be elaborated singly or as a mosaic, as in the case of some ambivalent behaviour, such as the zig-zag of the Stickleback, which involve elements derived from different sources. In the Gannet, bowing is an example of a ritualised display derived from at least two non-signal behaviour patterns and showing signs of conflict motivation. The role of environmental factors in influencing the form and orientation of some stereotyped postures is noted by Tinbergen (1952) and stressed by Crook (1962). The Gannet's size, strength and relative freedom from predators may have 'allowed' considerably more freedom in the evolution of signal behaviour than occurs in some species.

Gannet Behaviour.

There is no adequate account of Gannet behaviour; although Warham (1958) gives a valuable description of some behaviour patterns in Sula serrator, and Armstrong (1942); Gibson-Hill (1948); Perry (1948); Fisher & Lockley (1954) and Barlee (pers. comm.) have also written briefly on parts of Gannet behaviour.

Several behaviour patterns have not been previously described, and practically nothing has been written about causation, function and adaptiveness of the remainder. This study was therefore wide in scope, describing and attempting to interpret all the main features of Gannet behaviour at the breeding Colony.

In the Gannet site-acquisition and defence involves violent and persistent aggression, and an exceptionally high proportion of time spent in attendance. Apparent disadvantages to the species, if not the individual, result from these features; much of the Gannet's behaviour apparently represents an adaptive compromise between conflicting selection pressures.

Presentation follows the chronological account of the breeding biology; behaviour involved in site establishment, pair formation, incubation, etc.. Certain behaviour patterns (particularly comfort behaviour and the sky-pointing posture) do not fit in this pattern and their position in this account is a matter of convenience. The more general topics have been left to the end on the assumption that they are appropriately placed after the main account.

An effort was made to quantify seasonal changes in frequency and duration of behaviour patterns, together with sex and status differences, in part to complete the species-description and also to help in the analysis of function and motivation.

The Gannet shares many problems with other colonial sea-birds. Its 'solutions' are almost certainly peculiar to itself, but also throw light on other groups.

- 8 -

THE NEST SITE

Site Establishment.

It seems probable that Gannets, although now nesting on flattish ground as well as cliffs in many places, were originally, and are still primarily, cliff nesters. Since several of my reasons for believing this stem from their behaviour discussion of this topic is deferred, although it is important to keep in mind.

Before considering the details of behaviour involved in site establishment three broad predispositions of the species may be noted (probably shared by other sea-birds): to nest in the Colony of their birth, close to the nest from which they came and close to other nesting birds.

The tendency for animals whose life history involves dispersion or migration to return to the area of their origin is well documented and could clearly be advantageous in several ways. There own existence proves at least that successful breeding was, and probably is, possible there. Wynne-Edwards (1962) has also emphasised the potential value to the species of evolving local populations genotypically adapted to the particular environment, which may differ significantly from other areas within the species' range. So far as I know there is no case of a ringed Gannet recovered breeding in other than its Colony of origin. Fisher & Venables (1938) quote one instance of a bird ringed as a chick on Ailsa Craig in 1924 and recovered north of Shetland in 1926, and Baird (pers. comm.) recovered an adult in the Faroes ringed as a chick on Grassholm . This, however, was not breeding.

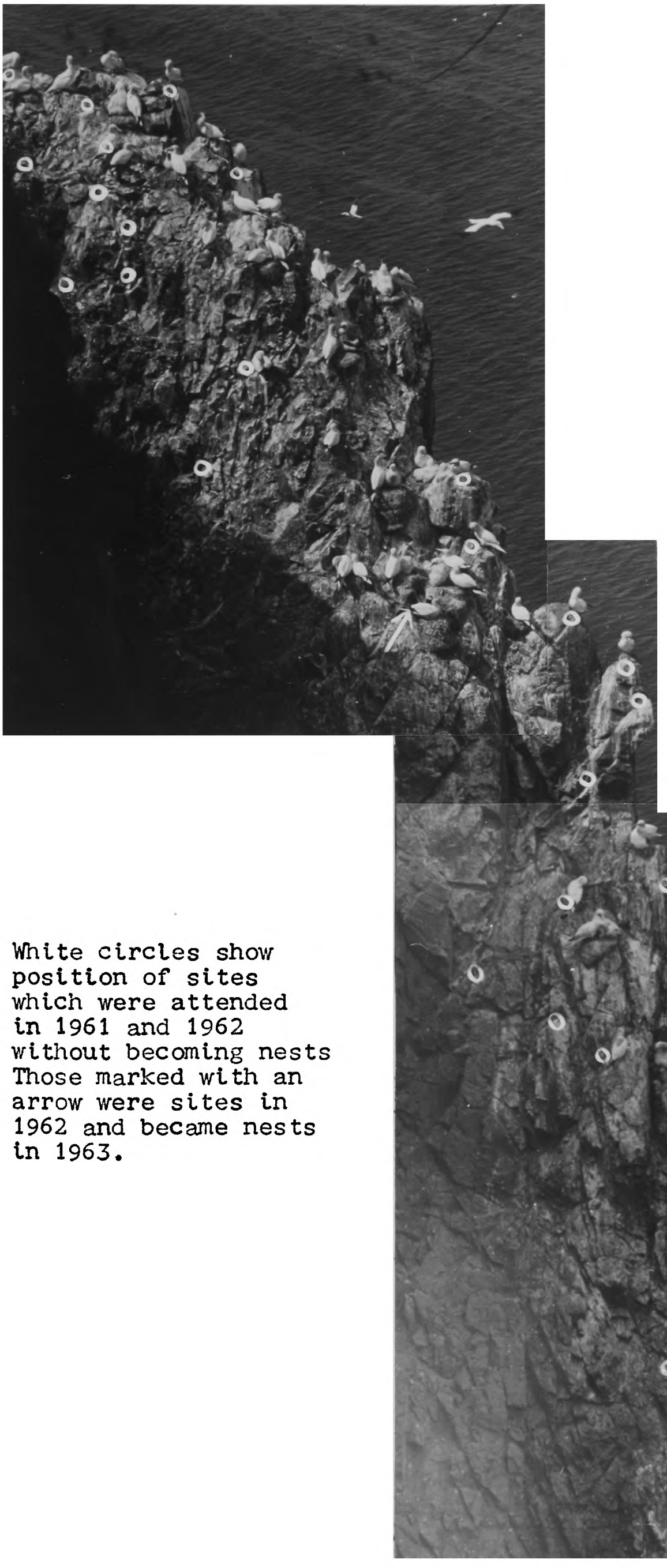
Because Gannets nest in comparatively discrete Colonies their tendency to return to their own may be particularly strong. There must, however, be many exceptions to this general tendency, to allow for extension of the species'

range or emigration in response to locally unfavourable conditions, and the absence of evidence really reflects the paucity of records. Fisher & Venables (1938) decided that the increase on Noss between 1914 and 1918 could not be accounted for except by colonisation from outside, and all new gannetries must be started by such pioneers. The nearest Colony which could have provided the Bempton (Yorkshire) pioneers is the Bass, more than 150 miles north.

The second predisposition is really an extension of the first. This study has shown that Gannets tend to return to the same limited area of the Colony in which they were born. Thus the high proportion of ringed birds (41%) establishing sites in the fringe between 1961 and 1963 could be accounted for only by assuming that most of the birds returning to breed for the first time had been ringed there as chicks (this area was particularly heavily ringed between 1955 and 1959). Further a chick colour ringed in 1960 landed several times in 1962 on the very ledge (an isolated one) from which it fledged. This would have been highly improbable on chance alone. Several other colour ringed chicks were seen flying repeatedly over their precise area of origin.

A further case is of particular interest. In 1961 an isolated and inaccessible stack 'The Needle' (PLate 8) held 35 nests and 35 sites. The latter were mostly on tiny projections or pointed pinacles (marked with white circles). By 1963 only two of these had accumulated nest material and become suitable for breeding. Many of them could never hope to do so, and several have been abandonned. Since there were available nest sites elsewhere on the Bass, it is inconceivable that they were forced to try these unsuitable spots. It seems more likely to be a rather unusual demonstration of the tendency of Needle offspring to return there, and in the absence of convenient ledges to attempt colonisation of highly unsuitable niches.

Plate 8 The 'Needle' colony, July 1963.



White circles show position of sites which were attended in 1961 and 1962 without becoming nests Those marked with an arrow were sites in 1962 and became nests in 1963.

The third important factor is the very strong tendency to nest close to birds already established. This is convincingly demonstrated by Plate 2 and is a common characteristic of colonial sea-birds, in some species supposed to derive from ultimate shortage of sites, but in many species the advantages are probably of another kind (e.g. anti-predator). Even in the first category it has often been remarked (e.g. Ashmole 1962) that perfectly suitable areas are neglected in favour of others, simply because the latter are nearer existing nests. In the Gannet it is an inevitable result of the tendency to return close to the nest in which it was reared. Nevertheless, it exerts a strong effect in its own right, and birds nesting in areas other than where they were reared nest near to existing breeders. Despite the attraction exerted by other nesters Gannets maintain individual territories (the area immediately around the nest) resulting in a characteristically regular dispersion within the group. It is important that Gannets <u>should</u> be capable of breaking away from the established group, and I have recorded a nest with egg 30 yards away from the nearest occupied nest, though this is unusual.

The details of site establishment are given next, and refer to birds newly-establishing sites, since it is their behaviour which is relevant. The behaviour of birds returning to previously established sites needs no special comment since they simply return and occupy their old sites, performing the ownership display when stimulated by intruders, etc.. The proportions of males and females are given in Chapter 3.

Before Gannets attempt to establish a permanent site, at the age of four or five, one may observe them flying low over and examining a particular group of nests time after time (see Plate 14A) and they must know the physiography of the Colony intimately as a result of innumerable flights over

each part (and probably particularly the one in which they eventually establish themselves).

Method of site establishment. During winter Gannets apparently range widely over the sea without territorial restriction. However, it seems that the acquisition and defence of a breeding site has required the evolution of intensely competitive, aggressive behaviour, despite inherent disadvantages. The effects of this aggression cannot be confined merely to the primary situation for which it was selected, and outcrop in ways which seem less adaptive but inevitable. A male, which because of outstanding aggression to other males, easily acquires and defends its site may also be unusually aggressive towards its mate and chick, thereby affecting their responses and thus the raw material from which signal behaviour can evolve. In this way one important behaviour system can influence much of the species' biology. Tinbergen (1956) has argued that agonistic behaviour in strongly territorial birds is so important that even a slight deficiency would seriously reduce an individual's chance of successful site establishment and breeding.

The male Gannet usually establishes and maintains a precisely located site for all or part of a season prior to that in which he first breeds (females do not establish sites), in contrast, so far as known, to all other British colonial sea-birds, except the Cormorant (Kortlandt 1942) and possibly the Fulmar. Arctic Terns, at the other extreme, may chose the nest site only a few hours before the first egg is laid (J.M. Cullen). Even S. dactylatra and S. leucogaster move about considerably in the site-owning but pre-laying period (Dorward).

The observation colony was clearly demarcated on the inland side and the boundary advanced each year from 1961 to 1963 (see Plate 2). The process of expansion could

therefore be closely watched and mapped. The following account is based on 53 sites established in the observation colony in 1961 and 1962, and mapped as soon as establishment was suspected.

Reconaissance. Apart from flying over the nesting group (p. 123) Gannets also reconnoitre from the ground by landing on an unoccupied nest or wndering along the fringe. I have recorded five different males occupying a vacant nest one after the other in a few hours and each being displaced by the owner (who had joined a widowed female nearby). This indicates the constant pressure of young males to take over empty sites, and the premium on guarding one's site. The length of time required by a new male to become sufficiently attached to a site to fight in its defence is hard to determine. It is certainly more than a few hours, and is probably two to three days, which about corresponds to the normal duration of absences at this stage. Rightful owners are therefore able to re-assert ownership without serious fighting.

Males establish sites either by taking over existing nests, squeezing in between them, or establishing a site in a new area - usually in the fringe of an existing group.

Taking over existing nests. The low adult mortality rate of 6%, and the female's continued attachment to the site if the male dies, mean that few nests are vacated each year. Within the group of ringed adults, therefore, only 4 cases were recorded, although the process is clearly responsible for maintaining the stability of gannet Colonies.

In some cases established females returned late to find that they had been replaced by new females whose attachment to the site, in the presence of the experienced male, quickly became strong enough to defeat attempts by the former owner to regain the site.

Lockley (in Fisher & Lockley 1954) states that young Gannets take up the outer edges of a colony and that

the inner section consists of older birds (he implies this for a stable population). Since there is no reduction in density in the old-established parts of the colony, it follows that, in a stable population, the first-time breeders are distributed throughout and not concentrated on the outer fringes. Where, however, a general or local increase is taking place, the expanding portion will, as in the observation colony, establish sites on the fringes. Unless, therefore, it is known whether the population is stable or expanding, one cannot deduce that the age of the birds in the centre of a colony is, on average, greater than at the fringe.

Squeezing in between existing nests, (see Plate 2). The density and regularity of old-established groups are greater than in newer areas, due partly to the tendency of new birds, in the beginning, to establish and defend a larger area than they later maintain, leaving gaps which are gradually filled during succeeding years until maximum density has been achieved. Nevertheless it sometimes happens that after many years a spot which has remained empty because of its small size or topographical difficulties is suddenly adopted by a male who, in the face of extreme hostility from neighbours, persists in establishing his site and forming a pair there. It is tempting to speculate that such males were born nearby and are, for some reason (possibly a conspicuous landmark) particularly prone to return there (see p. 122). On average only one male chick might be expected to survive to breeding over many years from the small area near such a landmark, thereby possibly explaining the sudden and tenacious adoption of such an unlikely spot. The habit of group consolidation in this way ensures maximum use of the habitat andccould be adapted to site shortage if this ever arises in the species, the Gannet possibly once having had a more extensive range than at present.

Establishing a site in a new area. Once having

recognised that the observation colony was expanding, twice daily observations were carried out and the presence of new birds recorded, particularly in the fringe, to find the pattern of establishment. The precise location of these sites and the area defended were pinpointed by reference to small features of the landscape. Newcomers were too wary to catch for colour ringing, although the eventual return of birds colour ringed as chicks (over 600 in the observation colony between 1960 and 1963) will provide recognisable individuals. A dyed male provided useful confirmation of some points deduced from unmarked birds.

Behaviour and the length of time spent on the site indicated whether birds were merely casual visitors. A male interested in a particular spot landed there and made a characteristic nest-biting movement. He threatened other males wandering nearby, frequently bowed (a site ownership display) and when doing none of these stood in relaxed fashion with retracted neck and preened or slept. On the other hand, a casual visitor landed without performing the nest-biting and stood in the anxiety posture, with elongated neck, scanning the neighbourhood, did not usually bow or show marked aggression towards nearby birds, but on the contrary was readily displaced by challengers. Since birds, later establishing themselves, first come to sites as casual visitors it is not surprising that the transition from one to the other was difficult to recognise. The longer a bird spends on a site the more serious he is about establishing himself and the more bitterly he will fight.

Period over which sites established. Table 31 shows the dates on which sites were established, and it should be noted that these are usually later than the return dates of established birds. In 52 out of 53 cases breeding did not occur until at least the season after establishment. Birds establishing a site

relatively early in the season spend more time on it than later birds, whose attendance may be sporadic (see Figs. 22 & 24). Birds late in establishing a site, but regular in attendance, usually bred the following year. Other late site-establishing males either abandonned the site in favour of a new one the following spring, or held it for a full subsequent season before breeding. Even after a full season's presence, however, sites now with nest material but which have not yet held an egg, are much more likely to be vacated during bad weather than those which have held one. Squeezed-in sites are more consistently guarded in the early stages and also returned to earlier in the following year than are fringe sites, possibly the result of social stimulation (p.54). The urge to establish these sites was obviously strong in the first place otherwise the local opposition could not have been overcome.

TABLE 31. Dates of site establishment (1961; 1962).

	Half-monthly periods.										
	April		May		June		July		August		Total
	1	2	1	2	1	2	1	2	1	2	
No. of sites established	5	8	12	13	10	1	0	0	4	0	53

Role of the sexes in defence of the site. After pair-formation both sexes defend the site. The details of aggression involved in site establishment and defence are better discussed under the separate heading of 'aggressive behaviour'. Its primary function in the male is undoubtedly to secure and maintain a site, and in the female, to keep a male as well as a site. Out of the 53 sites whose establishment was followed 34 were known to involve at least one fight. A total of 57 fights were recorded for them and this figure, of course, represents only a proportion of the real number.

Out of 29 fights recorded between established birds and rivals 24 involved females as a result of the male's polygamy. Therefore in both sexes fights begin only on or near the site or mate.

Site Attendance.

Site establishment is followed by a phase of site attendance, usually lasting for the remainder of the season but without breeding. During this period pair formation occurs and a stable pair bond is achieved. The attendance phase varies with time of year, the male's success in obtaining a partner, his age and the type of site (fringe or otherwise), etc..

Like many long-lived birds the Gannet forms a site attachment which is virtually permanent (see Table 7), but compared with most sea-birds it spends more time there (seasonally and as a proportion of seasonal time), defends it more vigorously and performs an ownership display (which probably lacks a precise counterpart in other species) more often. Indeed, the nest site focuses the breeding life of the Gannet more sharply than in other sea-birds and its importance is fundamental to an understanding of the behaviour of the species. The following section shows how site attendance can be measured and how it differs in different categories and between the sexes.

Seasonal duration. The main features of seasonal attendance at the breeding Colony have already been described in the account of the breeding cycle (Chapter 3). So far as the seasonal duration of time spent on the site is a criterion of site attachment, old males have the strongest, returning first and remaining longest. In all categories (i.e. experienced, successful breeders, failed breeders, newly established birds, etc.) males spend longer on the site than females, befitting their role as the sex originally establishing the site. Latimer's

(1954) claim that in the South African Gannet females arrive first and "males later escort them to the site" is puzzling and despite being based on evidence obtained from dissection, needs checking. It would be surprising if such an important difference existed between such closely related species. Figure 22 gives details of male, female and pair site attendance in experienced pairs throughout the season. Attendance in the male climbs steeply in March and then remains fairly constant until the middle of September, representing an extremely high attendance in total hours. The female shows a seasonal period of site attachment almost as long as the male's.

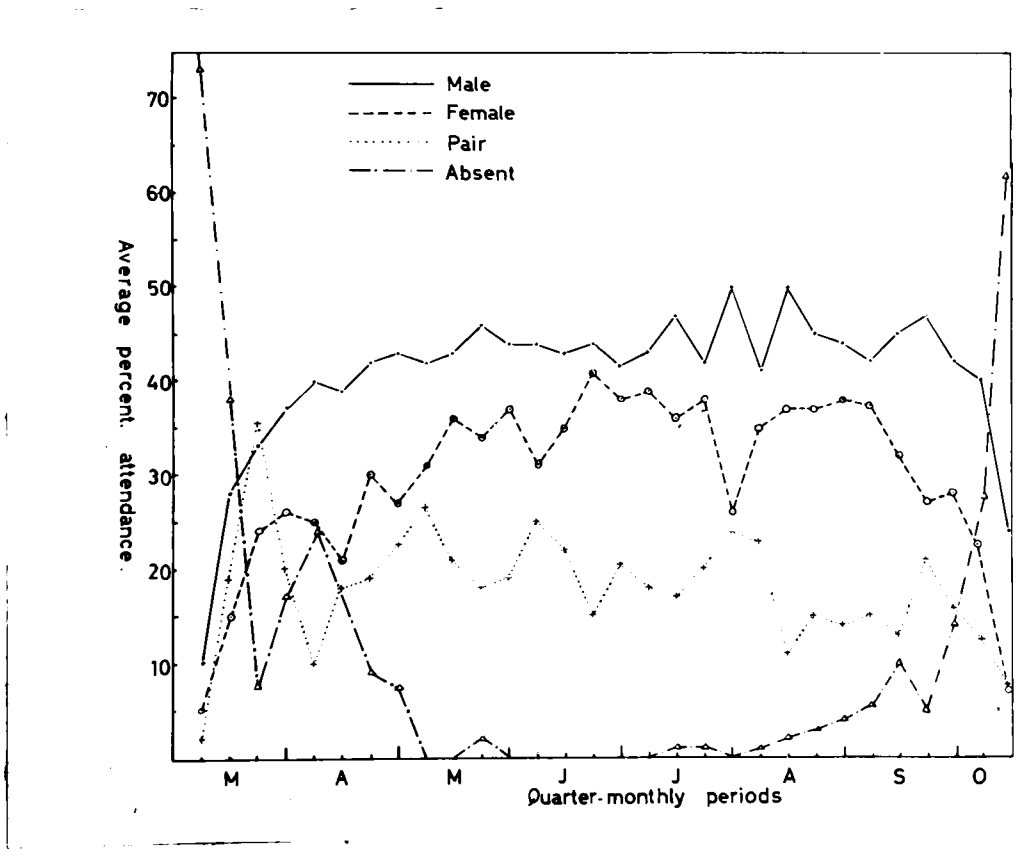


Figure 22. Seasonal site attendance in experienced birds.

Note : Total number of nest/observations 9,585.

In addition to seasonal duration of site attendance two other methods were used for estimating the strength of site attachment. First I recorded, for a few nests, the presence of male, female or pair at frequent intervals (sometimes two-hourly, or two or three times a day) throughout the season. Once the bird's general routine had been

discovered it was possible to interpret attendance spells more accurately. For example, if the male was present on two occasions six hours apart (and his arrival time was roughly known) it was safe to assume that he had been on duty the whole of that time. Also the large number of records involved minimises the final possible error.

A second method was to record similar information for a large number of nests of different categories. but once daily, or less often. These records do not show duration of spells, but over a long period reveal the pattern of attendance simply by the difference in the number of records for the sexes and categories. It should broadly agree with the more detailed information given by the first method, so long as the same categories are compared.

Length of attendance spells. Table 32 summarises the data on this subject. Attendance spells are calculated in each case with reference to the date of egg laying for the pair concerned, in an attempt to standardise the physiological condition of the birds.

Three main points are shown by the table :

1. Whatever the stage in the breeding cycle, the average duration of male spells of attendance is greater than of female spells (in the one exception they are of equal duration) Also the longest recorded spells are always by males. This suggests a summation of site attachment with other factors producing longer attendance spells in males (maximum recorded eight days).
2. There is a dramatic decrease in the duration of attendance during the first half of the fledging period, from 35.6 to 18.5 hours in the male and 30.2 to 18.8 in the female. This shows the effect of chick feeding. However, during the second half of the fledging period, the males' attendance spells rise to 23.7 hours whilst the females' remain at

18.8 hours. This difference could partly reflect some of the factors responsible for rising aggression and increasing tendency to perform the site ownership display at this time (see Figs.26 & 33).

3. After fledging the attendance spells rise significantly in the male, continuing the trend of the latter half of the fledging period, but rise less in the female. This fits with her weaker site attachment. The average number of spells is the same for both sexes at all periods; it is the length which changes.

TABLE 32. Comparison between male and female of experienced pairs in duration and number of attendance spells throughout the season.

Period	No. of days	Av. length of spells (hours)		Range of spells (hours)		Av. no. of spells	
		Male	Female	Male	Female	Male	Female
3 weeks before egg laying	21	44.6	39.6	4 to 197	2 to 134	6	7
Incubation period.							
First half	22	37.2	30.8	7 to 84	4 to 70	8.5	8.3
Second half	22	33.2	29.1	6 to 62	10 to 46	9	9
Average		35.6	30.2			8.7	8.4
Fledging period							
First half	45	18.5	18.8	4 to 58	7 to 50	31.2	30.6
Second half	45	23.7	18.8	5 to 103	3 to 70	25.9	26.1
Average		21.6	18.8			27.9	27.9
3 weeks post-fledging	21	33.2	20.8	3 to 127	2 to 96	8.7	8.8

Note : Based on 639 spells for males
637 spells for females,
from 12 nests.

Total occasions on which site attended. This information was gathered for eleven different categories of which three of the most important are analysed here, concerning experienced birds, newly-established birds and failed breeders.

Experienced birds. Figure 22 shows that in experienced pairs the male was recorded at the site consistently more frequently than the female throughout the season. On approximately 45% of all visits the male alone was on duty and on a further 20-25% he was at the site with the female. This picture agrees, as expected, with that from length-of-attendance records. It may be added that there is no significant daily rhythm except early in the season (Fig. 23) when males are mainly in attendance later in the day. The attendance of pairs also follows this pattern early in the season.

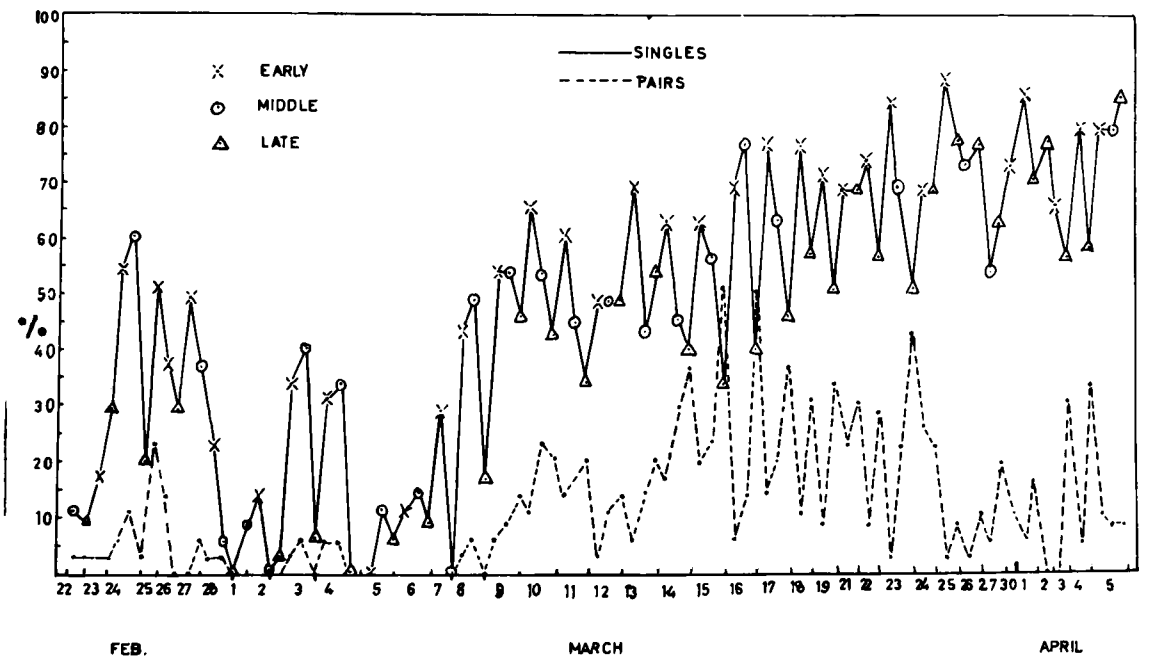


Figure 23. Attendance at nest of singles and pairs early in the season, in relation to time of day.

Note : Based on 35 cliff nests.

Newly-established birds. Figure 24 shows that, as in experienced birds, the newly-established male has a consistently higher attendance than the female, but is absent

far more frequently than were experienced males at the same period. By this measure, his site attachment is therefore weaker than their's. Nevertheless it persists at a high level until October, so that despite the absence of egg and chick the male alone was in attendance on about 30% of all counts and at the site together with the female some further 20% between April and October. This shows that the acquisition of a site in the pre-breeding phase is achieved by systematic attendance and is far from being the expression of incipient territoriality. In fact, during the previous two years the male has shown incipient territoriality in his club activities (p. 254). There is a suggestive decline in male attendance soon after pair formation, partly explicable by increased attendance as a pair, but also at one point falling slightly below the female's. This may be the result of the male's tendency frequently to leave the female in attendance soon after pair formation - perhaps to stabilise her site attachment as such, in addition to the pair bond (p. 186).

Failed breeders. Birds comprising this category lost their egg, and attendance has been calculated from the time of this loss (Fig. 25). Again the male shows a higher attendance than the female and compares favourably with that of experienced males breeding successfully, being little affected by egg loss. The female's attendance on the other hand was lower following egg loss, suggesting that for her the site as such has a less strong attraction than for the male. Other evidence already suggested the same thing.

Failed breeders spend longer on the nest as pairs than do experienced birds breeding successfully, doubtless because the parents have to attend to the demands of the chick.

Bowing as an index of site attachment. It will be shown later that bowing

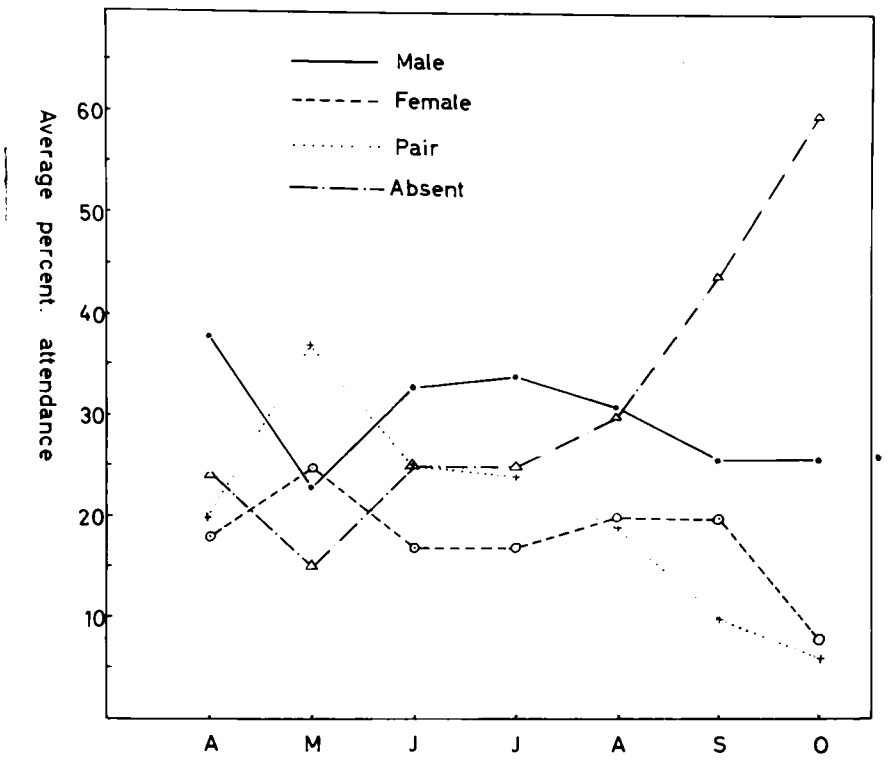


Figure 24. Attendance at nest-site of newly-established pairs (i.e. established during the season of the check). Attendance expressed as overall percentage (i.e. number of occasions, averaged for nests involved, on which male, female or pair present when checked). Based on 4,709 bird/observations.

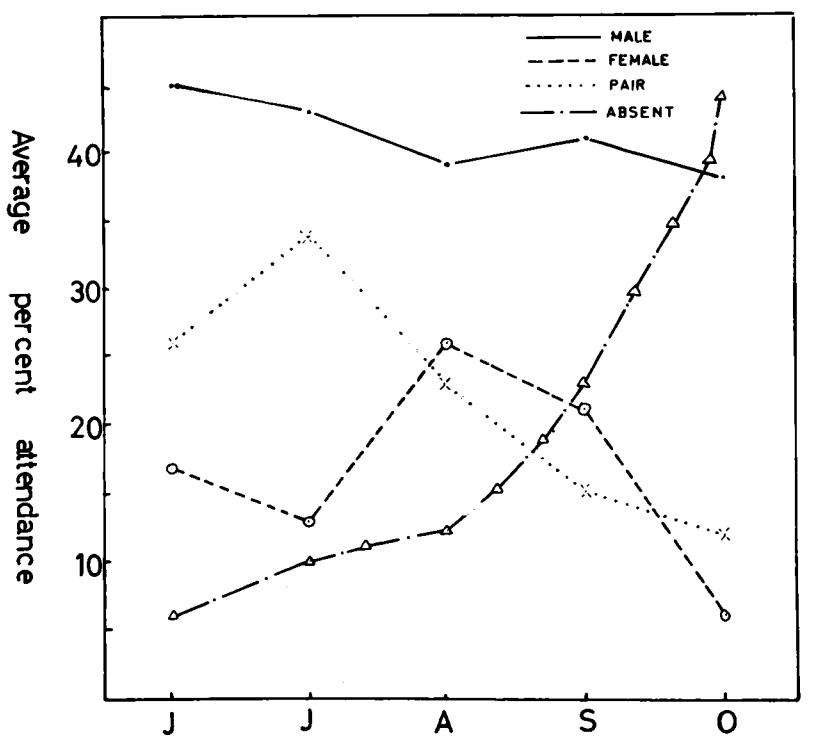


Figure 25. Attendance at the nest of failed breeders (after egg loss). Expressed as in Figure 24. Based on 781 bird/observations.

is undoubtedly a site ownership display, but its frequency and intensity do not increase proportionately with the strength of site attachment.

After site establishment, here assumed to have occurred when the male spends several hours on a site for three or four successive days, there are two main phases in his ownership display - before and after the first egg. In the pre-egg phase, which may last an entire season or more, bowing is more frequent than in birds <u>with</u> eggs (at the same time of year and sample period). After laying of the first egg bowing decreases. Although the site ownership display is at all times and in all categories strongly elicited by appropriate stimuli (intruders, the bowing of nearby birds, etc.) the effects of such stimuli are most marked in birds in the early stages of site establishment. Despite the fact that old-established males undoubtedly possess the strongest site attachment they bow less frequently than newer males, possibly because they are very rarely challenged and have no 'need' to demonstrate their status so frequently.

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THE NEST SITE (PART 2)

Limitation of Aggression to the Site Context.

It has already been suggested that the function of male fighting is in site establishment and maintenance. The site is the Gannet's only territory and is used for copulation, pair contact and breeding. The female defends the site, but also fights over the male and most female fights result from his acquisition of two mates.

It should be made clear that when the Gannet's aggressiveness is discussed, no attempt is being made to divide it into different 'kinds' of aggression. Hinde (1956[a]) argues for the essential unity of all forms of fighting, but not necessarily aggression. Here, however, aggression is qualified according to context and regarded as a single tendency (like fear), whose expression is modified by the sum of other tendencies and the external situation.

Food fighting, as reported in tits (Hinde 1952), corvids (Lockie 1956), Woodpigeons (Murton 1962) and Herring Gulls (pers. obs.), to cite a few examples, seems not to occur among Gannets, though it would be difficult in view of their habit of swallowing fish before surfacing. Nevertheless they rarely squabble when crowded together devouring trawler offal.

During communal gathering of nest material they may take material from each others' beaks, but I have never seen even the mildest fighting among such gatherings.

When breeding individuals meet on the fringe of the colony they are completely non-aggressive. Yet as soon as they reach their nests they become fiercely hostile. Even club birds show incipient aggression in defence of temporary sites.

Tinbergen (1956) has emphasised that agonistic behaviour is a balanced system in which selection favours a

particular combination of attack and escape tendency - not one to the exclusion of the other. Similarly Lack (1954) states that in territorial behaviour the avoidance response of non-owners is as important (or more so) than the aggression of the owner. Nevertheless, although it is true that in the Gannet all except serious contestants for the site react either by avoiding males guarding their sites or flee when menaced, severe fighting is probably commoner than in any other British bird. Indeed, all references to aggressive behaviour in sea-birds, which I have found, indicate that the Gannet is quite exceptional in this respect, although Tuck (1960) records "severe mortality" due to fighting, among Razorbills at Akpatok Island. The implications of this 'hypertrophied' aggression will be considered in the general discussion.

Having shown the site to be the main context of aggressive behaviour in the Gannet, we may now consider its forms under the sub-headings : method of fighting; fighting and the morphology of the sexes; threat behaviour and bowing.

Method of Fighting.

Gannets fight exclusively with their powerful bills. Exploratory model-experiments showed that it was not necessary for an intruder to present his bill before he would be attacked. A severed/head presented nape towards the owner was vigorously attacked. Nevertheless, since in threat display they confront each other with open beaks (Plate 9A) these focus the attack when threat develops into overt aggression (Plate 9B). Even when one contestant dives onto his opponent from the air, he usually attacks the beak. Other parts of the face, head and neck are also frequently gripped (Plate 9E), and sometimes wings, legs or feet (the webs are often torn). Males normally do not attempt to dispel other males, as they do females, by thrusting them away by the scruff of the neck (Plate 14B.). Although this may be partly

Plate 9. Fighting between males in site disputes.

A.

Male of newly-formed pair challenged by rival (slightly immature). Note withdrawn position of female and forward threat of male.

B.

Note the pushing method and extended neck of attacking male. Very new site, grass not yet worn away.

C.

Fight between rival males in fringe area (observation colony). Note bare earth but no nest material.

D.

A fight in which the contestants move many feet from the disputed site (marked with arrow).

E.

Fringe fight. Note that one male is slightly immature. Also the social stimulation provided by the fight (4 pairs mutual fencing, 2 birds bowing and several generally alerted).

because females face away from aggressive males, making it difficult for their beaks to be seized, it is also a real difference between the male's response to an intruding male and an intruding female.

Mandibles are strongly interlocked so that withdrawal is often impossible unless the contestants break off simultaneously (cf. the rapid, darting motions of Guillemots). With extended neck they then attempt to drive the opponent in front of them, the intensity of straining revealed by their taut postures and conspicuous muscle-ridges. The grip alternately tightens convulsively and relaxes, the dominant bird often shaking his opponent violently. Grips are altered with lightning speed and the usual position brings the tip of the upper mandible dangerously close to the opponent's eye, often grossly distorting the orbital ring. The eyelids are not used to protect the eyes during fighting, but the nictitating membrane (which is almost transparent) is drawn across as a reflex response to any anticipated contact with the eye. The lens can withstand strong jabs and must be protected by a strong conjunctiva and cornea. Gannets (unlike Shags, Snow 1963) do not avoid each others' eyes when mutual preening and certainly not when fighting (see below) and it is possible that their eyes are specially adapted to withstand the treatment meted out in fighting.

Marked deformities of the face region occur during fighting and the soft parts of the face are severely cut by the serrated edges of the mandibles. Gannets, caught whilst sleeping after a fight (p.244) were often found to bear severe wounds. One bird had much of the eye tissue hanging outside the socket (Plate 10), another had the socket filled with blood and a third had an opaque eye. Other wounds included deep cuts in the facial soft parts and a deep peck wound near the oil gland. One bird died from a peck wound in the lower breast. Extreme exhaustion and filthy, tattered

Plate 9F.

Fighting birds attacked by neighbours.

Plate 10.

Badly damaged eye - the result of a fight.

plumage underline the severity of these struggles (see Film).

Since differences in functionally equivalent behaviour patterns in different species are probably adaptive the Gannet's method of fighting deserves special comment on three counts. First, they fight with their extremely powerful beaks. They have relatively weak feet (cf. corvids) and their wings, though powerful, are long, and if used as a weapon (cf. Herring Gulls and Capercaillies Tetrao urogallus) would involve them in further punishment with neighbours in the restricted area around a nest.

Second, whereas Kittiwakes twist each other off the ledge, Gannets push with extended neck (Plate 9B) - a mechanically unstable method made practicable only because their necks are exceptionally powerful, probably as a structural adaptation for withstanding the shock of plunge-diving. This is a good example of the use, in one context, of an organ developed primarily in another. A further behavioural example is the way in which a bird occasionally displaces an opponent by diving onto him from the air, in a typical shallow fish-hunting dive (cf. the way in which Sparrow-hawks Accipiter nisus use hunting behaviour to break off twigs for nests, Bal 1950). Since the function of fighting is to evict the opponent, the main available methods are pushing, pulling or twisting. The two latter would be physically awkward for a Gannet and ordinary locomotion movements are far stronger and more effective.

Third, the main tendency is for one to push the other away from the site, regardless of its own position. Thus one bird often drives or chases the other many yards away (Plate 9D) and is itself attacked by neighbours (9F). Although it would seem advantageous, in a dense community, for one bird to remain on the site whilst using his long and powerful neck to thrust the other away, they do not behave in this way.

Females fighting in the presence of a male are unwilling to leave the site, not to avoid punishment from neighbours but to remain as close as possible to the male. They attempt to push up to him and accept sustained attack from their rival so long as they can retain this position. They may even attempt to mutual fence whilst resisting all efforts by the rival to displace them. In these cases the male, rather than the site, seems to be the disputed object.

When fighting in the absence of the male, females show the male pattern of fighting and will pursue an opponent some distance from the site.

In female fights the one willing to accept the greatest punishment without leaving the site usually wins, though not necessarily either the rightful owner or the most aggressive (by vigour of attack). In such fights the male tends to switch his attack to whichever female is losing at the time, and neighbours mainly attack the newer of the contestants, suggesting that recognition and acceptance of neighbours plays a part in the social life of the group.

It must be concluded that the male Gannet's fighting method is not adapted to displacing an opponent on flat ground whilst at the same time avoiding displacement and punishment itself. However, it seems well adapted to displacing the opponent from a cliff ledge which it effectively did in those cliff fights observed. It may well be <u>because</u> the fighting method is primarily geared to a cliff habitat that the fights on flatter ground are so severe and prolonged- a biologically undesirable feature. The difference between cliff and flat ground fights was well shown when a male made eight successive attempts to land and attack a rival on a ledge site and was forced away each time. When such fights do occur they are usually short-lived, whereas ground fights may last two hours or more.

I several times recorded fights continuing in mid-

air, and often on the sea. These were always birds continuing fights started on a ledge. Kittiwakes also fight on the sea, but they use their wings deliberately to buffet the opponent (Cullen) whereas Gannets continue to fight merely with their beaks. The reversion in the Kittiwake from its special ledge-fighting method may be a relic of the more generalised gull fighting method, since Herring Gulls also use their wings (and feet) when fighting.

Aerial pursuits occasionally culminated in renewed fighting. The infliction of a thorough defeat may lessen the chance of further challenge. This often required fighting after the dominance of one had been asserted and it was noticeable that a winning bird resisted any attempt by his opponent to break off the encounter. Also the winner was clearly recognised and normally not subsequently challenged by the defeated bird. Fighting is therefore an effective method of settling site disputes.

Fighting and the Morphology of the Sexes.

Although females do not establish the site they quickly form a strong attachment to it, possibly as a result of pair formation (p.167) and will then share in its defence. In birds in general, shared defence of territory is associated with morphological similarity between the sexes, just as in territorial species in which one sex is more aggressive than the other, the more aggressive is usually more conspicuously coloured. This is usually the male but may be the female, as in the Red-necked Phalarope Phalaropus lobatus. In most colonial sea-birds the sexes look alike, although defence of territory is by no means always (if ever) equally shared. Male Kittiwakes, for example, usually do most of the territorial fighting (Cullen). It is not completely satisfactory to suggest that the similar appearance of the sexes confers equal valence (through common possession of

threat releasers) as a deterrent to intruders, since the sexes (and often individuals) readily recognise each other. This is true, for example, in the Black-headed Gull (Tinbergen 1956) and the Kittiwake (Cullen) and certainly for the Gannet. Therefore a female may be little more likely to deter an intruding male simply because she resembles a male. In any case since she is herself aggressive such resemblance would be of slight advantage in this connection. In fact, on occasions it would benefit the female to differ conspicuously, since during female : female fights the male is often mistakenly attacked by one of them, and this mistake may decide the issue against her. Nevertheless, at this stage, the morphological similarity may be assumed to be connected with shared defence of territory.

Threat Behaviour, (Plate 11).

Aggressive behaviour in the Gannet consists mainly of fighting, incipient overt aggression with jabbing, stereotyped menacing and bowing. Only the stereotyped form of threat behaviour, termed 'menacing', will be analysed in detail since it is the usual (and extremely common) form between established birds.

The other form (incipient aggression) is intermediate between fighting and stereotyped menacing and mostly occurs as high intensity agonistic behaviour between newly-established pairs or strong rivals. The bill is widely opened (Plate 11A) and the lower mandible twitched erratically. It is accompanied by strident aggression/fright calling and, unlike the stereotyped menacing, frequently results in beak gripping, and occurs mainly when more serious aggression is likely to follow.

Form of menacing. Gannets menace from a standing, squatting or incubating position

Plate 11. Threat behaviour.

A.

Stereotyped menacing between newly-established birds.

B.

Pair : single menacing. Note withdrawn position of single bird and head twist of near bird of pair.

C.

Pair : pair menacing. Near pair have re-directed their movement to the chick.

D.

Mild beak gripping between established neighbours.

(Plate 11). In balanced encounters the beak is opened and thrust, with a marked sideways twist, towards the opponent and then withdrawn. It is noticeable that the withdrawal is a 'pre-set' part of the behaviour, and does not depend on aggressive reaction from the bird at which it was directed. Although one bird initiates the menacing bout, the movements of the participants often synchronise. The beak is opened to varying degrees, but normally not to its widest extent, nor with twitching of the lower mandible. It is quite distinct from the rapid jabbing and darting of Shags or Guillemots, which appear less stereotyped than the Gannet's menacing. S. dactylatra also make rapid thrusts at each other with open bill (Cullen pers. comm.).

From both Dorward's and Cullen's (loc.cit.) descriptions of the apparently analagous threat behaviour in S. dactylatra it contains an element entirely lacking in the Gannet. The former combines a slow sideways head wagging with a rapid up and down bill movement (to use Dorward's vivid description "as though indicating a slow 'no' and a vigorous 'yes' at the same time"). This, however, normally characterises the more afraid of the two and seems akin to the 'withdrawn' menace of the Gannet (Plate 11B) when one bird is more afraid (e.g. a single menaced by a pair). The form of the movement resembles food-begging of the young.

Menacing between hostile birds, when judged to be intensive from knowledge of the situation, is associated with head-shaking, frequent touching of nest material, repeated pelican postures and bowing.

Motivation. The form of menacing, the situations which elicit it, and the actual attack which it may lead to (and with which it is closely associated in time) show that it is at least partly aggressively motivated.

Although clearly hostile

~~fully ritualised menacing and fierce fighting occur) it~~ acquires certain overtones during the course of co-existence with neighbours. Whilst any infringement of territorial rights between neighbours immediately elicits full threat behaviour, perfunctory menacing occurs on countless occasions, sometimes without visible cause, at very low intensity and without calling. Figure 26 shows the seasonal incidence of menacing, estimated by systematic, five-minute counts of its frequency among two standard groups of 20 nests. The higher incidence towards the beginning and end of the season should be noted. It corresponds with a similar trend in bowing and is probably due to the relatively high level of external attack-eliciting stimuli at these times (wandering birds, prospectors etc.).

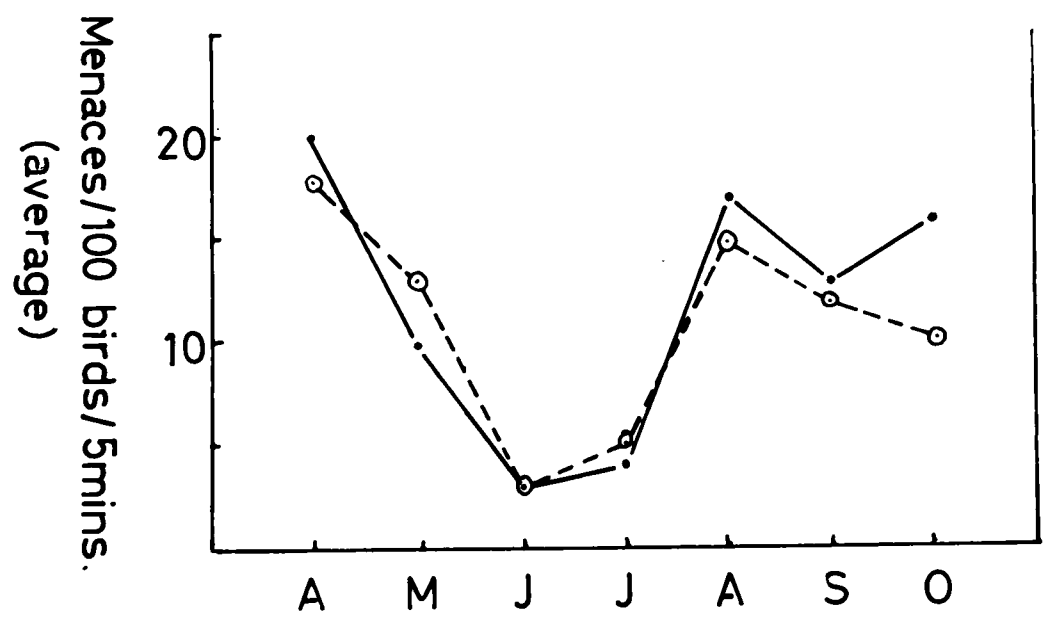


Figure 26. Frequency of threat behaviour (menacing) throughout the season.

To give an idea of the frequency of menaces the above data can be arranged to show that every bird, during the time spent singly on the nest throughout the entire season, menaces a neighbour more than once per hour during the hours of daylight. Pairs menaced pairs about half as frequently, but when they did so both birds menaced their own sex most, as one would expect from the nature of the

pair relationship. Singles were more likely to be menaced by pairs (if adjacent) than by other singles, and were also more likely to be seized.

Function. Menacing is an integral part of the behaviour ~~syndrome~~ ensuring spacing-out within the colony by maintaining inter-nest distances. The most intense and prolonged (half an hour or more) menacing bouts with calling occur when site boundaries are least well-defined, soon after establishment. It may, in extreme cases, prohibit successful breeding by squeezed in pairs, and in at least one case, hostility by neighbours drove away an old male and his newly-acquired female. The site has remained unoccupied since May 1961. Although perhaps largely responsible for the characteristic regularity of dispersion within breeding groups on flatter ground, each nest being just beyond practicable jabbing distance of the neighbours, inserted pairs, once accepted, may be tolerated at distances allowing the wing tip or tail of one actually to touch the other in certain positions. This could be important in the event of site shortage.

I believe (without having figures) that menacing is far commoner among flattish-ground than cliff-ledge nesters, probably because cliff ledges do not usually allow the same kind of contiguity (very broad ledges or outcrops must here be regarded as flat ground). It would be interesting to compare the incidence of different behaviour patterns between the two categories to trace the evolution of any intra-specific behaviour differences in response to habitat change.

Bowing.

One of the commonest and most conspicuous displays performed by the Gannet is a complex movement for which 'bowing' is a good descriptive term (this is the "wing-bow" of Perry (1948) and "curtsey" of Lockley (1954) and Warham (1958)). Since this movement plays an important part in the Gannet's social behaviour it will be described in detail

under the headings : form; sexual dimorphism; frequency; motivation; function and derivation.

Form. (Plate 12 and Fig. 27) A full, typical male bow is a strongly stereotyped movement taking 4 - 12 seconds, and performed from a standing position with neck slightly elongated, but not stretched as in the'anxious' long-necked position. The first movement is usually a sideways head shake (but may be the 'dip') starting slowly and increasing in speed and amplitude. The bill is inclined slightly downwards or, more rarely, horizontally. After 1 - 5 head shakes the head and thorax are bowed forwards and downwards. Sometimes the movement is a smooth sweep alongside either wing or foot (occasionally between the latter) at others it is slower and more hesitant*. The pelican posture (p.163) usually occurs on the same side as the bow. There is often an elevation of the tail (probably for balancing) which may be cocked vertically. Between each forward movement, of which there are three or four (termed 'dips' to distinguish them from the entire performance or 'bow') the head is raised and shaken rapidly from side to side.

During the bow the wings are held away from the body, either widely spread like a Cormorant's 'wing-drying', or merely loose at the shoulders. In a common intermediate position the wing tips are crossed and the carpal joints held well away from the body, the bird, from behind, resembling an equilateral triangle. As the bow proceeds the wings often open more widely. The normal wings-out position is adopted, in contrast to the special 'wings-busked' position peculiar to sky-pointing (see Plate 23).

After the final dip the wings are folded and the bird presses its bill tip tightly against its upper breast in a pelican position (65% of all bows were followed by a

* 44% dipped to the right and 56% to the left, 669 recorded. This difference is highly significant (p=.003) and completely puzzling. Warham (1958) also noticed this tendency, though does not give actual figures.

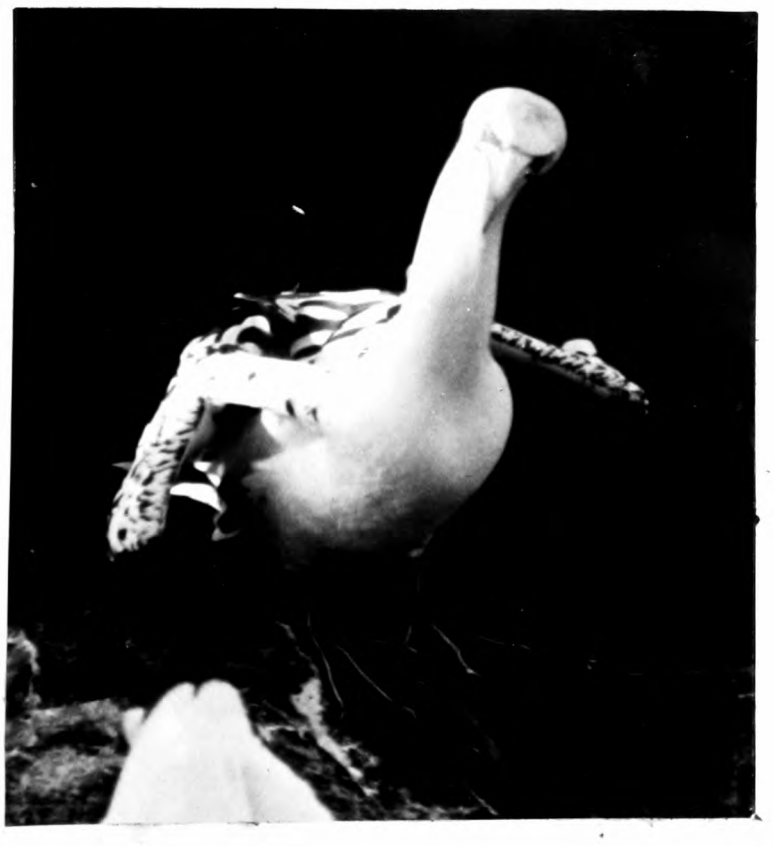
Plate 12 Bowing - a site-ownership display.

A.

Male performing head shake component of bow.
Note neighbouring bird almost in pelican posture.

B.

Male performing dip component of bow. Note neighbour in full pelican posture but looking at bowing bird.



C.

Three year-old male bowing.

pelican posture Fig. 32). Usually the bill tip lies to the same side of the median line as the dips (Table 33) and sometimes even points to the wing-bow. The pelican posture is held for two to four seconds, then gradually relaxed. Finally the tail may be shaken from side to side (24% of 372 cases). Often several bows are given in quick succession (27 in 27 minutes was the maximum recorded for one individual). During the bow the Gannet calls loudly with the typical 'urrah urrah', each bow containing between 10 to 30 separate calls.

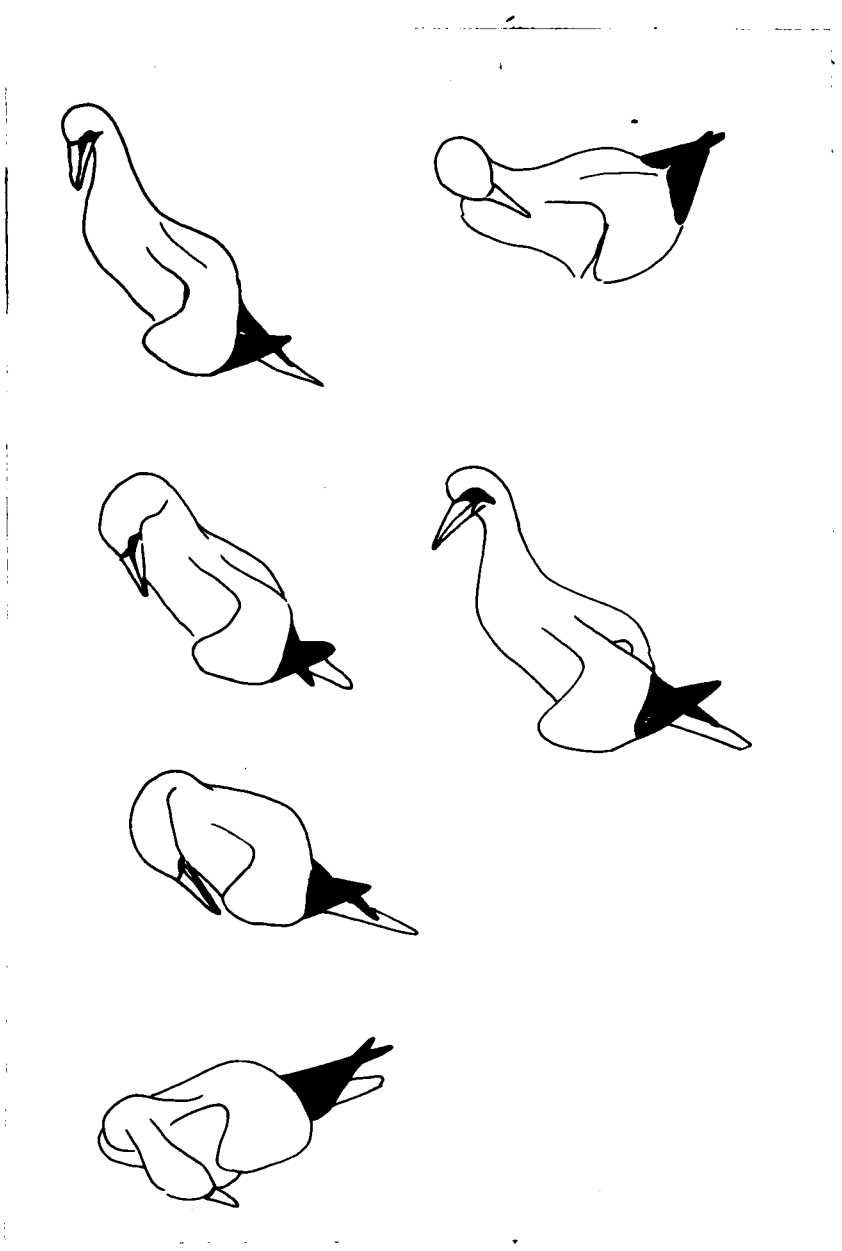


Figure 27. Sequence of bowing positions.

To analyse bowing into its components I counted the number of dips, classified four positions according to the extent of wing-opening, timed the duration of the pelican posture and divided performances into 'co-ordinated' and 'un-co-ordinated' (a measure of muscular control) in terms of jerkiness or smoothness, hesttancy or assurance, which was

useful in distinguishing between the bows of males varying in status).

TABLE 33. Correlation between orientation of dips and pelican posture (416 cases).

	%
Pelican posture and dips both to same side	65.9
Pelican posture central (but dips right or left)	27.6
Pelican posture opposite side to dips	6.5

Note : These figures refer to male bows, Female bows show similar trends.

Finally, it was usually possible to classify bows as either evoked by some external stimulus, such as a threat or a neighbour's bow, or performed without any obvious external stimuli, when for the purpose of this classification, it could be considered 'endogenous'.

Circumstantial evidence suggests that Gannets bow in the complete absence of external social stimuli. Subliminal stimuli may nearly always be suspected but seem highly unlikely when isolated males bowed for no obvious reason. Admittedly distant flying birds were in view, but nesting Gannets are always totally indifferent to these. Even more convincing evidence for spontaneous bowing came from sleeping birds, head in scapulars, which awoke, bowed and went back to sleep.

Correlation between bow components. These remarks apply to male and female bows. Sex differences will be discussed separately. The number of dips per bow (perhaps the most obvious 'intensity' measure) was correlated with :-

(a) the pelican posture - bows with most dips are most likely to have a pelican posture and one of longer duration (Fig. 28).

(b) wing position - bows with a single dip are often performed with wings closed, whereas those with three or four show higher wing positions (Fig. 29).

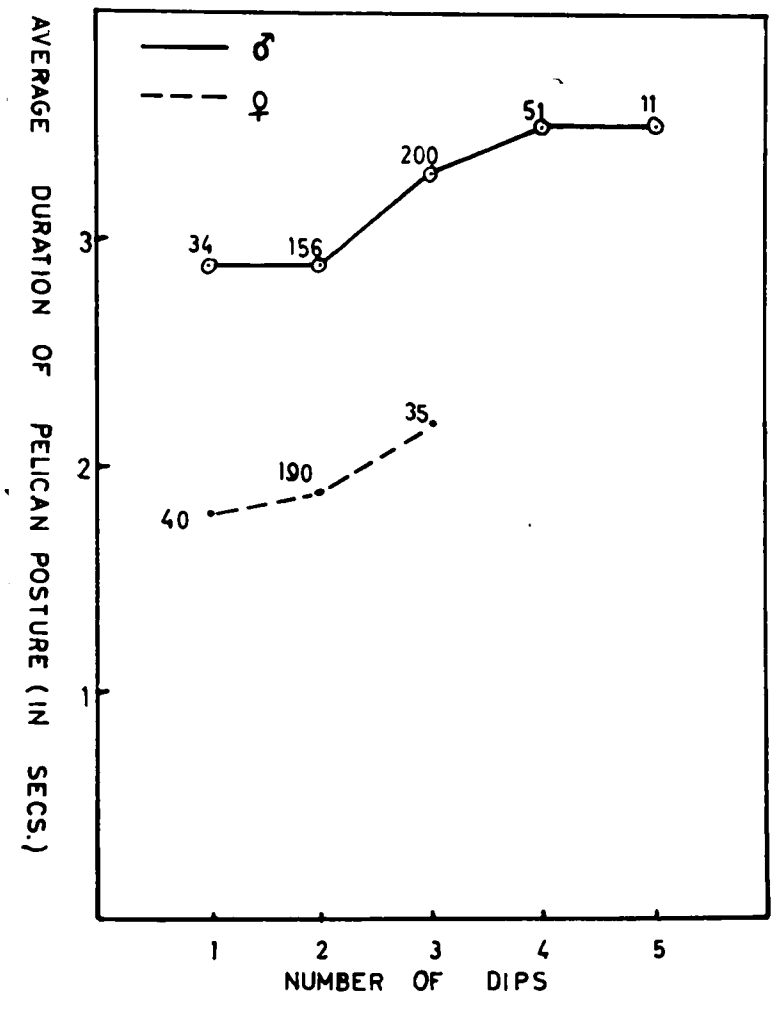


Figure 28. Correlation, in male and female, between the number of dips in a bow and the average duration of the pelican posture which follows. Females show shorter pelican postures. Numbers above points show sample size.

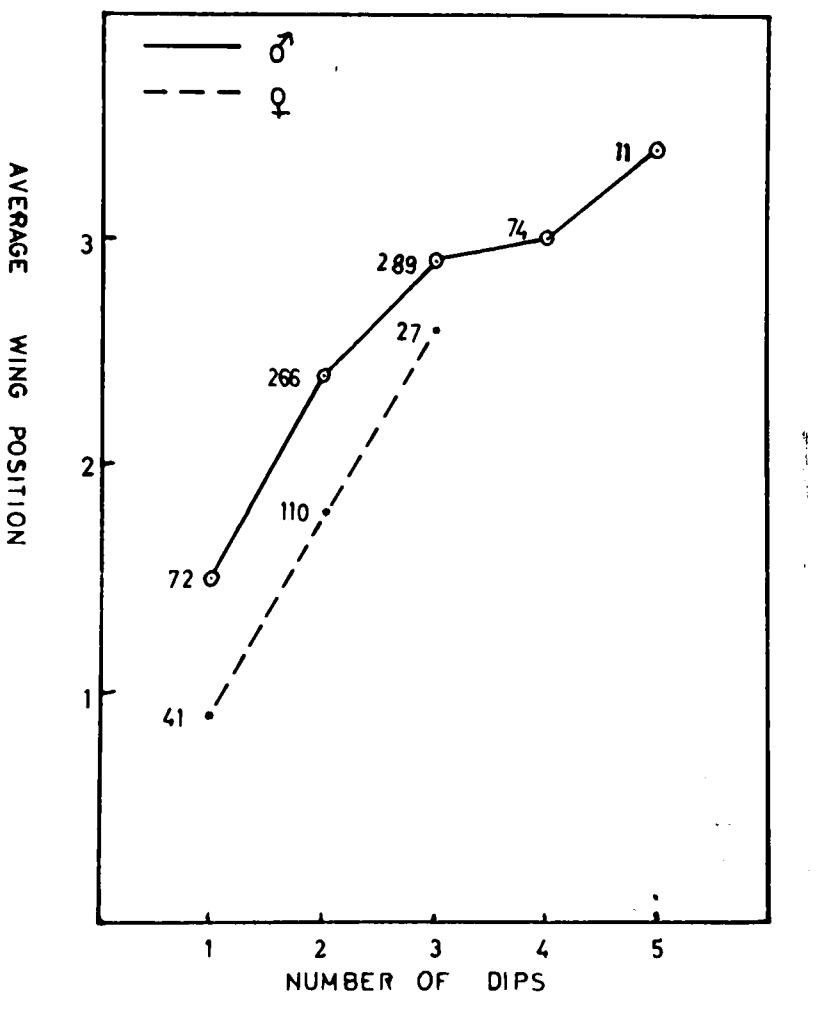


Figure 29. Correlation, in male and female, between the number of dips in a bow and the extent to which wings are held out during the bow. This is expressed by averaging the 4 discrete wing positions of all bows containing 1,2,3,4 or 5 dips.

(c) co-ordination - bows containing one or two dips tend to be more unco-ordinated than those with three, four or five dips (Table 34).

TABLE 34. Correlation between the number of dips and co-ordination.

	Number of dips				
	1	2	3	4	5
Co-ordinated	6	65	115	51	10
unco-ordinated	12	38	23	1	0

The number of dips, duration of pelican posture, wing position and degree of co-ordination are therefore linked, and collectively correspond to some ~~underlying~~ in-scale. tensity ~~in bowing motivation~~.

Further study is required to elucidate the factors which produce higher or lower bowing motivation at a given moment (seasonal variation can be explained to some extent), and also to account for independent variation in these components.

Individual variation in form. Certain individuals showed consistent and permanent peculiarities in some components of the bow. Male 501 had a high-flinging, rapid head shake; male 543 had a lazy bow in which the wings were only a little open and the number of dips never exceeded two; others were distinguished by stance, whilst speed, direction and extent of dip, movement of wings and silent bowing were other variants. Even within a stereotyped behaviour pattern, therefore, one finds individual differences, presumably heritable, which could form material for selective modification comparable to that which has produced the bow in its present form.

Sexual 'di-ethism'. There are clear measurable differences between male and female bows in the number of dips (Fig. 30), the wing position

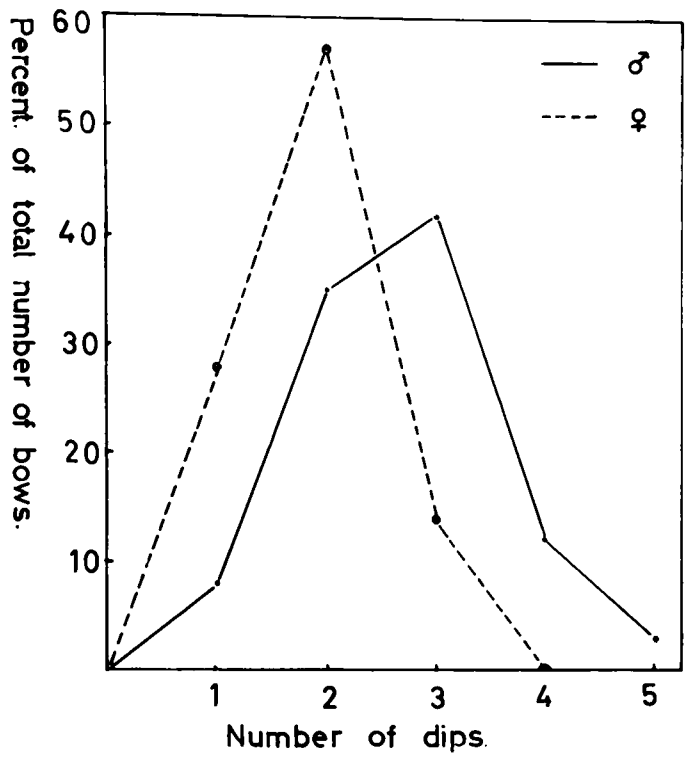


Figure 30. Differences between sexes in the number of dips per bow, male bows containing most.

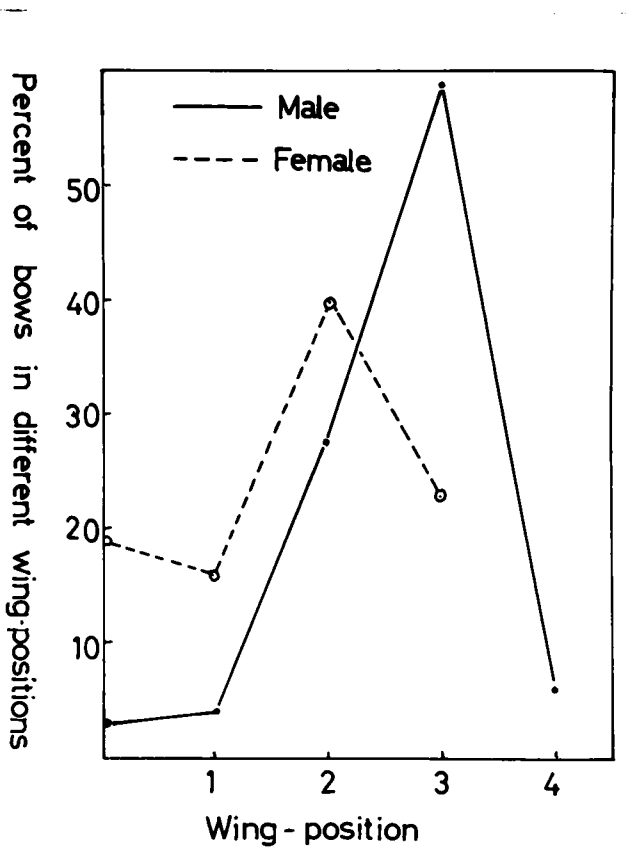


Figure 31. Differences between sexes in the wing position during bowing. Males bow more with wings widespread.

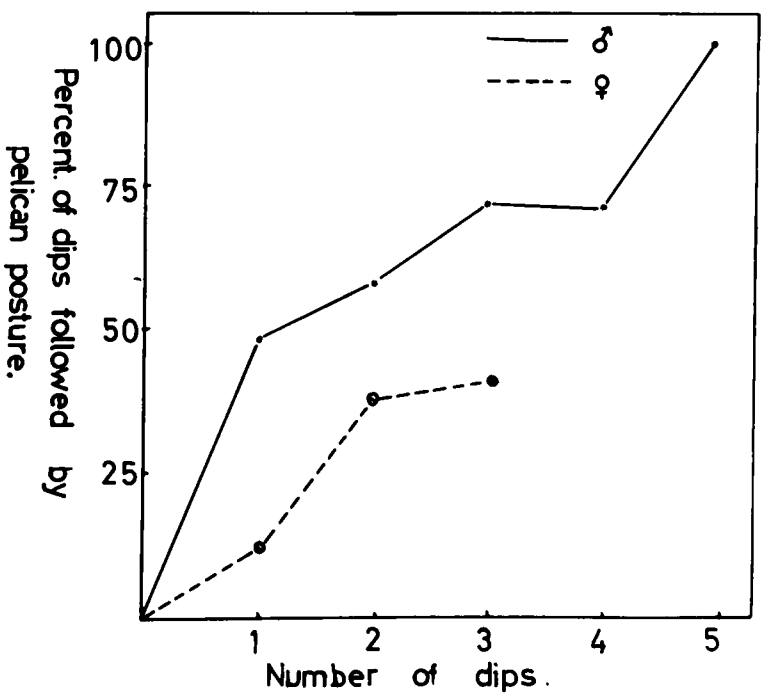


Figure 32. Differences between sexes in the percentage of bows followed by pelican postures. Males follow bowing by the pelican posture more often than do females.

(Fig. 31), and the pelican posture (Fig. 32). Female bows are also less co-ordinated than male bows.

The correlations between various features of the bow already described hold for both male and female. One may summarise the differences between the bowing of the sexes by saying that female bows are of lower intensity - resembling the incipient bows of club males. Females also bow less frequently.

Frequency.

Seasonal. Figure 33 illustrates seasonal changes in bowing, and shows that the frequency gradually wanes after first return to the site, even before the main egg-laying period, though it becomes less frequent during incubation. In addition Figure 34 shows that the basic seasonal pattern is reproducible from two small, separate groups. However, variations do occur and can be explained as differences due to position (the far circle usually had more birds flying low over it, etc.).

By comparing the incidence of bowing among birds with and without eggs, though otherwise similar, it can be shown that 'broodiness' inhibits bowing (Table 35). After hatching bowing increases, but only gradually, probably due to the difficulty of bowing whilst brooding a small chick. However, birds with infertile eggs show a rise in bowing as the season progresses, indicating an internal change (i.e. drop in broodiness or rise in bowing motivation, or both) despite the continued presence of the egg.

The gradual increase in bowing frequency following the incubation-low corresponds with a comparable increase in threat behaviour (see Fig. 26) and the length of mutual fencing bouts (see Table 39). These latter measures suggest a rise in aggression which, towards the end of the season, could be correlated first with a change in the external stimulus situation (presence of large chick perhaps, or

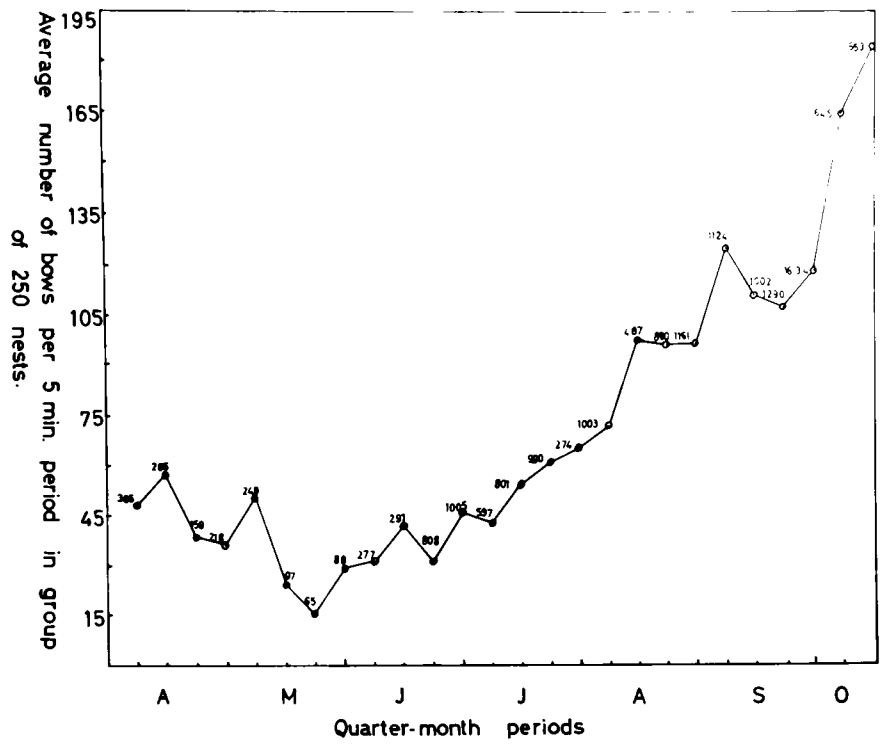


Figure 33. Seasonal pattern of bowing in a group of about 250 nests (the observation colony) measured by 300 five-minute counts. Numbers above points are the total bows averaged to obtain the point.

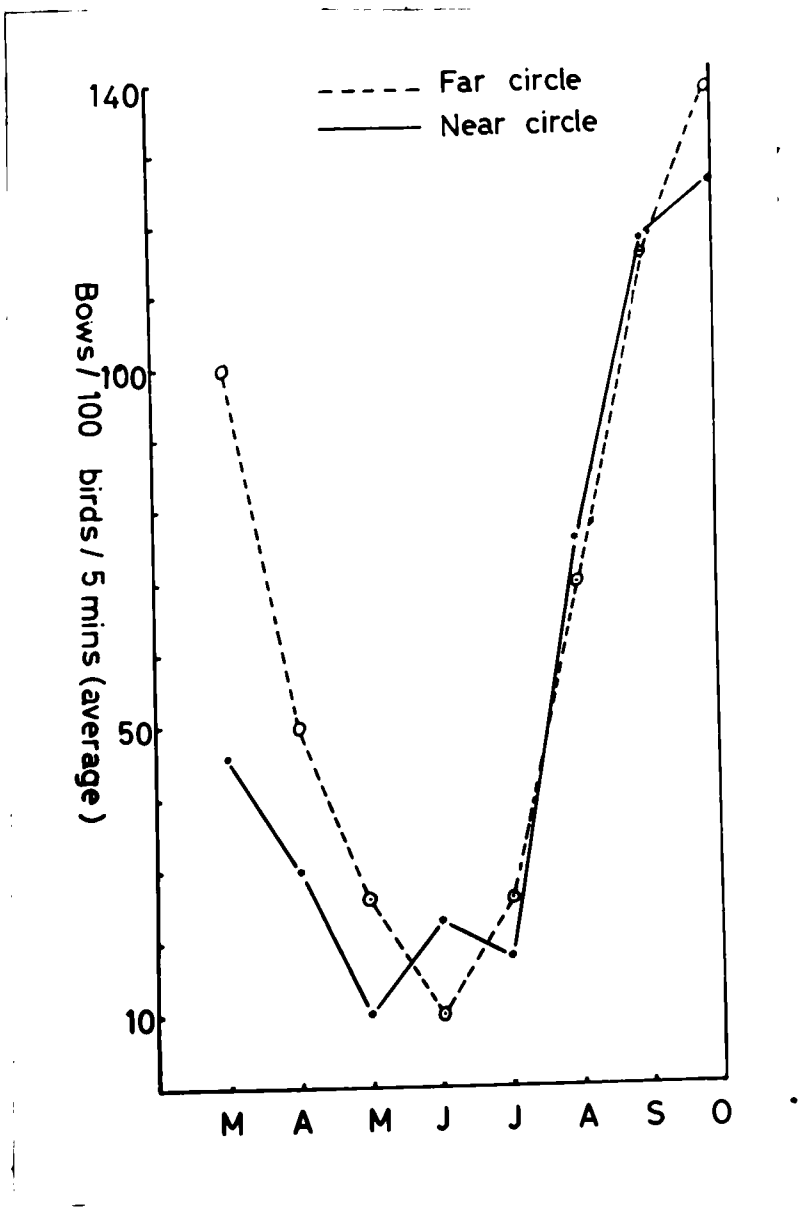


Figure 34. Seasonal pattern of bowing measured in two separate groups of equal size.

increased trespassing of some adults) and also with a rise in the internal contribution to aggressive behaviour, perhaps the result of decreasing inhibition of aggression by sex-motivation and/or broodiness.

TABLE 35. Comparison of bowing frequency (as ratios) in birds of differing status.

		Status			
			Experienced birds with :-		
Month	No. of bows involved	Newly-established	No egg	Egg	Chick
May	84	12.0	-	1.0	-
June	924	6.4	5.0	1.0	-
July	780	1.8	2.64	1.0	0.92
August	644	1.6	3.7	-	1.0

Note : Ratios were obtained by measuring the frequencies of bowing in the different categories and, knowing the number of individuals in each category, bows were then related to a standard frequency of 1 for birds with eggs (or, in August, with chicks). Because of of the way the ratios were calculated differences between months for a particular category can be misleading.

However, for some unknown reason, the increase in bowing towards the end of the season goes beyond its early season level. This late-season exhibition of territorial behaviour would seem a highly unusual reversal of the normal tendency in most species to show a rapid decline, even before the culmination of breeding and certainly soon after. Thus Shags were not noted to show aggressive behaviour after the chicks fledged (Snow 1963) and Kittiwakes desert the ledges soon after the chicks become independent. In the Gannet this late peak cannot be accounted for by any combination of external stimuli, since there are no significant differences between the March and October situations, except the presence of a few chick stragglers in the latter. The prolonged post-breeding stay at the site is not a quiescent period but a very active one.

Diurnal. Unlike the ~~epideictic (Wynne-Edwards 1962)~~ displays and songs of many species (passerines, 'lek' species, etc.) Gannet displays do not show marked activity peaks in the post-dawn hours. Activity is slightly lower in the evening, but at all periods arrivals and departures maintain the tempo of activity (Fig. 35) and certain late-evening counts were very high (though this is not revealed in the figure). Since prospecting females and site-establishing males are present in and around the colony all day it is not surprising that the ownership display occurs throughout. The morning and late-evening increases which do occur are correlated with a marked increase in the number of arriving and departing birds at these times (see Table 47). Very hot weather sometimes reduces the mid-day level of activity.

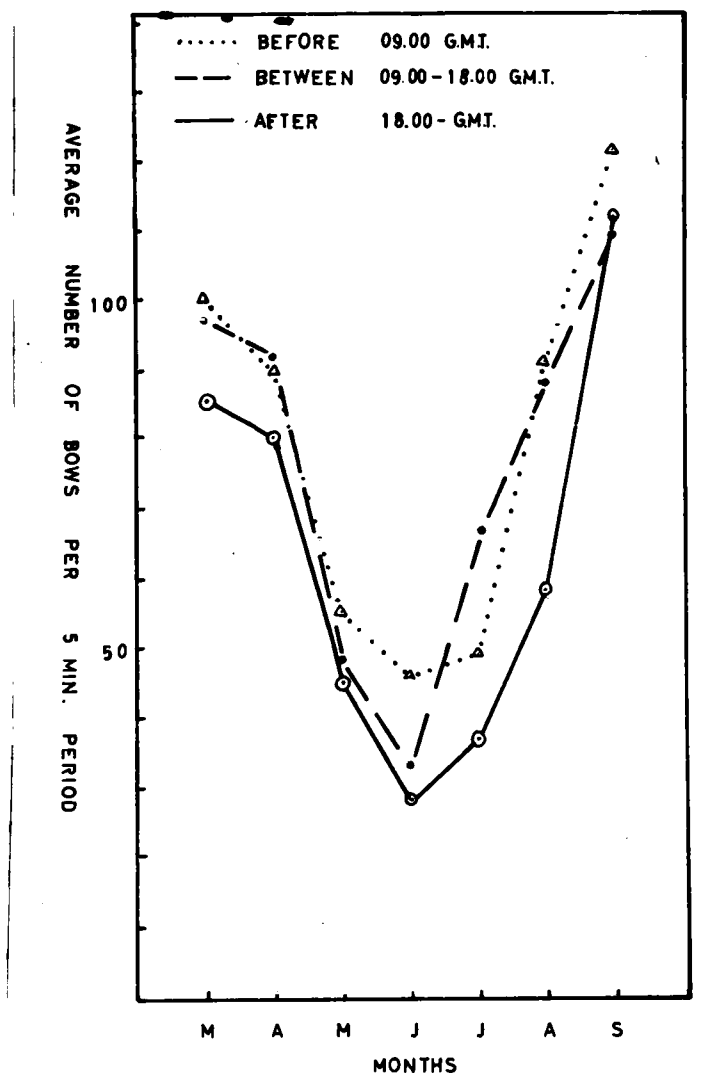


Figure 35. Diurnal periodicity in bowing activity. measured as for Figure 33.

Status. Two sources of observations reveal something about the effects of status (and its associated

conditions) on bowing: First the bowing activity of different categories of birds within the observation colony (see Table 35), and second, that of males in the clubs. In the former interpretation is complicated by position effects: newly-established males, for example, are usually in the fringe of the colony and receive less than average social stimulation. Such effects are, in practice, extremely difficult to assess quantitatively. Nevertheless the higher frequency of bowing by newly-established males in May and June is shown, despite, if anything, fewer surrounding birds. Stronger late-season activity of experienced birds without eggs, compared with newly-established birds, is also indicated.

Club birds settle temporarily at a number of places on the Rock and show incipient breeding activity (p.254). Males perform a female-type bow, with fewer dips, wings out less, a shorter pelican posture and less co-ordination than established males. Since the sexual and territorial behaviour of these males is highly transitory (the places where they alight are dictated by wind direction) it is not surprising to find a territorial display less intense than in established site-owners.

Motivation. The form of a movement may indicate motivation e.g. when obviously related to attack, fleeing, etc.. Other measures include the kind of behaviour with which it is associated, either over a long period or closely. (Tinbergen 1959 discusses the criteria to be used in assessing the kinds of motivation involved in agonistic and pair formation displays). Evidence will be given here for considering bowing to be aggressively motivated display in which a fear component and a 'site effect' are also involved.

Aggressive.

(a) Form. Although bowing does not immediately look like a hostile act, it closely resembles nest-bitting (to be discussed)

which is certainly aggressive.

(b) External factors eliciting bowing. Bowing is the response of a site owner to territorial infringement. Thus the frequency of bowing increases tenfold when non-breeding birds fly over a nesting group, especially if some crash in down-draughts. Even birds landing on their own sites cause an increase in bowing in the neighbourhood - presumably a re-iteration of ownership elicited by the approach of another bird and socially induced by the bowing of others.

(c) Long-term association with overt aggression. The seasonal pattern of bowing follows that for threat behaviour (see Fig. 26). It is usually acepted (see, for example, Andrew 1963) that acts occurring together share some of the same causal factors, although this correlation must be made with care. In the case of two or more behaviour patterns varying in the same way throughout a season, parallel long-term changes in motivation are probably involved.

When plotted against each other over the season, bowing and menacing show an evident relationship, which does not, however, show on a short-term basis. Plotting the frequency of bowing and menacing within the same five-minute sample periods, over a month, gives a wide scatter (Fig. 36).

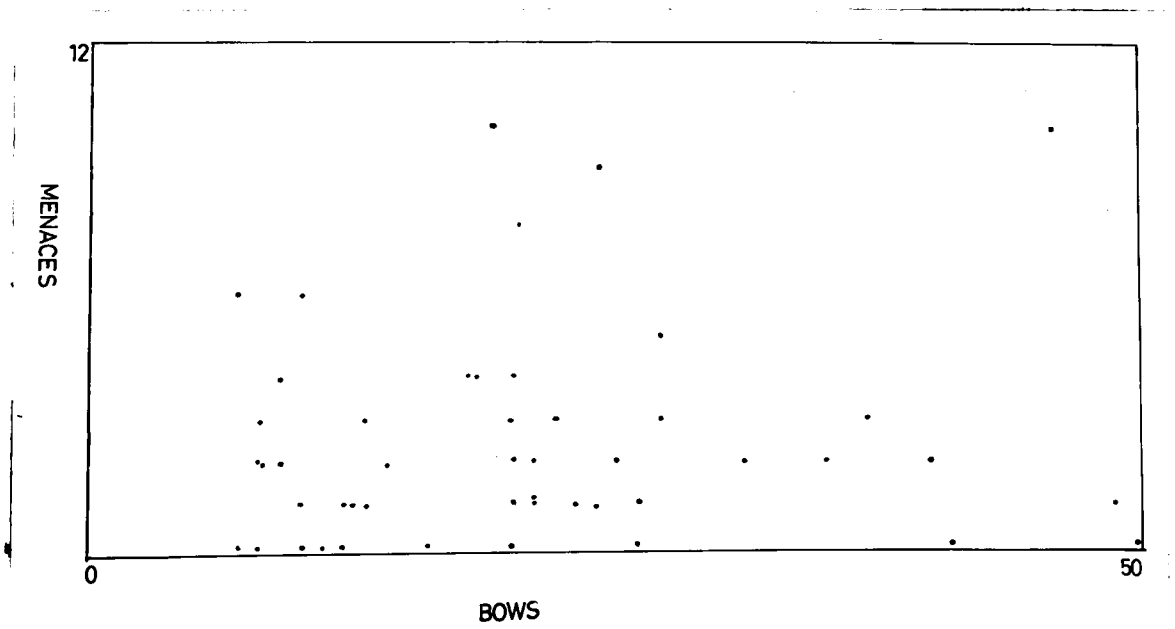


Figure 36. The frequency of bowing and menacing in the same five-minute check periods, within a standard group, during one month (September), showing the lack of short-term correlation.

This however fits with the direct observation that the stimuli eliciting the two behaviour patterns are not the same; for example, a bird arriving two nests away may cause bowing from neighbours but not menacing.

When bowing is most frequent mutual fencing bouts are longest; this length is correlated with the amount of aggression between the sexes (p.179).

However, one cannot necessarily conclude that when bowing is low (e.g. during incubation) aggression has declined. The overt expression of a tendency (hunger, fear aggression, sex, etc.) reflects the strength of the readiness to respond as well as the immediate external stimulus situation and this is further complicated by the interaction of other ~~drive systems~~ motivation Factors. Sevenster (1962) for example, clearly showed that the aggression of a male Stickleback Gasterosteus aculeatus to other males may remain high, or even rise, at the same time as his aggression towards a female declines. These points may make it unnecessary to invoke complicated seasonal fluctuations in the internal motivation causing bowing.

(d) Short-term correlation with aggression. Bowing is highly predictable in certain situations closely associated with overt aggression, which it accompanies or follows rather than precedes. After intense fights (see below) the winner bows frequently; bowing is interspersed between menacing and jabbing; it often accompanies overt attacks on chicks; males often bow after alighting at their unguarded nest-sites, a situation in which they commonly first perform aggressive nest-biting. Also, if the female is on guard, the male bites her fiercely before taking part in the meeting ceremony, mutual fencing (itself

probably derived from bowing).

After a fight only the winner, now occupying the disputed site, bows, but if the contestants are neighbours both with sites of their own and ready to continue the fight, both will bow. Occasionally two males fight each other to exhaustion and both leave the disputed site, in which case neither bow. Thus without aggressiveness and/or the nest site with which it is associated, Gannets do not bow. The F.A.M. theory of the motivation of displays may be inadequate to explain the site-factor in bowing.

The male Gannet is more aggressive than the female (he also has a stronger site-attachment) and accordingly bows more often (3.5 times as often in a sample of 1,068 bows).

The increased frequency of bows after fighting does not merely reflect a general arousal of all behaviour. Other behaviour patterns (except nest-touching and aggressive nest-biting, from which bowing is probably derived) are absent immediately after a fight and only reappear as bowing wanes.

Fear. In many animals aggressive displays are also thought to necessarily involve some element of fear or escape. ~~motivation~~. In the Gannet matched antagonists consistently bow away from each other, which probably indicates some avoidance of a potentially dangerous opponent.

Bowing by a rival on a disputed site is very likely to elicit strong attack from the opponent, and it would be hardly surprising if a fear element should form part of the motivation of such bows. Many fights are started or renewed in response to the challenge of disputed ownership, signalled by bowing. We might therefore look for a component most exaggerated when occurring in response to extreme fear and perhaps reflecting escape or appeasement behaviour in some form.

The pelican posture is just such a regular and conspicuous component of bowing. Often when a pelican posture

occurs by itself it does so most intensively in frightened birds. Its position at the end of bowing therefore fits with expectation, since at that point the bowing bird might be attacked. This view also accords with the observation that 'stimulated' bows incorporate pelican postures more often than 'endogenous' bows (70% as against 57% in the male, 34% as against 21% in the female). Further the pelican postures were of longer duration when following stimulated bows.

Finally 'stimulated' bows were more likely to be unco-ordinated - a feature which might be expected from behaviour performed under some stress (here probably fearful rather than anything else).

It must be admitted that there are inconsistencies about this fear component as a usual part of bowing. It will be remembered that one of the characteristics of high-intensity bows mentioned earlier was that they are particularly likely to be followed by a pelican posture and that these are of relatively long duration, although there is no obvious sign that such birds are frightened. Probably, as in some other displays, certain elements which originally occurred as occasional features under certain 'critical' conditions have now become 'frozen in' to the more stereotyped form of the display, thereby ceasing to be a sensitive indication of motivational state.

The pelican posture, therefore, varies with situation, and precisely those situations most likely to involve the bowing bird in overt aggression elicit 'stress-type' bowing with the most marked pelican posture. If its function is to appease, this seems reasonable.

Function of bowing as a site ownership display.

Field observations often provide circumstantial evidence for the function of displays, but direct proof is seldom possible.

Bowing is one of the Gannet's predictable responses to certain recurrent situations, and a mass of indirect evidence suggests that it functions as an ownership display of the 'distance-evoking' type, to repel potential trespassers. Some of the main points may be reiterated. Bowing is closely linked with the site and with infringement by neighbours (birds 'dashing' to the edge of the group, wandering birds or even flying birds which crash in downdraughts). Indeed, (apart from obvious exceptions) bowing is the only behaviour pattern entirely restricted to the site. The chance observation of an unusual incident confirmed site and bowing relationship in a striking way. At sea an adult alighted on a piece of wood and bowed several times. Two or three others attempted to displace it - one succeeded and immediately bowed. Yet the usual behaviour after alighting at sea is rotary head shaking - never bowing. He, in turn was deposed and the new'owner'bowed. The piece of wood was clearly treated as a temporary territory.

Bowing is most marked where there are strong ownership ties plus the need to display ownership. Thus males do it more than females, and especially males establishing a site when there is more liklihood of challenge. Thus males newly establishing themselves bow more than males re-establishing themselves on sites held previously. Also, those periods when most trespassing occurs (early and late in the season when birds are taking advantage of absentees to steal nest material) are precisely when bowing is most frequent.

Turning to the effect of bowing on other individuals, we find that the necessary choice situations cannot be observed except by rare chance. The simple question "which of two birds, one bowing and the other not, is avoided by a third ?" is meaningless in the situation as it occurs. All birds within the breeding colony are 'avoided' by all others except their mate and rivals. In the latter case

bowing elicits attack rather than avoidance. Yet we would not say that bowing functions in attracting rivals. Rather it is because the rival 'recognises' the display that he attacks and disputes the other's claim. In much the same way, some song birds will permit a rival on their territory so long as he does not make some provocative gesture like singing. This attack-eliciting property of bowing in a balanced aggressive situation is very striking and leaves no doubt that the bowing has effected a response, of a kind entirely to be expected where both are 'rightful' owners. Only in unequal situations should one expect to find that bowing repels the inferior bird.

The above evidence supports the view that bowing is connected with establishment and defence of site (or territory). In this respect it is equivalent to the agonistic displays of many passerines, gulls, waders, etc.. A difference of note, however, is that in many passerines, gulls (the Kittiwake is particularly comparable because of its colonial and cliff nesting habits) and even the Red-footed Booby (Verner 1961) the 'song' or ownership display is also the advertising display, whereas in the Gannet the two are quite distinct, although the advertising display is a modified form of bowing (p. 167). However, other members of the Sulidae appear to lack a specific and frequently performed ownership display, having nothing comparable to the Gannet's bowing. Male S. dactylatra and S. leucogaster, for example, (Dorward pers. comm.) do not perform any specific behaviour when alone on the site, though they will of course react to females and intruders. This lack may be correlated with relatively weaker territorial behaviour in the boobies.

To sum up, the situation in which bowing occurs, the conditions which increase its frequency and the effect on other birds may be consistently interpreted to show that it functions in signifying site ownership and preventing site

usurpation. It is typical territorial behaviour (see Hinde 1956).

Derivation. Tinbergen (1952,1959) has discussed in detail the ways in which displays may be derived from simple behaviour patterns (intention movements, displacement reactions, re-directed activity, etc.) which may then become exaggerated or changed. The study of derived activities within a group is valuable in showing how one species may modify a derived component in one direction whilst another modifies it in another - both under the influence of different selection pressures arising from their way of life. The Sulidae are excellent material for such an investigation, and the bow of the Gannet is a particularly interesting example since it is a composite display of various ~~semi-independent~~ components, derived from different sources and changed in form (and apparently motivation also) to varying extents.

Head shake. This part of the bow is similar to the ordinary sideways head shake (see p. 240) and probably derived from it. After displacement of an intruder, when the dip becomes aggressive nest-biting, head shaking is often far more vigorous becoming a head flinging movement like that used to dispose of nest debris. Thus the situation determines the type of dip and the stimuli resulting from this determine the type of head shake. This interaction of stimuli may be compared with the aggressive grass-pulling of Herring Gulls passing into nest-building. It could clearly form one of the steps in the progressive ~~ritualisation~~ schematisation and ~~emancipation~~ of a movement later to become fully stylised as part of a complex display.

Dip. This conspicuous movement is probably derived from nest touching (or biting), which, according to Van Tets (1961), is found in many Pelecaniformes, and also in Herons, as an after-landing behaviour pattern. Apart from similarity

in form between the dip and bending to touch nest material (which is any case is not much greater than between dipping and bending the head to preen the flanks) I base my conclusion on the following points :-

(a) After landing on its empty site the Gannet performs a nest touching or biting movement (see p.196 for distinction). This passes uninterruptedly into normal bowing except that subsequent dips may also include this nest-biting feature. The transition from nest-biting, to dipping with nest-biting, to ordinary bowing suggests the progressive stylisation which may have occurred in evolution. Bowing after landing (announcing ownership) and bowing after displacing an intruder (evicting a rival) are the most predictable and probably the phylogenetically oldest bowing situations. In both, bowing involves the touching (or biting) of nest material. Although the highly stylised form of 'ordinary' bowing includes dipping <u>without</u> touching nest material, it seems justifiable to conclude that the dips are homologous with those of the primary situations.

(b) Further association between bowing and touching (or biting) nest material is that both occur in aggressive situations. Also the touching of nest material is often part of the dip. In fact, birds bowing on bare rock sometimes go through the motions of handling nest material.

It is also possible that postural facilitation plays a part in bowing. At the end of a dip the bird is in the right position for handling nest material, which could therefore occur as a 'transitional activity' (Lind 1959). Alternatively when bending down to handle nest material the Gannet brings itself into a similar position to one stage of the dipping movement, which could then trigger off the rest of the bowing sequence. No doubt both these alternatives happen on occasions, but/~~postural facilitation, rather than~~

but in most cases, the dipping movement does not result in the handling of nest material, nor does the handling of nest material usually trigger off bowing.

Pelican posture. All Gannet appeasement postures probably reflect the fact that the bill is the only weapon of attack. Thus of the four available methods which a Gannet could use to remove its beak from the attack position (pressing it into the chest, pointing it vertically upwards, turning it to one side and withdrawing the whole head onto the back) the first three are commonly used and the last-named is used occasionally.

The form of the pelican posture (Plate 13) strongly resembles chick beak-hiding, and the two postures probably share common causal factors, though occurring at different times in life.

When attacked a chick usually hides its beak by tucking it medially beneath its body, at the same time crouching or lying (S. dactylatra does exactly the same, Dorward, Plate 8B.). This is the first (ontogenetically), and the most extreme, appeasement posture which the Gannet ever performs.

The adult pelican posture, which is not shown by the chick, differs in form from chick beak-hiding mainly in degree, since it is performed from an upright position and the head is not bent so far beneath the body. Whilst it is possible that the adult pelican posture may be derived from the chick beak-hiding, I cannot, of course, show this conclusively. The difference in form between the two is associated with a difference in the degree of aggression. Adults in the pelican posture are often partly aggressively motivated and in a position to defend themselves. Chicks, on the other hand, are completely non-aggressive to adults and, by beak-hiding, make themselves incapable of self-

defence. Evidence for the derivation of the pelican posture from beak-hiding would not be sufficient to prove that the pelican posture was ritualised. Although it occurs as part of the bow (which is ritualised) it also occurs alone and it is not possible at the level of the present analysis to demonstrate its ritualisation in the latter circumstances. However, it is a stereotyped movement and probably, also, has a signal effect.

Facing-away differs from beak-hiding in that the head is turned sharply to one side and the position, though less upright than the pelican posture, is nevertheless a standing one.

The pelican posture and facing-away are absolutely distinct, differing in beak position and, radically, in context. Whilst facing-away is almost entirely confined to females responding to aggressive males, the pelican posture is used by both sexes in a variety of situations. The main advantage of the pelican posture seems to be that the performer can still scan his normal visual field from which the stimulus evoking his posture came - possibly a hostile neighbour or an intruder, etc.. He can therefore retaliate or withdraw as necessary. Both chick beak-hiding and female facing-away place the performer at a disadvantage in this respect, but since the chick is unable to defend itself and the female is strongly inhibited from doing so (p. 188) this is of no consequence. The question still arises : why has the female evolved a special appeasement posture instead of using the generalised pelican posture and it may be suggested that by so doing the beak is removed more effectively from the male. Chance's (1962) 'cut-off' theory might also be applied, but seems unnecessary.

Summary. Bowing is a mainly aggressive agonistic display, complex and highly stereotyped, whose function (as a signal) is to repel potential intruders. It

consists of certain movements which no longer require their original context, and are in that sense emancipated. On these criteria bowing may be considered ritualised. It signifies site-ownership and is performed by both sexes, but more frequently and intensively by males, who also have a stronger site attachment.

The Pelican Posture.

This has already been discussed as part of bowing. The following is an account of it in all other situations.

Form. (Plate 13) The bill tip is pressed into the upper breast, centrally or to one side, resembling the resting position of a Pelican Pelecanus pelecanus. This position may be held for 20 seconds or more before the bill is lifted slowly and carefully as though the bird were striving to avoid moving it suddenly. In some situations the slow bill-raising accompanies an equally slow turning away from an opponent. An obvious comparison is the deliberate foot-raising used when Gannets move in the sky-pointing position (p. 246). The same slow foot-raising sometimes occurs in conjunction with the pelican posture. In one aggressive encounter with a neighbour, a male withdrew in this extremely cautious manner, and when clear suddenly dashed back to his site and attacked his mate. When a Gannet moves in the pelican posture it does so slowly and with wings busked as in sky-pointing (p. 245). It never moves in a pelican posture with wings held out sideways, as, for example, in the extreme bow position. Nor does it run in a pelican posture, as S. dactylatra does (Dorward).

Motivation. Pelican postures occur regularly in most ambivalent agonistic situations, including those in which fear is stronger than aggression and vice versa

Aggressive situations. Pelican postures occur in the aggressive bird during and following aggression of male

to female (re-directed aggression, aggressive copulation, the new-pair situation, or the eviction of unwanted females) or of either sex to some other species (e.g. Herring Gull whose territory is invaded). In the first named examples the pelican posturing bird is almost purely aggressive.

Fear situations. Hostile behaviour from neighbours elicited in a variety of ways (landing badly, establishing a site among established pairs, blundering through the colony in an attempt to take-off) produces prolonged pelican postures from the birds threatened or attacked. A male landed in the fringe and performed a deep pelican posture; it was startled by a bird flying overhead, flinched and assumed a deeper pelican posture; it came out of the pelican posture, was menaced and assumed another deep pelican posture. This series of pelican posture reactions to threat stimuli is characteristic.

Conspicuously ambivalent situations. Whilst the above instances probably involve ambivalent motivation, a number of situations clearly evoking both fear and aggression also elicit the pelican posture. Thus it frequently occurs in evenly-matched aggressive encounters between site-establishing birds; in birds displacing intruders (with, in many cases, strong possibilities of resistance); in birds trespassing to attack a chick, or approach a threatening female. In all cases there is an obvious source of both fear and aggression. Birds landing on their empty sites are aggressive but also elicit threats. They show marked pelican postures, during which (as their conspicuous eye-movements show) they scan the neighbours. In all these situations it occurs whilst the bird is relatively safe from attack, not during it.

The pelican posture as an ambivalent agonistic behaviour pattern fits its occurrence, not only as an independent behaviour pattern, but also as part of the bow, where it was suggested to be partly fear-induced within a pre-

dominantly aggressive behaviour pattern (see especially its connection with 'stress'bowing p. 157).

In all the above examples the bird performing the pelican posture is therefore :- (a) mainly aggressive but at the same time trespassing and slightly afraid of retaliation, or(b) mainly afraid but attempting to aggressively maintain its site, or (c) in an evenly balanced situation as in reciprocal menacing bouts.

Finally it may be added that neither site, mate, the near presence of any other Gannet nor the performance of any specific behaviour pattern are necessary to evoke a pelican posture. It may be suggested, however, that a specific direction, or perhaps, rate, of change in the proportions of contributory tendencies could be necessary, for it is precisely where considerable fluctuations in motivation are occurring that the pelican posture is performed.

Function. Since the pelican ppsture often occurs in situations 'requiring' an appeasement posture (and looks like one), the possibility that this is in fact its function should be considered.

The pelican posture (since most birds fight with their beaks) clearly fulfils one requirement of an appeasement posture - that the weapon of offense should be held in a position markedly different from that used in attack. It is therefore not surprising to find, for example, that the Kittiwake (Cullen) in which the bill sharply focuses attack, has convergently evolved a bill-hiding appeasement posture. Despite the fact that the pelican posture occurs in such a wide variety of situations, and ~~includes aggression besides fear~~ is ambivalently motivated, the most fitting interpretation of function is that it tends to reduce the liklihood of attack or retaliation, and is therefore an appeasement posture.

As usual in interpreting the function of a display

it is difficult to measure its efficacy. It often fails to prevent attack or retaliation and certainly does not stop attacks already launched; nor does it necessarily inhibit the performer from attacking. It is not possible with my data to decide whether the performer lowers its chances of eliciting hostile behaviour, but it may well do so. It clearly removes the bill as far away as possible from an antagonist whilst at the same time maintaining full readiness to retaliate. It seems (p. 138) unlikely to function in protecting the eyes and does not remove the potential attacker from the visual field of the bird performing the pelican posture (cf. Chance's 'cut-off' theory 1962).

It is, however, restricted to the above situations. Appeasement postures in other situations are completely different in form. It may be significant that these situations also lack the aggressive motivation, which may well be necessary to evoke the pelican posture.

Derivation. See p. 161.

Plate 13.

An extreme form of the pelican posture.

- 10 -

PAIR FORMATION AND RELATIONSHIP

Pair-formation may be studied from many angles. It is a phase in the bird's life during which variation may be particularly subject to critical selection pressure in a way not equally true for some other behaviour patterns. The incorporation of agonistic behaviour into courtship displays reflects just one of the delicate adaptive compromises which must be achieved between aggression towards intruders and acceptance of potential partners. The subtle differences between the agonistic components occurring in different contexts in the Black-headed Gull are still being worked out (Tinbergen & Moynihan 1952; Moynihan 1955; Tinbergen 1959; Manley 1961). At the group level the Larids are perhaps the best known animals so far as adaptive differences in agonistic and pair-formation displays are concerned. Crook's (1962) fruitful study on pair-formation in weaver-birds shows how the process of contact and pair-bond development may be related to the bird's feeding habits, dispersion type and sexual or seasonal dimorphism. Many more such integrated and adaptively orientated studies of species-groups would be welcome. The Sulidae are excellent for comparative work, and already the relationship between the method of pair-formation, which will be described in this section, and differences in nesting habits suggests itself. From the literature and for reasons summarised on p.264 it appears that the Gannet (or perhaps the gannet super-species including capensis and serrator) is the most aggressive and densely-nesting member of a family in which this characteristic appears to vary in some way with the type of nest site and the density of the nesting group.

Male advertising. In many birds the same display functions as male ownership display and male advertising to attract females. Boobies, apparently

have an advertising display but no ownership display (Dorward; Verner 1961), whilst the Gannet has a male advertising display distinct from, though resembling, the ownership display. This rather surprising difference may be connected with the Gannet's very strong site attachment (Chapters 3 and 8).

The first stages of pair-formation, bringing about the meeting of the sexes, involve 'prospecting' by the female and 'advertising' by the male. As already mentioned meeting occurs only on the male's site, which fortunately allows the initial stages of pair-formation to be observed more readily than in most species (cf. the complicated aerial manoeuvres of terns worked out by Cullen). The process of site establishment has been described in detail in Chapter 8 and the account is now taken up with the description of male advertising.

Form. Gannet advertising (Plate 14) resembles partly inhibited bowing with the headshake exaggerated, the wings closed and the dip reduced to a slight downward movement of the head directed towards the female eliciting the response. The male does not take a step towards the female, though he makes slight reaching movements with lengthened neck. S. dactylatra, by contrast, wanders rather more prior to pair-formation and will move towards a female, rather like Gannet club males, which are also not tied to a fixed spot. However, even dactylatra shows a strong tendency to stay on one spot (Cullen pers. comm.).

Motivation. It has proved a useful ~~concept~~ in the analysis of displays to consider them produced by particular levels of arousal of fear, aggression ~~or~~ and sex motivation. In particular, the occurrence of hostile displays directed towards females now seems hardly surprising in territorial species in which the sexes look alike. Why this has not led to the development of distinctive plumage in the female is a problem briefly considered on p. 141 and in Appendix A. It

Plate 14 Pair formation.

A.

Prospecting females (or males looking for sites) fly over the colony scanning the ground for landing spots. Note depressed tail to increase drag.

B.

Sometimes male is hostile and forces female to leave site. Female usually faces away and is gripped by skin of head or neck. Note female is immature.

C.

Advertising male on right. Note the head shake and upright position. Wings closed and the aggressive dipping movement of the bow is inhibited.

must, however, be emphasised that the male can recognise females from a distance of several yards, despite similar plumage and the absence of obviously distinctive behaviour. Dorward also records male dactylatra displays to flying females. Here it is sufficient that a female Gannet elicits a form of aggression from the male (bowing but with the aggressive component reduced and the 'friendly' one exaggerated, see p. 242) and is often bitten when she joins him on the site. The male's aggression is strongly inhibited by sex motivation. Thus in many cases males copulate during the first meeting with the female and always mutual fence with her (a 'friendly' meeting ceremony, partly sex-motivated).

Function. A natural choice situation is often presented to the female, who has the opportunity to respond either to an advertising male or a male, equally near, who is not advertising. Thus from a total 74 cases in which females were advertised to in the fringe, 32% approached the male who was advertising rather than a nearby passive male, a further 41% displayed interest in the advertising male but did not approach and 27% ignored such a male. None approached a passive male. These figures therefore show that male advertising has a real effect in attracting females.

Female prospecting. The male advertising display is released mainly by young, unmated females who carry out special searching behaviour here called 'prospecting'. This behaviour, though impossible to follow continuously in the very early stages, may be reconstructed

from fragmentary observations and can be adequately followed in the critical stages.

Like territory-seeking males, prospecting females are mainly four or five year-olds, but tend to be younger than the males (see Table 10). They are not present at the Colony in large numbers until April; in February and early March unmated (bereaved) males may wait more than two weeks before acquiring a new female whereas later several have been known to visit one male during a few hours.

Although only easily followed after landing in or at the edge of a breeding group, they often fly over beforehand and probably land and take off many times before approaching a particular male. At all events, females (from behaviour probably prospectors, see below) taking flight from a vantage point may be watched as they fly over the colony several times. They know the layout of a particular area well, as indicated by the certainty with which they return to a site once acquired, even in the absence of the male. This knowledge is important in areas which do not permit exploration on foot to correct a landing in the wrong area. Where practicable, prospecting females may land on the fringe of the nesting group and wander about. Alternatively they use a temporarily vacant nest; a space between nests or a natural vantage point, not necessarily near an advertising male at all. Having reached such a spot they peer about in the long-necked anxiety posture (Plate 23b). There is nothing specially distinctive about the posture of a prospecting female (as against an 'anxious' bird) and male advertising is certainly not directed exclusively towards them.

The male's advertising response frequently stimulates the female to approach, often hesitantly and with small-amplitude head shakes before finally rushing up in the facing-away position. Sometimes instead she merely cranes forwards and delicately touches the male's beak before grad-

ually increasing this to the full meeting ceremony (p. 176) with no prior facing-away.

Two characteristics of prospecting females are particularly noticeable. First, they are initially ready to accept almost any male, so that should the site change hands (which new sites often do) they are prepared to stay with the new male. One female began mutual fencing with a new male whilst her first mate was at grips with a challenger. Their extreme responsiveness is also highly adaptive in facilitating pair-formation within the colony, where males are confined to their sites and have only an inconspicuous behaviour pattern with which to attract females. Initially, prospecting females show little preference for a particular male, and may copulate with five in less than two hours. This indiscriminate sexual behaviour is similar to that shown by immature females in the clubs. It has obvious disadvantages and leads to the formation of both kinds of triangular and multilateral associations (Table 36). Also the female's tendency to break the first few pair bonds she forms requires the male to continue advertising after he has acquired a female. This again leads to severe female conflicts (out of 57 fights concerned with establishing new pairs 31 were between females). However, the advantages of female opportunism and high responsiveness must, presumably, favour these traits.

The second characteristic of prospecting females is the astonishingly high tolerance of punishment by males and their reluctance to retaliate (p. 187) which sometimes wins acceptance from a hostile male.

Motivation. See 'male advertising', and 'mutual fencing' (p. 184) for comments on motivation involved in the first stages of pair-formation.

Ambivalent sex and fear motivation are probably mainly involved in the female's approach towards a potentially

TABLE 36. The number of different males and females involved in new as against old nest-sites.

Status of site	Number of cases of nest-sites involving :-						
	1M.1F.	1M.2F.	1M.3F.	1M.4F.	2M.1F.	2M.2F.	2M.3F.
New	1	7	-	2	1	7	3
Old	45	5	3	1	3	4	3
	2M.4F.	2M.5F.	2M.6F.	3M.1F.	3M.2F.	3M.3F.	3M.4F.
New	3	2	-	1	3	3	5
Old	-	-	1	1	-	2	-
	3M.5F.	4M.3F.	4M.5F.	5M.1F.	5M.2F.		
New	-	1	1	-	1		
Old	1	-	-	1	-		

Notes : (i) M = male, F = female.

(ii) In the cases of old sites involving several males and/or females, the 'original' pair had been disrupted.

TABLE 37. The extent of female facing-away and male aggression in new and established pairs.

	Meeting followed by :-		
	Much aggression and facing-away	Normal aggression and brief facing-away	No, of cases
	%	%	
New pairs	75	25	48
Established pairs	5	95	473

aggressive male. Her approach is clearly fearful even though the male does not usually threaten her. Her appeasement posture (facing-away) is strictly (in adults) a female's response to an aggressive male and indicates some fear, as does the flurried, flinching nature of her mutual fencing, in which she may also face-away repeatedly. Occasionally females show slight aggression, though this is usually not detectable (correspondingly I could not recognise male fear in the new pair situation).

Function. The female Gannet must perform the initial searching to obtain a mate, since the male cannot contact her away from the site (excluding fortuitous meetings). Guillemots, Razorbills, Puffins, Kittiwakes and terns, for example, all perform aerial flights together at some time before pair formation; Black-headed Gulls have special pairing territories (Tinbergen 1956); Shags (Snow 1962) may lead the female to the nest after contacting her away from it (many passerines also do this - e.g.-tits house-hunt together, although there the site and territory are not synonymous as they are in the Gannet). In the Gannet, territorially extremely aggressive, the male remains on the site and the female must come within range of his inconspicuous advertising display. The female's prospecting method fulfils these requirements, and also ensures replacement of deceased female breeders whilst allowing the male to maintain continuity of site. There is nothing intrinsically improbable about the idea of Gannet aerial courtship and, in fact, S. dactylatra and S. leucogaster both occasionally continue their ground advertising display in the air (Dorward). The male's strong attachment to site may be one factor preventing this in the Gannet.

Female Facing-away in Response to Male Aggression.

Form. The female reacts to male biting in the pair context by 'facing-away', turning her head side-

ways and presenting her nape to him, at the same time pushing hard against him (Fig. 37), or (occasionally and only as a reluctant alternative) by actual fleeing.

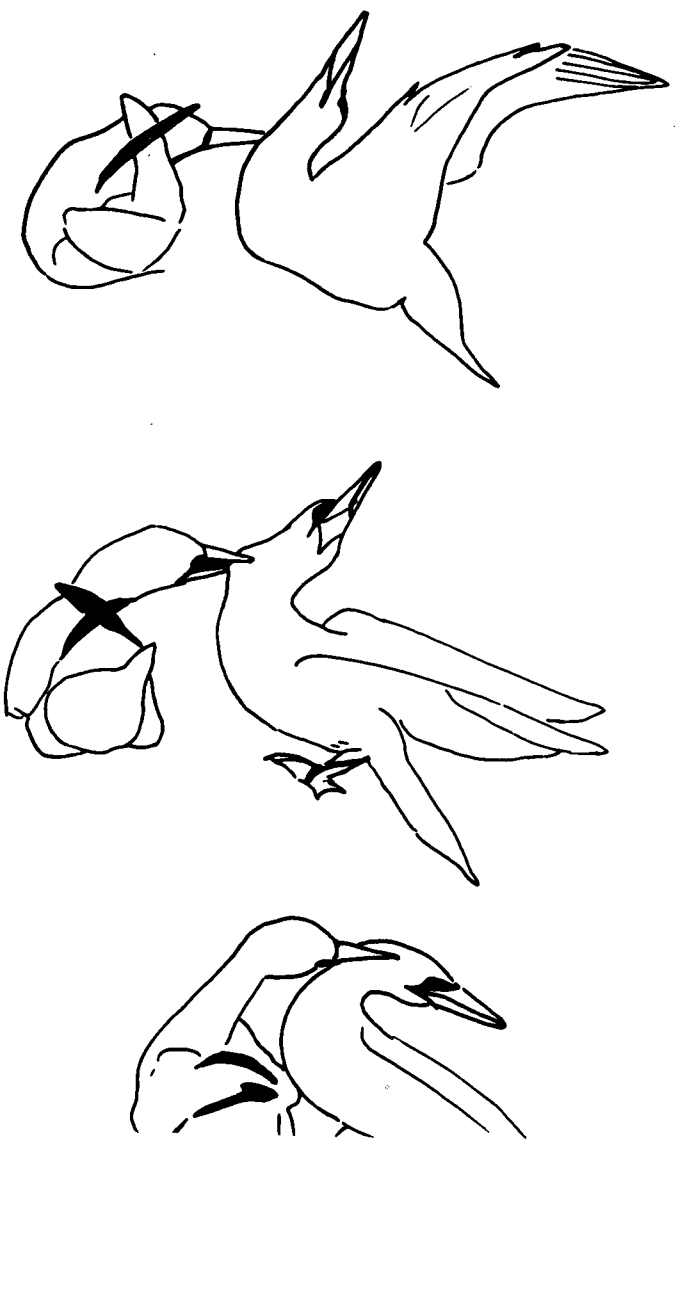


Figure 37.

Female seized whilst approaching aggressive male, pushes closer and faces-away.

Occurrence. This female appeasement behaviour occurs in any pair when they meet on the site, following aggression (biting) from the male. For a short time after pair-formation, however, females are often attacked on meeting with more than usual severity and consequently face-away strongly (Table 37). Even when a female is simultaneously attacked by a male and another female she restricts her facing-away to the former. Very rarely, males ~~have been~~ were seen fleetingly to face-away from females.

Motivation. Facing-away is a fear-induced behaviour pattern, as clearly shown by its form (avoidance) and context (response to fierce attack by the male). Nevertheless, since it does not occur in female fighting, the sex motivation involved in the pair situation

may be involved, although a particularly high level of fear and low aggression may be sufficient to account for it.

Function. Since the main function of facing-away is presumably to reduce the intensity of male aggression (and possibly female retaliation), critical during pair-formation, it should be emphasised that it is only effective in balanced cases in which the male is neither strongly hostile nor very receptive. In these cases it effectively stops the male's attack, although before beginning the mutual fencing ceremony he may strenuously attempt to push her off the site (Plate 14B). The female's tendency to push against the male is conspicuous in female : female fights where the male is present (p. 140). The female does not retaliate to male aggression when she has approached him, but if driven off the site often then returns his menaces without coming to grips.

Derivation. This is discussed (because of its association with other appeasement postures) on p. 162.

Facing-away in new pairs. Facing-away was followed by cessation of male attack in 12/41 cases and failed to stop them in the remainder. It cannot be compared with situations in which the female did not face-away, since these are so rare. Although a fair representation of the efficacy of facing-away, these figures do not bring out the important point that it functions most effectively in 'border-line' cases. Facing-away may be considered effective appeasement behaviour and highly adaptive if it succeeds (as it does) in permitting pair-formation even in a proportion of cases which would otherwise have failed.

Facing-away in established pairs. It is possible to interpret male aggression towards a new mate as a result of strong territorial behaviour, elicited by the female as an intruder, but

it becomes a matter for special remark that males should continue to display aggression to their mates (Plate 15A) throughout the period of attachment (see Table 37). Some Gannets probably mate for life and others certainly for many years, yet in 98% of 294 cases recorded, incoming males bit their females, and in 75% of 253 cases incoming females were gripped by the male. The difference in proportions is probably due to the greater difficulty of biting in the latter situation. Among these hundreds of observations there was one record of a male being bitten by a female, startled by his arrival. These figures apply to males landing without nest material in their beaks and exclude cases in which neighbours interfered with the normal procedure. Females respond to incoming males by rapid head shaking and face-away before he lands - sometimes lying almost prone in the chick facing-away position. Presentation of the nape does not prevent the male biting, but removes any risk of the female retaliating and releasing serious male aggression - important enough in the early stages, and possibly also in established pairs. It should be added that pair members clearly recognise each other; there is no question of all females being treated as intruders until their response to biting proves them otherwise, (the calling of an incoming bird may evoke head shaking from its mate, though not from neighbours).

In 87% of cases in which males arrived with nest material females did not face-away whereas males <u>without</u> nest material failed to elicit facing-away in only 10%, showing conclusively that this reaction is related not merely to the arrival of the male but to his arrival and biting capacity. Although males of established pairs would not attack so persistently that the female was compelled to face-away, it

Plate 15 Pair relationship.

A.

Male arriving at nest and biting female, who faces away from him.

B.

Mutual fencing. Note birds standing close to each other and calling (bill of right bird slightly open).

C.

Mutual (allo-) preening. Note half-closed eye of bird on nest.

nevertheless seems that facing-away has remained a response to genuinely aggressive biting by the male.

Intruding females. Females intruding onto a male's territory (e.g. when two males independently acquire the same site and different females, one of whom returns to the 'wrong' male) or there when he returns, are usually displaced (78% of cases recorded) despite conspicuous facing-away and acceptance of male aggression. In this situation, therefore, facing-away is relatively ineffective as an appeasement posture.

To sum up : facing-away is the female's response to male aggression; it is primarily fear motivated and has an appeasing function at a critical period in the pair relationship. It is apparently without parallel in other Sulidae which appear to lack a specific female appeasement posture, although possessing the infantile beak-hiding from which facing-away may be derived.

Mutual Fencing.

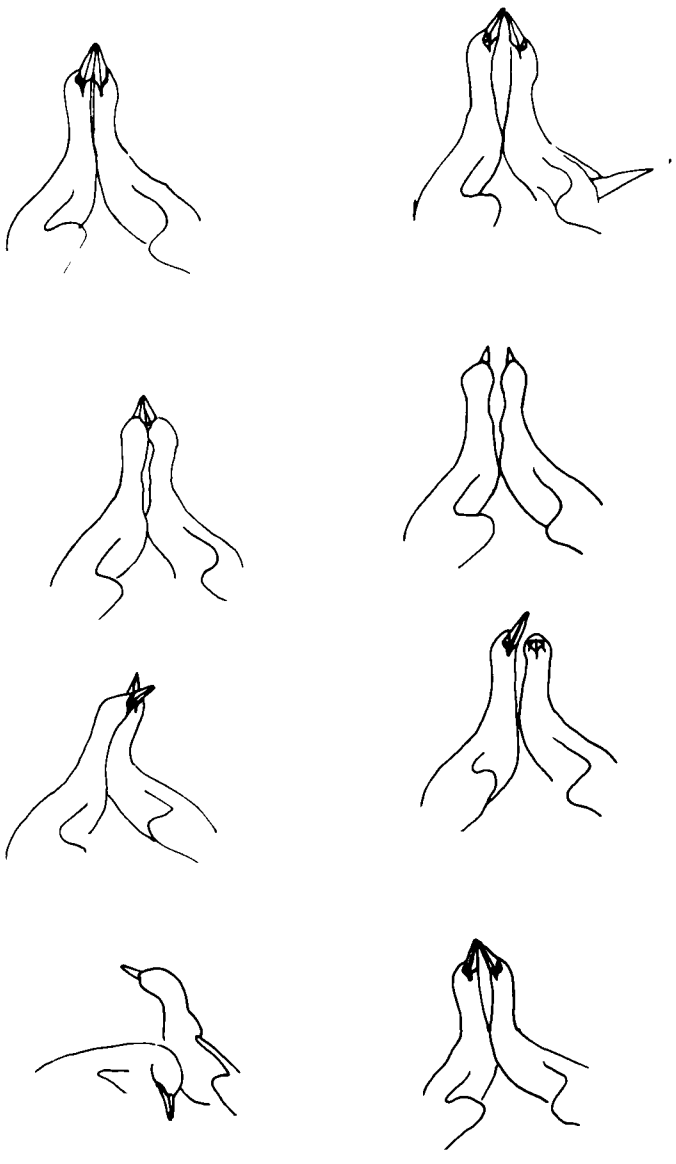
Mutual fencing between mates (Plate 15B.) is one of the Gannet's most conspicuous behaviour patterns and seems to have been considered the 'main' display by the few authors describing Gannet behaviour. It occurs most commonly as a meeting ceremony following arrival at the nest of one member of the pair, usually from flight, but sometimes on foot. When the pair are present it also regularly follows an aggression-eliciting stimulus (e.g. a menace from a neighbour).

Surprisingly, S. sula, S. dactylatra and S. leucogaster apparently lack a comparable meeting ceremony, although Dorward saw a pair of dactylatra "sparring" which he considered a mild form of fighting and "bill-touching" which he also considered aggressive. Both these may be related to the Gannet's mutual fencing. Similar greeting ceremonies are found in many other, particularly colonial, species. The

Openbill Stork Anastomus oscitans has a meeting ceremony much like the Gannet's in form, lasting for four to five minutes with calls (Loke wan Tho, via Huxley 1962); Herons show a sort of fencing, biting each other's bills, obviously not so elaborately ritualised as the Gannet's (Lowe 1954); albatrosses knock beaks together on meeting (Rice & Kenyon 1962) and many other species employ beak touching, rubbing, biting, etc. in less conspicuous form than the examples given. The 'triumph' ceremony of geese, though not exactly comparable, is also a form of meeting ceremony (Johnsgard 1961).

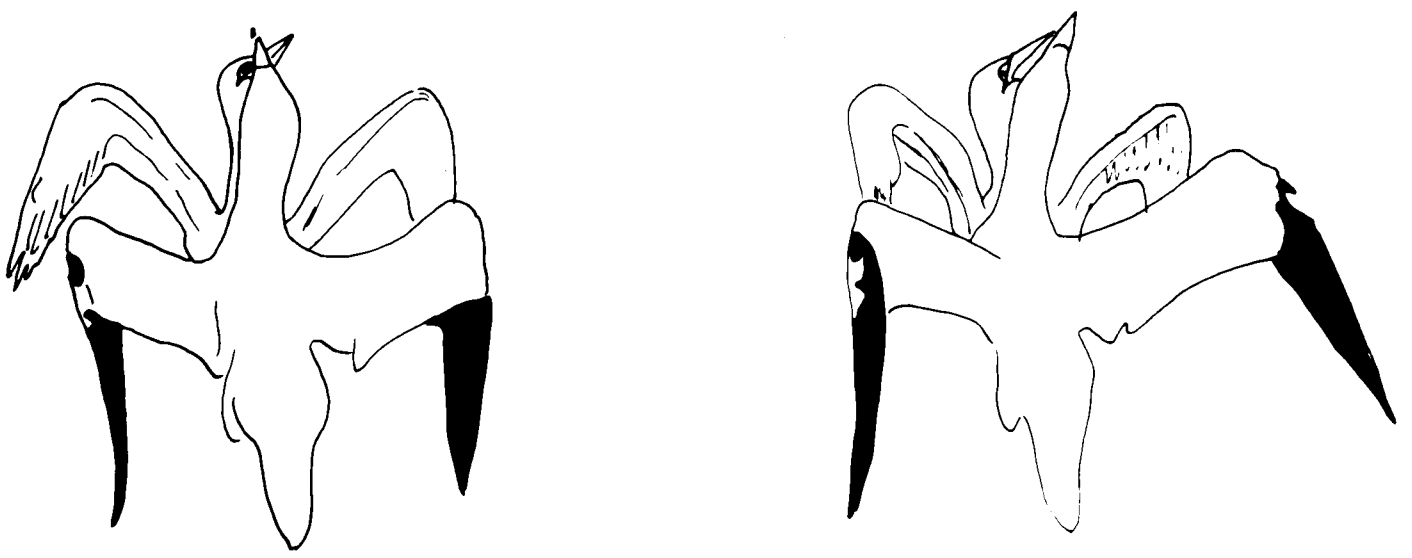
Form. The inflying bird of either sex calls stridently at about 4/second, in response to which the bird on the nest head shakes rapidly and, if a female, faces-away in anticipation of the bite to be delivered by the male.

As the male lands, perhaps even before, he grips the female, sometimes so fiercely that an observer unfamiliar with Gannet breeding behaviour would certainly interpret the action as overt hostility intended to drive off an intruder. Following this the pair typically stand breast to breast, and with wings widely spread and bills inclined upwards, perform a rapid fencing or 'scissoring' movement with their bills, calling throughout - loudly when displaying vigorously and more softly as display dies down. Interspersed with this bill-fencing are downward movements of the head, perhaps as far as the nest material or only a little to one side, which often result in one bird reaching over the neck of the other in a sinuous 'neck-smoothing' movement. As a vigorous bout of mutual fencing dies down the wings are held closer to the body, heads more horizontal and head movements become slower and less extensive. In mutual fencing between birds new to each other the partners stand rather far apart, their movements are characteristically nervous and jerky, and the male intersperses slight biting of the female. Together with the



A.

B.



C.

Figure 38. Mutual fencing. A. Different head positions. B. The dipping movement. C. Three grades of 'wings-out' position in intense mutual fencing.

duration of the display (usually two to three minutes, but 40 minutes of unbroken display was once recorded) and the number of nest touching movements involved, all the components listed above can be quantified to analyse seasonal and status differences in mutual fencing. Details of several bouts were recorded on a tape-recorder and analysed on paper.

In form, mutual fencing conspicuously resembles bowing, and will be considered to be a modified form of it. The implications of the differences will be discussed under motivation and function. In form, these differences are not merely imposed by the partners' positions (standing breast to breast). Whereas, during the head shaking in bowing, the bill is usually held slightly below horizontal, in mutual fencing it is pointed upwards; this difference may be associated with the bird's greater aggression in bowing (see Andrew 1961 for a discussion of bill-position in relation to motivation). Mutual fencing contains fewer, more haphazard dips than bowing, and the head shake is rather less regular, possibly due to physical interference with each other's movements. In the female's mutual fencing during the pre-laying period this head shake frequently alternates with the soliciting head shake which precedes copulation, and occurs nowhere else.

Length and intensity of bouts. Mutual fencing between the pair continues throughout the season; the length of bouts varies, reflecting the vigour of the whole performance, and was recorded as an aid to analysis.

Considering only established pairs and dividing records of the length of mutual fencing bouts resulting from meeting on the site into early, middle and late periods of the season (March and first half of April; latter half of June and July; September and first half of October) gave the results shown in Table 38. Records came from thrice-daily

checks.

TABLE 38. The average length (in seconds) of mutual fencing bouts in experienced birds at different times of the season.

	March to mid April	Mid June to end of July	September to mid October
Long absences	208 (30)	30 (38)	88 (11)
All absences	180 (35)	29 (56)	87 (13)

Notes : The figures in brackets represent the number of cases involved.

'Long absences'= 6+ hours.

'All absences' include those of unknown length.

The differences are significant and show that mutual fencing bouts tend to be shorter in mid-season than at the beginning or end. It is only at the beginning or end of the season that even very short absences may be followed by long (2 mins.) mutual fencing bouts. In fact bouts become shorter soon after egg-laying, and during part of the chick stage they may be very short (10 seconds). If a pair lose their egg their mutual fencing bouts suddenly become much longer again. This seasonal difference in bout length is also present in new pairs.

Other measures of the vigour of mutual fencing (roughly graded A, B, and C according to a composite intensity measure involving wing-position, amplitude, speed and inclination of head movements) showed the same seasonal pattern as the duration of bouts. Thus mid-season displays showed a ratio of 1 : 1.5 : 12.5 of A, B and C grades respectively, whereas late-season ratios were 1 : 0 : 0.3. The rise in mutual fencing towards the end of the season could be correlated with a rise in aggression. It is obviously a non-personal factor in the sense that recognition of each other between pair members will be as good or better at the end of

the season than at other times.

Sex differences. There are sex differences in the form of mutual fencing. Males tend to dip more (Table 39) and this difference is significant.

TABLE 39. Sex differences in the dip component of mutual fencing.

	Mean no. of dips/bout	Range	No. of cases
Male	11.6	3-27	27
Female	4.6	0-21	27

Note : Out of a further 39 cases in which the actual number of dips were not counted, it was noted that the male dipped more than the female in 28, and the female more in 11.

However, the fewer dips in female mutual fencing are no indication that females mutual fence at a lower intensity than males (cf. their bowing which is of lower intensity, Chapter 9), since in two other measures females show more vigorous mutual fencing than males (Table 40). Thus females mutual fence with wings held out more widely and show greater persistence in maintaining the display. Also, female mutual fencing probably shows a higher proportion of head shakes, though I was unable to measure this satisfactorily.

TABLE 40. Sex differences in wing position and persistence in mutual fencing.

	New		Experienced	
	Number of cases in which :-			
	Male more	Female more	Male more	Female more
Extent to which wings held out	3	17	13	47
Persistence in maintaining mutual fencing	6	12	10	24

Status differences. New pairs show longer mutual fencing bouts than experienced ones (Table 41) at the same time of year.

TABLE 41. Status differences in the length of mutual fencing bouts.

	Mean duration of bouts (in secs.)	Range (in secs.)	No. of cases
Established	45	5-150	31
New	97	10-180	9

Note : These records are mid-seasonal only and length of absence has not been taken into account.

Thus one never sees new pairs, re-united after a long absence, perform the relatively perfunctory display occasionally seen in old pairs. It seems reasonable to suppose that as the pair get to know each other the mutual fencing bouts do not need to be as long. This, however, is only reasonable if certain assumptions about motivation and function are made, which will now be discussed.

Motivation. Mutual fencing is restricted to male/female interactions, almost always between pair members. Aggression (male biting) and fear (female facing-away) are involved when the sexes meet and are particularly high in new pairs, and early and late in the season. These facts suggest that aggression and fear between partners has to be overcome; that they are reduced as the pair-bond strengthens (i.e. in old pairs) and that they will be most difficult to overcome at the beginning and end of the season.

The seasonal and status differences in mutual fencing already described (bout lengths, vigour, etc.) are all consistent with the facts given in the paragraph above, if it is assumed that mutual fencing intensity is correlated with the strength of aggression and fear between the pair. This is further confirmed by the fact that aggression-eliciting

stimuli, such as threats at the pair, call forth renewed mutual fencing. It may also be illustrated by two examples:-

(i) A male attacked his mate for 15 minutes and tried to drive her off the egg. The female faced-away most of the time, but also retaliated three times and almost drove the male away. After the third retaliation they began high intensity mutual fencing which lasted for 4 minutes 25 seconds. The new 'outlet' for the aggression which both had previously shown, completely prevented any further attack.

(ii) The male of a new pair returned, mutual fenced, copulated and was then menaced by a neighbour and turned on the female in violent re-directed attack. At the first pause this passed into intense mutual fencing lasting several minutes.

These show the aggression of the male prior to mutual fencing which then forms an outlet for the fear/aggression tension between the pair. The male's aggression in mutual fencing is further shown by the higher number of dips (the dip is probably an aggressively motivated movement, as in the bow).

Besides aggression (in the male) and fear (in the female) sex motivation is also involved in mutual fencing. Early in the season, in at least 90% of cases, copulation follows mutual fencing. Also, the female mixes the ordinary head shaking with 'soliciting' head shaking.

Finally, since mutual fencing takes place only on the site this may be a necessary part of the external stimulus situation, though it is difficult to disentangle the effects of site and aggression. These ~~four sources of~~ evidence for the motivation of mutual fencing may be tabulated as follows :-

Male	Female
1. Aggression.	
Bites female.	May (rarely) alternate attack on the male with mutual fencing.
Performs aggressive movements (dips) in mutual fencing.	Performs aggressive movements (dips) in mutual fencing.
Reacts to aggression-eliciting stimuli by mutual fencing.	Reacts to aggression-eliciting stimuli by mutual fencing.

	Male	Female
2. Fear.		
	No overt expression of fleeing tendency.	Faces-away initially.
		In new pairs occasionally faces-away <u>during</u> mutual fencing.
3. Sexual.		
	Returns to female	Returns to male.
	Often copulates afterwards.	Allows copulation.
	Allows female to remain in proximity.	Mixes soliciting head shake with ordinary head shake.
(4. Site.)		
	Performed only on the site.	Performed only on the site.
	Frequently touches nest material during mutual fencing.	Frequently touches nest material during mutual fencing.

Since the balance between fear and aggression etc. will be different in male and female it is reasonable to find that their mutual fencing behaviour also shows differences (in number of dips, etc.) and that these tend in the direction expected if the male is more aggressive than the female and if mutual fencing bears some quantitative relationship to the amount of aggression/fear to be overcome between the pair/members. However, the form differences seem much less than would be expected from the radical differences, for instance, in the aggressiveness of the partners.

Before concluding this account of motivation it

is worth making a further point. Mutual fencing in the Gannet is only part of its meeting ceremony, which rightly also includes the male advertising (leading to the first meeting of the pair). Male advertising, it may be recalled, resembles the aggressive ownership display though the aggressive elements have been reduced. Yet no appeasement has been incorporated; nor has male appeasement been compounded into his mutual fencing. Thus, considering the whole meeting situation in the Gannet, we find that its advertising (and probably also its mutual fencing) is an example of a pair-formation display derived from a relatively low-intensity (Tinbergen 1959 "more timid") threat display by suppression of certain aggressive elements. This fits with the gull work. Thus in the Black-headed Gull the pair-formation involves 'song' (aggressively motivated) by the male, approach by the female, agonistic display by the male, appeasement (distance reducing) display by the female and then mutual appeasement (head flagging) by both members. The comparable sequence in the Gannet is advertising by the male (derived from aggressive agonistic display), approach by the female in facing-away (appeasing) posture, aggression by the male, further appeasement by the female and a mutual meeting ceremony. It is interesting that natural selection should not have eliminated the male Gannet's continued hostility to his mate - a fact doubtless related to the general aggression of the species, and particularly the male (see general Discussion).

Function. The discussion of motivation has already implied that mutual fencing must be interpreted as a 'friendly' meeting, or pair-bond strengthening, ceremony, in which the aggression/fear between the sexes is reduced. For example, the longest bouts follow long absences and repeated short trips for nest material are followed only by perfunctory mutual fencing and a much lower tendency for the male to bite; marked aggression by the male invariably

causes the female to attempt mutual fencing as though to overcome the aggression; pairs which have already performed the ceremony do not do so again except in response to stimuli which elicit aggression; etc..

The circumstantial evidence all points the same way - the more aggression there is to be allayed (and the means of ascertaining this are independent of the intensity of mutual fencing elicited) and the more prolonged and intense are the mutual fencing bouts.

Summary. Females clearly elicit aggression when the sexes meet on the site and are themselves afraid. Their initial appeasement behaviour is followed by a mutual display which itself expresses sexual attraction mixed with aggression in the male and fear in the female. Variations in form, intensity, and seasonal incidence, together with status differences, agree with the suggestion that mutual fencing reduces tension between members of a new pair, strengthens the pair-bond and is the ownership display when both members are present.

Extension of Female's Attachment from Male to Site.

Whereas males acquire sites, females are attracted to and acquire males, only later forming a permanent attachment to the site. Thus a female sometimes follows a male if he moves away soon after she joins him. Also females will accompany their male if he changes site more permanently, though he seldom does so. Since the female is initially attracted by the male's advertising rather than the site itself, she leaves it for other advertising males, or even spontaneously, if the male goes off to sea, therefore males frequently lose the first female who joined them and must continue to react to prospecting females after acquiring a mate. Eventually the female must become firmly attached to a site to guard it effectively; the formation of this attachment may be one function of the long pre-breeding period of

site ownership.

Soon after pair-formation, and only then, the male behaves in a way which could condition the female to remain on the site alone; he leaves and returns to the site repeatedly in a short period. In addition to the gathering of nest material after copulation - behaviour common to males of all categories - males of new pairs often move a few feet from the nest, suddenly rush back, bite the female and perform the meeting ceremony. If the location of the site does not allow this, short aerial excursions and returns to the site are made instead. A dyed male, conspicuous at long range, carried out nine such flights in less than half an hour. This repeated return and mutual fencing is likely to strengthen the pair-bond and accustom the female to the male's departure and return.

After the first few prolonged male absences the female begins to take regular spells of attendance - necessary to accumulate nest material which is robbed from unguarded nests. Eggs are occasionally laid on bare earth, but have a lower chance of survival. Females bow and also fight against other females in defence of the site quite as strongly as males fight against males. They may even change sites and then fight bitterly to evict other females from the old one. Thus, after the initial phase when her interest is centred on the male, sites are defended as such. However, females probably have a weaker attachment than males (see p.129 for attendance details as a measure of attachment, and also p. 32 for long-term fidelity to it).

Later Stages in the Pair Relationship.

The changes occurring in a pair relationship with time are extremely little known. In most species for which the details of pair formation have been studied subsequent interest has centred round nest building, incubation behaviour, and parent/young relationships. Perhaps few species are

suitable for the analysis of such changes, the pair simply 'settling down' together. Yet the changes must occur and are of great interest. Do the pair members come to know each other better and better; how does this affect their behaviour; is aggression reduced and if so by what mechanism ?. The Gannet's pair relationship can be looked at with these questions in mind. As in pair-formation, it is sometimes necessary to know the previous history of the individuals concerned to avoid wrong conclusions.

The aggressiveness shown by males during pair-formation continues throughout the relationship (e.g. an established male attacked his female, with whom he had nested at least two years, for one minute after her return from a flight, as late as mid-September). The factors affecting the pair relationship will be changes in motivation, many of them independent of the partner, and also changes expressing the personal relationship. Thus males of new pairs are more aggressive than males of old. Then they become less aggressive, but within this framework show a pattern of aggression - stronger early and late in the season. The late-season resurgence cannot be due to males becoming less familiar with their mates - they don't for instance see less of them in mid-season (see Fig. 22) - and must be a 'non-personal' change. Some consequencies of male aggression in the pair context (length of mutual fencing bouts, biting of the female, female facing-away) have already been described. Other aspects of aggression and the pair relationship, including preference, are discussed here.

Aggression between pair members. The highly adaptive female tolerance of male aggression has already been mentioned when discussing pair-formation. Females were known to absorb male aggression for up to 20 minutes without retaliation. Later in the pair relationship, apart from the bite received on meeting (no

mere token) females are occasionally attacked by their mates often as re-directed aggression stimulated by outbursts of activity in the neighbourhood. Her reaction, even under the most severe male attack, is merely to face-away. It must not be supposed that females are incapable of successfully resisting males; they can on occasions vanquish males not their mates. Even when provoked to retaliate however, inhibition frequently re-asserts itself and they break off successful aggression to resume facing-away. This tolerance contrasts with ths situation in many passerines (e.g. Chaffinch Fringilla coelebs and Greenfinch Chloris chloris) in which, after pairing, the male will tolerate female aggression and she can supplant him at food, etc. (Hinde 1953).

Position effects. Females (and also chicks) are more likely to be attacked when slightly off the drum. One male alternated between two sites, each with a female, and consistently attacked whichever female happened to be off the site he was occupying whilst mutual fencing with the other. He was therefore attacking a female one minute and mutual fencing with her the next. This tendency may explain the female's initial hesitant approach to an advertising male, followed by a quick rush, pushing and then facing-away (see Fig. 37). Similarly, the female is powerfully inhibited from attacking an intruding male if he can once gain access to her site, where she usually tolerates him. More unexpectedly, a female is more likely to attack an intruding male (or even menace her own mate) when she herself is off the site. This is probably due to the removal of the powerful inhibition against attacking a male which all females seem to experience when on the site.

Flexibility of pair response. Despite the permanence of the pair-bond and the strong reaction against intruders, both male and female remain remarkably receptive to the other sex, with attendant advantages and disadvantages. It allows both sexes to respond

to a large number of suitors in the early stages and later also allows partner replacement, but it encourages triangular associations (see Table 36). In almost all cases where eggs simply disappeared (and all obvious possibilities could be ruled out) at least one owner of the nest concerned was known to be 'interested' in a third party; the egg was therefore more likely to be left temporarily unattended. This egg loss and the many fights resulting from such associations are two obvious disadvantages of persistent receptiveness in both sexes. The system is probably adjusted to the Gannet's dense colonial nesting and the male's aggressiveness, both of which increase the liklihood of several 'abortive' pairings before a stable bond is formed.

However their receptivity is not entirely predictable and poses interesting questions about individual preferences (Richdale 1951 records personal preferences in penguins). Males have a marked receptive period at the beginning of each season, and become highly selective later on, although a second receptive phase occurs towards the end of the season, but within this framework there is much variability.

After pair-formation receptivity is substantially lower, but may be retained, even in long-established birds, towards particular individuals with whom some previous relationship has existed, and who are clearly still recognised. One male not only accepted his previous mate back again after a year in which they had both successfully bred with new mates, but also drove away his mate of one year's standing in favour of his original one. On the other hand another male completely rejected his original mate when she returned to him after an estrangement of less than two months. In some cases relationship with two females turned on the outcome of the fight between them. Usually the loser did not return, but when she did was often forcibly rejected by the male. Again, however, in some cases, the precise opposite occurred -

the loser returned, was accepted and had to be ejected again by the victorious female. It appears that individual likes and dislikes play some part in determining the choice of a mate, just as in other higher vertebrates.

Where male or female are attached to two sites they show normal pair relationships with mates on both. Even when one site has an egg the other is also visited and intruders repelled. In one case where the two-site triangle involved two females and each produced an egg, the male incubated both but favoured the female who first laid to him, even though she was not on the site where he had bred the two previous years. The newer female therefore inevitably lost her egg. Even then the male continued to visit the site and repelled many site-establishing males with great determination. His dual attachment caused at least ten fights in one season, though he eventually lost the site.

Site and mate attraction are clearly both strong forces and the striking variability in response to both seems to be the result of opportunism with its attendant advantages and disadvantages.

Mutual (allo-) Preening.

Members of a pair often follow mutual fencing or copulation by mutual preening (Plate 15C) in which each delicately nibbles, with the tips of the mandibles, the head, neck and throat feathers (occasionally the wings and back) of its partner. The eyes are often closed but probably not as a protective measure. The head is heavily infested with Mallophaga, but mutual preening does not appear to remove them and may perhaps persist because of its association with pleasurable tactile stimulation. It is infrequent when compared with ordinary preening, occurring mainly in established pairs. It is unlikely to be appeasement behaviour since it usually occurs after mutual fencing has removed any tension between the participants, but it also occurs in connection

with aggression as clearly indicated in unstable pairs when it may alternate, in the male, with overt aggression. ~~and might have a signal function here~~. Once an intruding male preened the female and then showed intention movements of copulation. Copulation in this situation is often aggressive and as mounting approached his preening became rougher and finally graded into biting prior to copulation. The reverse also happens - a male starting with attack often ended by preening. However this may be in part an expression of postural facilitation, the biting grading into nibbling and preening as a result of the bill being brought into the 'correct' position. Similarly, when adults attack chicks they alternate this with preening them.

There is a tendency for females to preen males more frequently than vice versa as in Jackdaws Corvus monedula (Lorenz 1931) and many other birds (C.J.O. Harrison in prep.).

- 11 -

NEST BUILDING AND ASSOCIATED MOVEMENTS

Nest Building.

Gannets accumulate large, compacted nests of seaweed, grass, moulted feathers and 'oddments' (string, paper, straw, children's toys, etc.), and add to it any earth they can reach around the nest. The drum, or pedestal, occasionally measures more than four feet from rim to base (Gurney 1913 records a nest five feet high) - the product of many annual increments - though in most cases a well-established nest is about one to two feet high, with a firm, shallow cup 'lined' with grass or sometimes seaweed, and often containing feathers (see Plate 20B). The finer material in the cup results from removal of larger items rather than a deliberate choice of fine material, much as in the Shag (Snow 1960). However, there is enormous variation not only in the size but also in the quality of the nest. Some females lay and incubate on large, well-lined nests, others on a patch of muddy ground with a few scraps of material. The sides of the pedestal are heightened by a continuous 'gardening', the birds reaching down and drawing loose earth and debris up the slope to the rim (Fig. 39). This elevation can be highly adaptive under some conditions. Low-lying nests on flattish ground tend to gather drainage water during heavy rain and the young become soaked and chilled. I have seven records of young from such nests, too old to be effectively brooded but still protected only by their down, dying during cold N.E. winds and rain in June and July (see also p. 218). In addition high nests provide take-off points - useful in flat areas, since nesting Gannets do not allow free passage to birds departing on foot (see Plate 23E).

Nests are not systematically or'deliberately' added to by the birds' own excrement, which is usually voided well clear by both adults and well-grown young, though Armstrong's

(1942) statement that the young are "fastidious" in keeping the nest clear is exaggerated. However, on many occasions adults lower their tails and excrete onto the side of the nest. It is usually the more viscous residue from the alimentary tract which is 'directed' in this way, the faeces containing a higher proportion of uric acid being squirted clear. Nevertheless, on small, sloping ledges where nest material sticks with difficulty, the cementing action of excreta is unquestionably valuable in providing a base for subsequent accretions. Indeed, were it not for this and the use of earth and humus (often pulled up with grass) nests would never stick onto some of the sites used (see Plate 8), a measure of the potential value of this habit to the species. Shags' nests, which lack this 'cement', could not accumulate on some sites used by Gannets, whose adaptability, compared with some cliff-nesters, is worth special mention, and could be significant in permitting extension of range. The Kittiwake has an even greater ability to stick nests on small projections, and Cullen & Ashmole (1963) have suggested that the Black Noddy, because of its ability to attach nests with excreta, can utilise nesting sites denied to its relative the Brown Noddy Anous stolidus. However, quite apart from ability to stick nests, the Gannet could never use certain kinds of sites open to the agile Kittiwake, and its choice may often be limited by its manoeuvrability.

Bringing nest material. Gannets collect nest material, mainly grass and seaweed (273 records of grass against 131 of seaweed in 1961 and 1962, with more grass than seaweed in both years), from January to the beginning of October, and indeed may be seen carrying seaweed every month of the year (F. Marr pers. comm.), though mainly from the end of February to October. This seven to eight month interest in nest material is remarkably long, and the

Gannet's concern with it, shown in other ways also, should be stressed. Stealing is common throughout the season and reaction to the sight of nest material is so strong that birds sometimes try to rob each other both when gathering it and even in mid-air.

102 five-minute counts of the frequency with which nest material was brought to a group of 250 nests showed that this rose steadily in April (averaging 2, 2, 3 and 4 per five-minute period in the four quarters), was lower in mid-season and rose again in August.

The rise before egg laying is associated with the increased rate of copulation, and is to be expected since copulation ~~this~~ is usually followed by nest material gathering. Some days before egg laying, females spend longer on the nest with the male, thereby facilitating copulation and the attendant nest material gathering - a chain of events producing a well-built nest just prior to laying. Prior to laying nest material is brought by the male only (231 visits by males, 0 by females), but subsequently by the female also, though never so frequently as by the male. Males, but rarely females, bring nest material to their sites even in the absence of a mate to guard it between collecting trips.

For the remainder of the year gathering is scattered, although sudden rain elicits a marked outburst of nest building. During rainy weather in August 1962, for example, in five minutes 28 birds arrived with nest material at the group of 250 nests, only about 40 of which were attended by pairs. Since Gannets do not normally leave their nests unattended, three-quarters of the possible total were gathering nest material at the time of the count. This activity continued for hours - a spectacular response (Kittiwakes react to a similar extent,Cullen). The function may be to elevate the nest and keep the egg or chick drier, though even pairs without egg or chick respond in this way.

Nest-building Movements. (Plate 16)

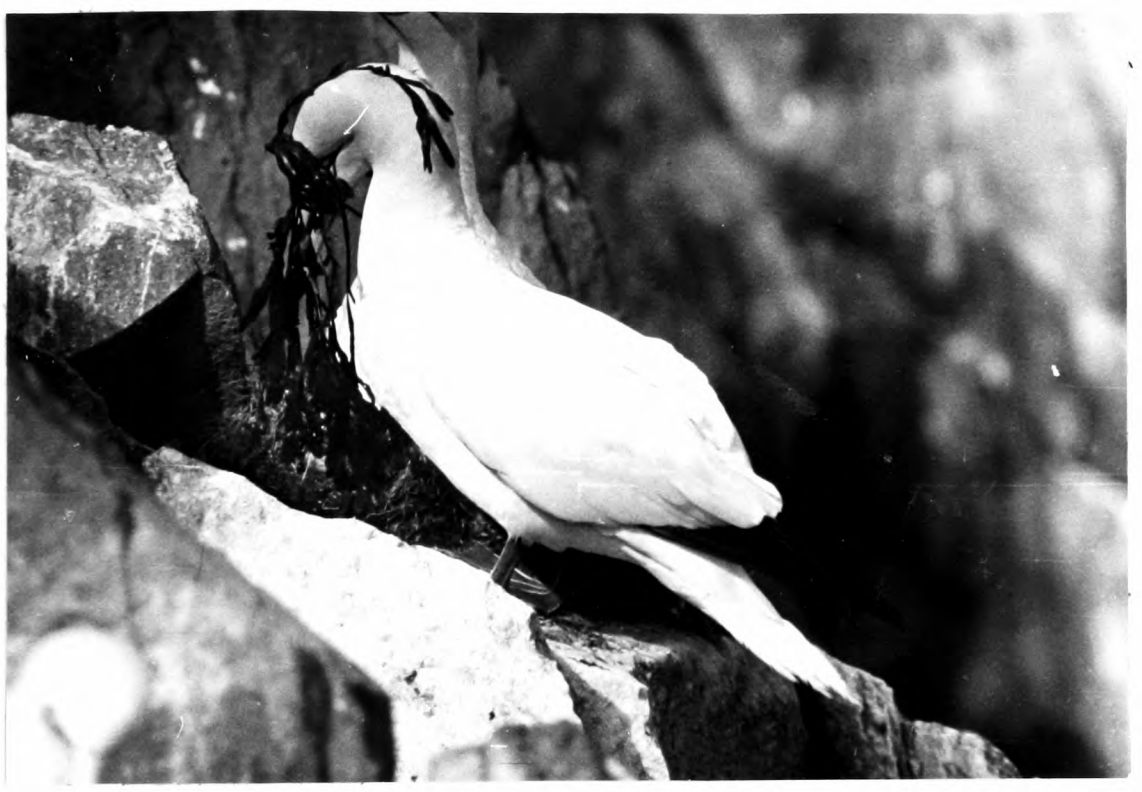
Gannets spend much time arranging nest material throughout the season (see, for example, Table 45). They have no complicated method of interweaving the material, merely placing it in front or to one side, whilst standing or sitting (16E), and with rhythmic, small-amplitude, sideways head movements and trembling of the mandibles pushing it into place. The presence of a cup or hollow is not necessary to induce nest building movements, but the bird must be actually on the site. I noticed that after shifting the egg and settling to another spell of incubation, they seemed particularly prone to arrange nest material around the breast and flanks, tucking small pieces delicately between themselves and the nest, perhaps to 'seal in' part of the warmth. After depositing and arranging the material in this way, the mandibles are characteristically opened and vibrated (16E) to dislodge any material sticking to them, followed by a quick sideways head shake, varying in vigour with the stickiness of the material. Sometimes material is placed in position without any sideways building movements. Mandible vibration is not strictly confined to the context of nest material handling. It also occurs when dealing with regurgitated fish and was recorded, for example, from an aggressive female menacing a male in a high intensity conflict situation.

Nest maintenance involves behaviour which I termed 'nest digging' (Plates 16F and 16G), in which the mandibles, slightly parted, are thrust into the floor of the nest and used as a probe to dislodge hard lumps. It is performed with concentration and vigour, and seemed to become more frequent during the hatching and tiny chick periods, when it may be adaptive in removing sharp objects which could injure the egg or chick. Snow (1963) recorded it in the Shag and suggested it might 'sift' ectoparasites out of the floor of the nest, but its form in the Gannet suggests it would be in-

Plate 16 The nest.

A.

Nest material is gathered communally. Note vigorous grass-pulling.



B.

Large masses of seaweed are brought.

C.

The male occasionally brings small scraps from nearby.

Plate 16 The nest (D. - G.). 1956

D.

Loose material from the base of the nest is placed on the rim.

E.

Mandible vibrating follows deposition of material.

F.

Nest-digging. The nest bottom is deeply probed.

G.

Hard lumps are placed on the rim or flung away.

efficient for this purpose.

Gannets sometimes toss or juggle pieces of stick, etc., apparently playing with them. The quick, jerky head movements and dexterous manipulation of the object resembles the way in which fish-eating birds orientate their prey before swallowing it; the movements used are doubtless similar. Adults and well-grown chicks both do this and it could be of use to the latter in perfecting movements which will later be used in dealing with prey. Unemployed birds in the fringe juggle much more frequently than breeders.

Nest-touching Movements and Nest-biting.

Whereas the nest-building movements already discussed play some part in maintaining the nest structure, there are two distinct forms of non-functional nest-touching. In the commonest,nest material is touched with the bill or briefly handled, often with associated vibrations of the mandibles and sideways nest-building movements. In the more aggressive form, nest material or the ground is actually bitten vigorously.

Ordinary nest-touching movements. These occur in a variety of conflict situations, in which nest material may be handled and put into place, handled aimlessly or merely touched, and their relevance (in terms of nest maintenance) in the first category must be decided for each occurrence.

Nest-touching movements often occur in severe menacing bouts and other high-intensity agonistic situations in which the bird performing it (or performing it most) is slightly inferior or under stress. However the winner of a severe fight (and hence aggressive) usually mixes nest-touching with bowing, and an aggressive male trying to repel a female frequently touches nest material. Also, it occurs in the male during female : female fights on his site.

Table 42 shows that nest-touching commonly follows menacing, but less often in pairs than singles, pairs instead following menacing by mutual fencing.

TABLE 42. The occurrence of touching nest material following menacing bouts.

	Number of menacing bouts after which :-	
Menacing between :-	One or both parties touched nest material	Neither touched nest material
Single : single	63	77
Single : pair	13 singles 10 pairs	37
Pair : pair	8	19
Totals	145	133

Nest-touching also occurs in the female after copulation (60% of cases), during mutual fencing, particularly in the female and, on occasions, in bowing (though most bows do not actually involve touching the nest material). Therefore any simple generalisation about its occurrence would be premature.

Aggressive nest-biting. Immediately after alighting on their empty nest or site Gannets, and particularly males, bite the nest material, ground or even bare rock (Plate 3C includes a male doing this), at the same time calling aggressively, with outspread wings and making irregular foot-lifting movements.

29% of 91 such landings were followed by full aggressive nest-biting and a further 64% either by touching nest material or bowing (itself derived from nest-touching, probably of the aggressive kind) Table 43. The alightings of frightened birds were followed by fewer nest-touching movements or bows. In early February 1962, when occasional 'panics' still occurred, 19 out of 27 birds showed an anxiety posture as the first behaviour following landing, only three touched nest material and none bowed; these were not included

in the analysis. Birds landing away from their sites and birds without sites landing in the fringe never show aggressive nest-touching movements.

TABLE 43. Behaviour following landing alone at the site.

Nest touching (without bow)		Nest touching (plus bow)		Bow alone		Pelican posture alone	Total
57		19		9		6	91
Nest biting	Normal	Nest biting	Normal	Pelican posture	No Pelican posture		
12	45	14	5	8	1		

Note : The sexes were not distinguished in this analysis and only birds returning 'naturally' were included.

Apart from landing, a conspicuous form of aggressive nest-biting occurs when birds return on foot to their sites after some disturbance within the colony (e.g. landing off-site and being attacked, knocked off by a nearby fight, etc) and also during aggressive (but non-fighting) encounters, and following fights.

Motivation of Nest-touching Movements and Nest-biting.

Nest-touching movements which do not result in nest-building, and therefore appear 'irrelevant', result from fear, aggression and mating conflict situations. Since, in the Gannet, they occur only on the site this may also play a part in the motivation, although site and aggression are so closely linked that it might not be possible to separate their effects.

Using the symbols FAM and fam to denote much or little fear, aggression and mating tendency, in the absence of M (as in male : male menacing encounters) nest-touching movements are most likely to occur with either F or A, or both (e.g. between newly-established males) and are less

likely to follow fa situations (e.g. perfunctory menaces between long-established neighbours).

In Fa and fA situations (e.g. a single bird threatened by a pair) the former is more likely to touch nest material. Bowing, following a severe fight, is followed in the winning bird (fA) by touching nest material but not in the loser (Fa), who, however, is not on a nest-site.

In FM situations (e.g. when the female is afraid in aggressive copulations) nest-touching occurs in the female, but may be partly due to postural facilitation. In AM situations (e.g. in the male during the aggressive type of mutual fencing) nest-touching often occurs. Therefore FM and AM may both elicit irrelevant nest-touching. Tinbergen's (1952) definition of displacement activity includes the idea that it arises when "an activated drive is denied discharge through its own consumatory act(s)". Irrelevant nest-touching movements would seem, in many instances, to fit with this.

Why should nest-touching, rather than anything else, be the irrelevant behaviour performed in the situations described ?. Possibly because nest material is a convenient directing stimulus in these circumstances. If the conflict occurred at sea, for example, bathing could perhaps become the irrelevent action, and in fact, fights ending on the sea are invariably followed by excited bathing in both participants (common too in many water-birds). On this supposition preening, rotary head shaking, scratching, etc.

could all be considered as 'likely' as nest-touching, but may have been excluded because they would reduce the bird's ability to defend itself in precisely the situations requiring vigilance against attack.

If irrelevant nest-touching is the result of nest material 'directing' the behaviour resulting from conflicting tendencies, possibly of different kinds under different circumstances, rather than the result of a specific kind of conflict situation, one would expect (as one finds) that it is elicited by a variety of conflict situations.

Aggressive nest-biting may contain an element of re-direction (perhaps also in biting the female) since incoming birds are often menaced by neighbours.

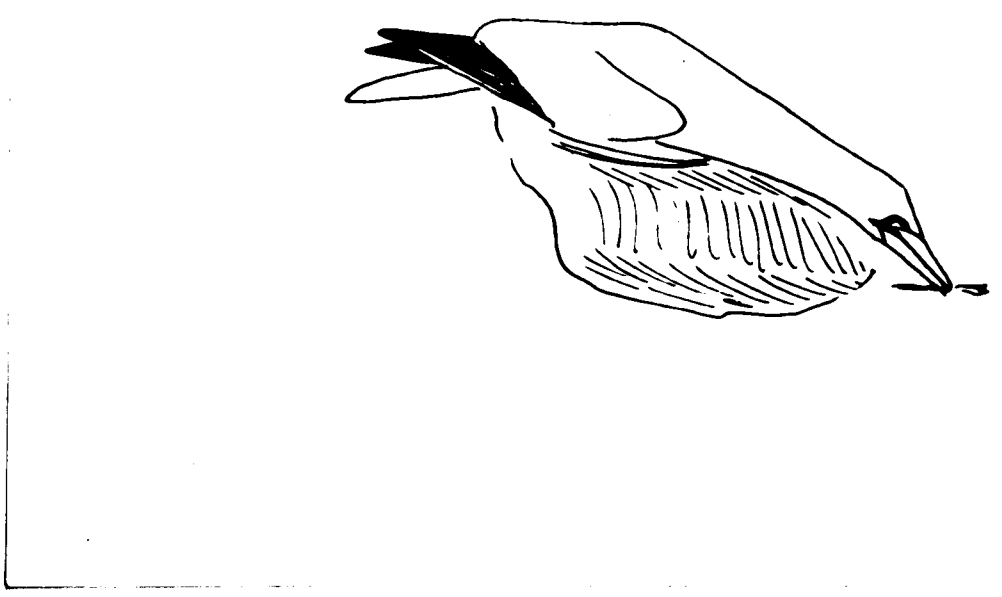


Figure 39. Heightening nest by drawing up material from base of pedestal.

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COPULATION, EGG LAYING AND INCUBATION

Copulation.(Plate 17 and Fig. 40)

Copulation occurs only at the nest site and is usually solicited by the squatting female with violent, rapid sideways head shakes of such amplitude that the bill tip sometimes points along the back to the tail; these continue to some extent during the copulation. Prior to copulation the male points his bill towards the female's head, makes slight head shaking and feet pattering movements, grips the female's head strongly and mounts, usually from the side.

From placing one foot on the female's back to dismounting takes 15 - 35 seconds (average 24 seconds, 180 measured). During copulation the female head shakes repeatedly (in only 1% did she not head shake at all) and occasionally arranges nest material, whilst the male waves his outspread wings and patters noisily with his feet. The feet move singly or in unison - in the latter case the male rests on his tarsi - and must be a powerful tactile stimulus to the female, perhaps aiding the synchronisation of their copulatory behaviour. The totipalmate foot is surprisingly prehensile and by clenching the toes the claws provide an effective grip on the females' plumage. S. dactylatra and S. leucogaster males do not patter or grip the female's head.

To achieve cloacal application the female lifts her tail and the male bends his to one side and beneath hers (Plate 17B) with rapid, shuffling movements. The female's cloaca dilates and contracts whilst the male's everts to facilitate intromission (this was clearly seen on two occasions). Upon contact (and presumably ejaculation) the wings are closed and the male remains immobile for several seconds, afterwards giving the female's head, upon which he retains his grip, several strong shakes. The occurrence of these later stages was my criterion for successful copulation. He may then

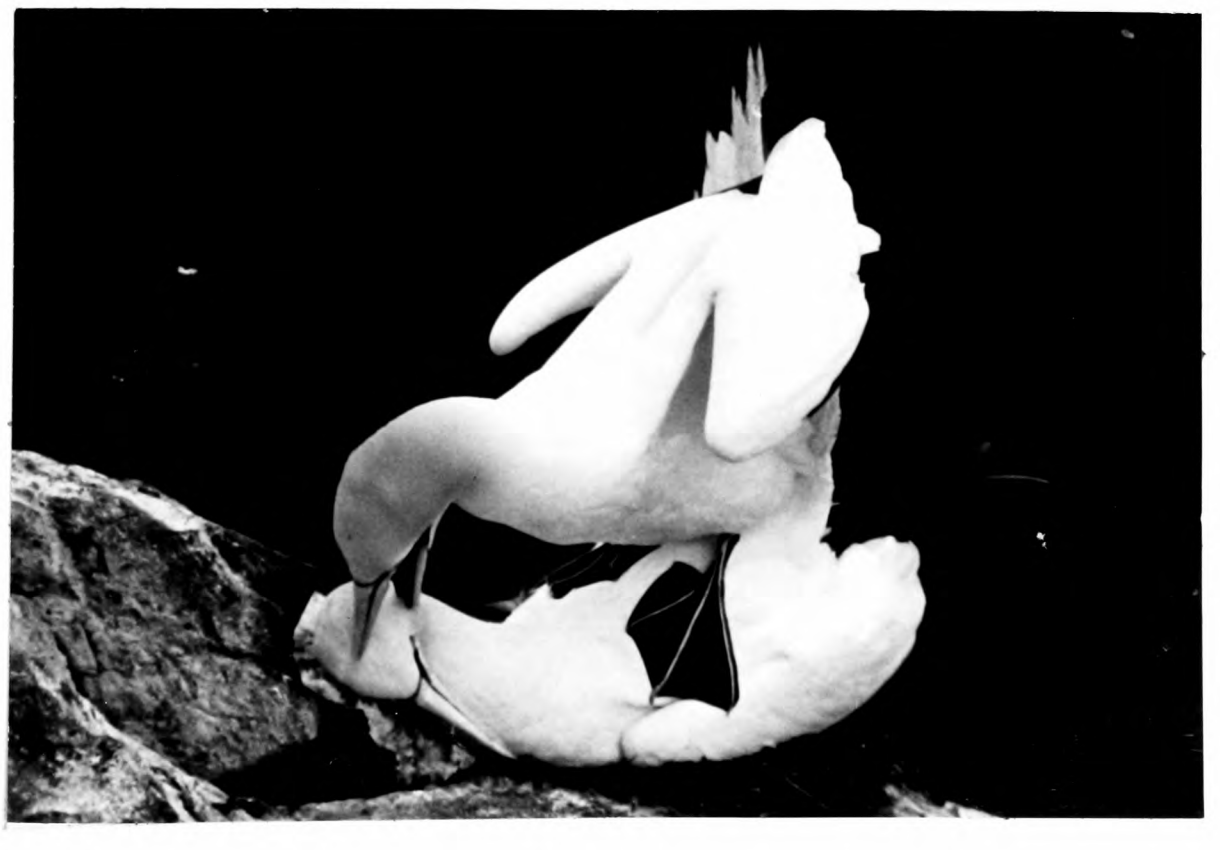
Plate 17 Copulation.

A.

Male mounting. Note powerful grip and female's tail already raised.

B.

Cloacal contact. Female facing away from male.



C.

Male about to dismount.

relinquish his grip and sky-point four or five times before dismounting, fly straight from her back or dismount normally.

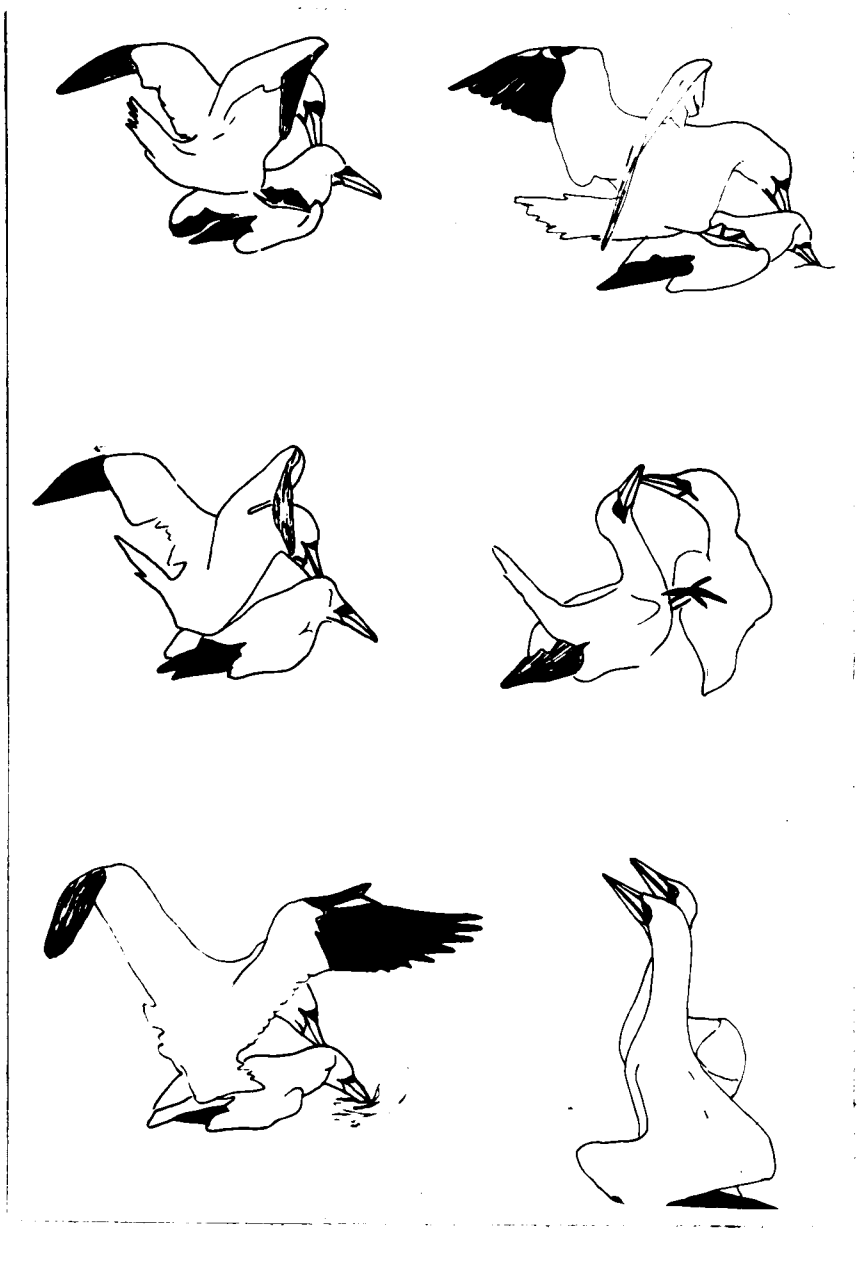


Figure 40.

Sequence of events in copulation. Note female's beak pushed into ground, and the mutual fencing after copulation.

Copulation behaviour varies considerably. An owning female may solicit copulation from an intruding male, who is attacking her (though this is not usual); such a male may copulate, but afterwards continue his attack. Although copulation is always accompanied by biting, this may be extremely fierce in some cases, usually in new pairs or between non-mates, when the female tends to show fear and may prevent cloacal application by lowering her tail. Clearly male copulation behaviour and aggression (and female copulation behaviour and fear) are less incompatible than in other species where hostility must be eliminated before copulation can occur. This is another way in which aggression has been incorporated into normal pair relationships. If the more aggressive males have been favoured by natural selection, as seems likely, it is not surprising that, as a corollary, high

female tolerance has likewise been favoured.

Only one reverse copulation was recorded out of many hundreds seen, although they are much commoner in the Phalacrocoracidae (cf. Shags, Cullen pers. comm.; and Cormorants, Kortlandt 1942).

Copulation (male role) with chicks is not uncommon. Between August 8th. and September 19th. (1961 and 1962) 12 cases of males copulating with chicks were recorded, in two of which the female was also present, so that apparently this behaviour occurs even in the presence of the normal releasing stimuli. In nine cases the chicks were 10 - 11 weeks old and the youngeat was six weeks. The age of the chicks suggests that it may be necessary for them to approximate to adult size and shape. The female did not interfere.

Although reverse adult copulations were so rare, I recorded 12 cases in which females copulated with chicks. This happened between August 9th. and September 9th 1961 and 1962, and in 11 cases involved chicks from 9 - 11 weeks, the youngest being 8 weeks. The male was present on one occasion and did not interfere. Females gripped chicks in the male's usual manner and in three cases copulations passed into preening of the chick's head.

Copulation period and frequency. Copulations occur over a period of some seven months (earliest and latest dates 10th. March and 28th September respectively) corresponding with the unusually prolonged period of site attendance and social behaviour. In any one pair, the period is usually about four to six weeks before egg laying with a small late-season resurgence. In addition to this extensive period during which copulations are frequent, there is a high individual rate (probably a 100 or more per pair are achieved in the period before egg laying). No comparable data seems to have been published for other species, but Cullen (pers. comm.) found that Shags

mount at about the rate of 9 - 12 per day at a period about three weeks before egg laying. This figure includes unsuccessful attempts, whereas these are rare in the Gannet. Figure 41 shows the changes in copulation rate within the observation colony in April and part of May. The peak in the third week of April reflects the immediate pre-egg laying period (mean) for the colony. After laying (mainly spread over about a month) copulations virtually stop for the pair concerned, probably due to the inhibitory stimulation of the egg (see below).

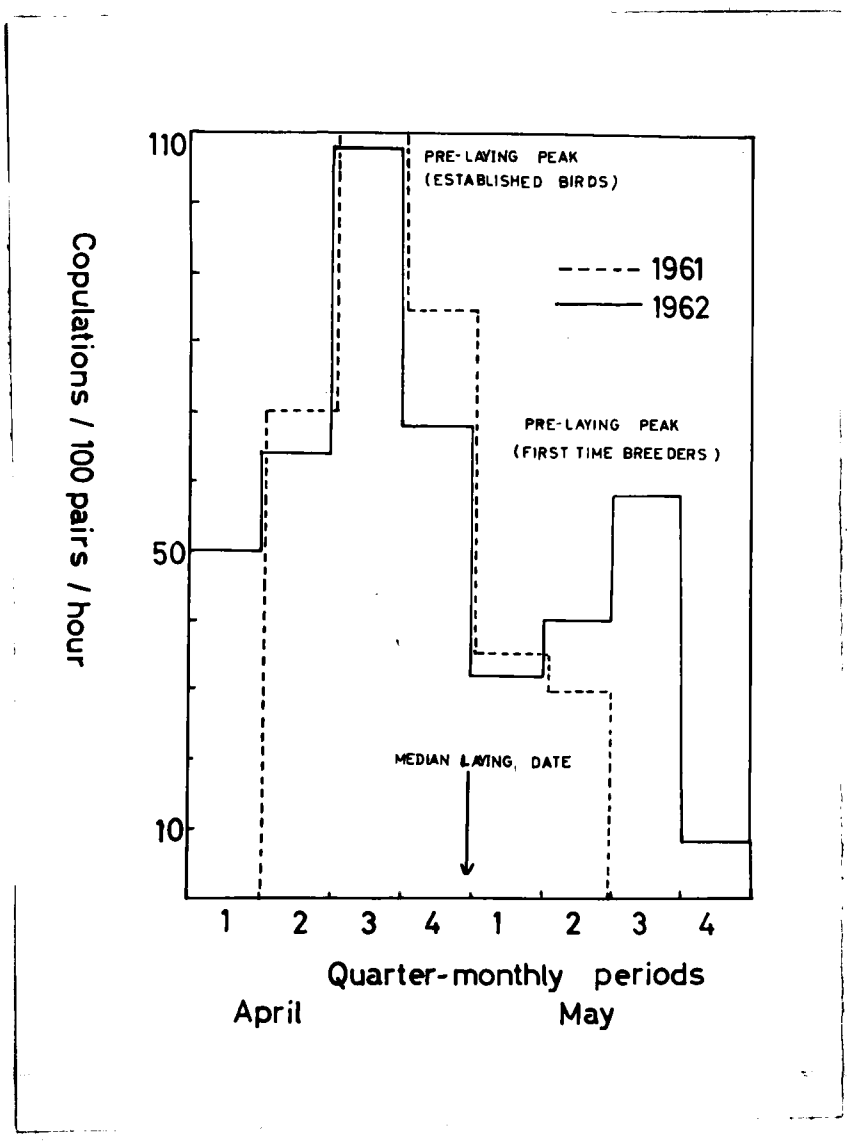


Figure 41.

The seasonal pattern in copulation frequency (479 five-minute checks on a group of 250 nests)

Note : The proportion of pairs present are taken into account.

The drop in copulation rate after egg laying is very striking, particularly since copulation reaches a peak probably 10 to 14 days prior to egg laying. An isolated instance, in which a female in a triangular situation laid an egg to one male but allowed copulation with the other 13 days afterwards, suggests that the male may be the inhibited sex. Occasionally males returning to the nest soon after the egg had been laid made copulation intention movements but actual mounting did not occur, although (from other records) it very probably would have done so in the absence

of an egg.

Lost eggs are usually replaced in about a fortnight (see Table 12) though re-laying can occur six days after loss if the first egg was never incubated. This about corresponds with a peak in copulation 10 to 14 days before the main laying period if females are particularly prone to stimulate copulation at the time when fertilisation can occur (i.e. at ovulation). Copulations restart within 24 hours of egg loss irrespective of the degree of incubation achieved (e.g. in one case 32 days after laying). This was a regular and remarkable phenomenon, indicating that the egg as an external stimulus, and not spermatogenic regression (even after some time) is responsible for the abrupt cessation of copulation after laying (although it is possible that apparently successful copulation (see p. 201) could occur even though there had been regression). The suddeness of the change does not rule out the possibility of hormonal mechanisms being involved. Lehrman (1959) mentions the possibility of external stimuli reflexly causing changes in hormonal secretion.

~~Seasonal changes in the size and histological character of the male gonads occur mainly in birds with distinct breeding cycles~~. All changes in the reproductive systems of birds result from the interaction of environment, gonads and central nervous system. The factors inducing breeding condition may well have received more attention than the regressive phase. Marshall (1959) says that the post-nuptial stage involves a regenerative phase (sexual quiescence) during which the testis does not produce spermatozoa. It is possibly the Gannet's prolonged period of site attachment and aggressive display (both of which probably require a relatively high androgen level) which ~~keeps~~ require the gonads to be active for a much longer period than in short-cycled species. It would be interesting to know whether other long-cycled species are

similarly capable of fertilisation for such an extended seasonal period.

Late in the season, when the chick is well-grown or fledged, copulations begin again, though they never reach the pre-laying peak. They are often successful and do not differ in any noticeable way from early ones, except that the female never showed the intense soliciting behaviour found before egg laying.

The individual frequency (highest rate 4 copulations in 40 minutes) seems not unduly high for sea-birds, though quantitative comparative evidence is lacking. Herring Gulls may achieve 7 cloacal contacts in three minutes, but without dismounting (pers. obs.).

Copulation success. Successful copulation (i.e. insemination) can probably be reliably detected by behaviour. Abortive efforts do not produce the cloacal contact and final immobile stage characteristic of complete sequences. There is seasonal variation in copulation success (Table 44).

TABLE 44. Seasonal variation in copulation success.

Period	No. of pairs involved	Percent unsuccessful
March	49	22
April - May	55	12
June - July	87	67
August - September	29	67

Note : The figures for 'unsuccessful copulations will be minimum, since a proportion of apparently successful copulations may well be unsuccessful.

Thus the period during egg laying is, as would be expected, that in which copulations show a higher success rate.

Pre and post-copulation behaviour. Copulation commonly occurs within ten

minutes of the pair coming together on the site after an absence of more than a few (0 - 3) hours. It almost invariably follows mutual fencing in the pre-laying stage. The copulation soliciting behaviour of the female is apparently extremely stimulating to the male (see p. 202) and almost 'forces' him to mount even though he may be aggressive. One cannot be certain that the male has not first shown copulation intention movements and hence elicited the soliciting head shake, though this seems unlikely in view of his aggression. The female Gannet seems so conditioned to male aggression that she responds to it as a 'usual' part of the pair relationship, and particularly the pre-copulation situation.

After the male dismounts the female often touches nest material and makes nest building movements (in 60% of all cases recorded up to ten seconds after male dismounting), the male did so in 20%. On the other hand, males sky-point more often (35% in the same sample, females 0). Nest touching may be partly due to postural facilitation, the female, sitting in the nest cup, is in the normal position for arranging nest material. The male sky-pointing is correlated with his tendency to leave the site for nest material soon after copulation. This involves movement away from the site, in which context sky-pointing usually occurs (see p. 250). Post-copulation trips to gather nest material vary from a few inches to over a mile. Mutual fencing follows copulation (see Fig. 40) in about 40% of cases.

Female facing-away follows aggressive copulation in some cases, and the male (rarely the female) often assumes the pelican posture, which is probably an ambivalent agonistic posture (p. 163). Thus even in the 'purest' sexual activity, there are clear signs of the complicating tendencies which are such a feature of pair-formation displays prior to copulation.

Egg Laying.

See Chapter 3 for the influence of external factors on the time of laying.

The act of deposition was observed on five occasions on all of which the tail was depressed and guided the egg into the cup - important in view of the Gannet's poorly developed retrieving ability. In three cases the female crouched in a tense position with wings held up and out, tail raised and slightly to one side with strong cloacal contractions. Once extrusion was preceded by ten tail erections, during the last four of which the female fell forward with one wing asprawl. In another the female fell forward as the egg emerged. The remaining cases were less violent. The one accurately timed laying took two minutes. Eggs may be laid at any time of day, and possibly, also, at night, though I had no definite record of this.

Incubation.

Form. Gannets (and apparently all Sulidae) lack brood patches, and incubate their single egg beneath their webs, which become highly vascularised and hot during incubation (cf. S. dactylatra Dorward). Non-breeding birds caught during the breeding season had cool webs, but no known breeders were caught off the nest, so it was not known whether webs remain hot. Howell & Bartholomew (1962), however, showed that the mean internal temperature of incubated eggs of S. sula was 36°C. and the foot temperature 35.8°C. and suggest that the feet do not provide the main source of heat for incubation. They are vague in their alternative, and the difference in the temperatures they record would seem too small to disprove the conventional view. The egg temperature achieved by this method compares favourably with that of brood-spot incubation (e.g. 36.6°C. for the surface temperature of Herring Gulls' eggs, Baerends 1959).

The egg is relatively small and thick-shelled and

the surface area of the webs, about 46 sq. cm. is certainly enough to cover the exposed part. The egg is brooded lengthwise or crosswise, though more frequently the former, the webs being placed one after the other on either side of the egg and overlapping. The incubating bird then settles, adjusting its position with slight rocking, which I call 'nest settling movements'. Positions are shifted several times an hour and nest settling movements made more than twice as often. During very warm weather the egg is sometimes transferred to the upper side of the webs or the incubating bird stands with the uncovered egg between its webs, presumably to cool it.

Although some single-egg laying species (e.g. the Laysan Albatross, Rice & Kenyon 1962) are incapable of hatching two eggs the Gannet (like most Sulidae) can do so. The hatching success of nests containing experimentally doubled clutches was equal to that of singles (87% and 85% respectively), though the average incubation period was 46 days compared with 44 days for singles. This was probably due to less efficient covering rather than chilling resulting from egg transference. Transferred single eggs did not take so long to hatch. The two eggs were incubated in almost any position, provided the egg long axis was horizontal. The incidence of rising and settling greatly increased after donation of an extra egg (cf. Beer 1961). Incubation is less efficient in first-time breeders (p. 40), in that a lower percent of eggs hatched. One such female at first incubated the egg on top of her webs and later lost it. However, there is no difference in incubation period between first-time breeders and experienced pairs.

Behaviour during incubation. Except when sleeping Gannets rarely incubate for more than ten successive minutes without also performing numerous other behaviour patterns, (Table 45). Spells of activity alternate with spells of rest. Certain activities are linked

(e.g. menacing, touching nest material and bowing) and when one occurs at much higher frequency within the 30 minutes so do the others. Other activities (e.g. nest digging) occur in concentrated spells or may be entirely absent (cf. rotary head shaking which occurs at a fairly uniform level in all counts). The commonest activity was touching nest material, since this occurs as a displacement activity in conflict situations as well as autochthonously. Preening and ordinary head shaking are the two other commonest behaviour patterns.

TABLE 45. Behaviour during incubation.

Preen* (No.of mins.)	Head shake	Rotary head shake	Nest dig	Menace	Bow	Touch nest mat.	Nest settle movts.	Shift position	Shift egg
0	30	0	19	3	0	10	0	0	1
8	4	2	16	2	3	26	13	9	2
21	0	1	0	4	0	0	9	1	0
0	18	0	2	3	0	19	5	0	1
14	2	1	0	2	1	9	5	5	1
12	5	2	0	3	1	4	4	1	1
18	11	3	0	0	2	2	6	0	0
1	2	1	0	0	1	3	8	3	0
16	13	1	1	29	5	32	14	1	1
14	1	2	0	0	0	1	7	0	0
18	31	5	4	0	2	27	17	5	3

Notes : (i) Each row shows the frequency of different activities by a single bird in half an hour.

(ii) *Preening is expressed as the number of minutes (out of 30) during which preening occurred (continuous or not).

During incubation quiet spells are usually ended by a sudden stimulus (e.g. the arrival or departure of a neighbour). The activity resulting (e.g. menacing) then leads to another activity (e.g. egg shifting) as a result of changed position, etc.. However, some activities occurred without any such observable stimulus.

Part played by external stimuli. The onset of incubation might be released by the external stimulus of the egg in the nest and might also require the birds to be in a particular hormonal state, or

conceivably, in the female, require the prior act of laying. To test this 21 eggs were donated to different nests in the pre-laying period and the reactions of the birds recorded. Where the egg was rejected the date on which their own egg was subsequently laid could also be noted. The substitutions were of fressh Gannet eggs (except for three pot eggs, smaller than a Gannet's, and one Shag egg).

There were 12 outright rejections, involving both male and female, in which the Gannet gripped the egg between its mandibles and either placed it on the rim of the nest with mandible vibrations (as in deposition of nest material), jabbed it in the bottom of the nest, pushed it over the rim or ignored it. 11 of these nests were subsequently laid in : 6, 9,(four cases), 10 (two cases), 14-19, 20, 21, and 27 days later.

The remaining 9 eggs were accepted (3 by males, 2 by females and 4 by birds of unknown sex), but 5 of them only temporarily. Birds which continued to incubate and hatch the foster eggs failed to lay their own - an inhibitory effect known in many other species. Of the five which accepted the foster eggs only temporarily, one did not lay and the remaining four laid : 4, 5 and 9 (two cases) days later. In other words of birds which did lay subsequently those which accepted the foster eggs were closer to laying their own than those which rejected them. Beer (1963) also found this for the Black-headed Gull. The tendency to incubate, as one would expect, increases with the laying of their own egg. However, the fact that some individuals rejected a donated egg some days before laying, whilst others accepted one at a similar time may suggest (if incubation depends on a specific hormonal state) that this is reached by different birds at different times in their cycles. Incubation tendency increases with seasonal gonad development, but the response to the egg is apparently present for some time before required.

This need not have been the case. Certain aspects of female breeding behaviour can develop independently of others, though all under the influence of oestrogens. Alternatively incubation behaviour might conceivably have depended on reflexly initiated hormone activity, triggered by the sight or 'feel' of the egg.

Whilst such a strong tendency to reject eggs near to the laying date might not be expected, it was even more surprising to find that a female rejected a donated egg nine days before laying her own, which she then lost, then again rejected a donated egg, but re-laid 20 days after this further refusal. She had therefore recently experienced both laying and incubating, and was within three weeks of laying again, yet rejected a substituted egg. This strongly suggests that incubation tendency is closely linked with the deposition and presence of the egg and quickly wanes in its absence. Of three other eggs donated after natural loss two were accepted (one a Shag's) and one rejected only two days after the recipient's own had been lost.

Egg-shifting and nest-settling movements. The position of the egg beneath the webs is frequently altered, using the lower edge of the closed (or slightly open) bill, pointing backwards between the webs. This behaviour occurs about twice an hour during incubation (see Table 45).

Settling movements, altering the position of the webs on the egg, are common and invariably follow egg-shifting. Only rarely are they followed by leg or wing stretching, so that they would seem to be concerned with incubating rather than relieving muscle cramp. Nest-settling movements occur even before there is an egg in the nest and become commoner just before laying. Like some of the adjusting movements in terns (Poulsen 1953) the Gannet's settling-movements do not seem to alter the position of the egg but, unlike the terns,

are caused by feet, rather than body, movements.

Egg-retrieving. (Plate 18) Poulsen (1953) concludes that in all ground nesters with shallow nests and liable to displace their eggs, egg-retrieving is well-developed. The Gannet, only partially a ground nester, and with its tall, pedestal nest, shows little retrieving ability if the egg is knocked or experimentally placed out of the nest. This may be because recovery is generally impossible - either the egg rolls into a deep valley between nests or falls over the ledge, and in any case their is very little loss due to accidental displacement. However eggs placed on the rim of the nest are rolled back into the cup and the bird also attempts to retrieve those just within reach though a little below the rim. In this it is usually unsuccessful since, even with low rims, the egg rolls away from the beak. Gannets seem to lack the steering movement of the egg-rolling Greylag Goose Anser anser and are very quickly discouraged. S. dactylatra (Dorward) apparently rolls nearby eggs into its nest and may accumulate several, but it does not build any nest. I have a single record of a male Gannet which had just lost its egg attempting to roll a neighbour's unattended egg into his own nest. Whereas Herring Gulls will build many separate nests around their displaced eggs until eventually incubating them several yards from the original site (pers. obs.) Gannets do not attempt to incubate outside the nest even where this is possible. Such a response would rarely be useful.

Role of the sexes in incubation. When the female first vacates the egg, which, if the male is present, she usually does soon after laying, he immediately begins his first incubation spell, the sight of the egg apparently releasing the appropriate behaviour. The early change-over may be partly due to the female having already spent a long pre-laying spell on the nest. A similar

Plate 18.

Egg-retrieving experiment. Despite low nest, incubating bird was unable to roll the egg back into the nest and quickly abandonned the attempt.

procedure occurs in many other species which habitually take long incubation stints (e.g. King Penguin Stonehouse 1960; Laysan and Black-footed Albatrosses Rice & Kenyon 1962; Adelie Penguin Sladen 1958; Yellow-eyed Penguin Richdale; etc.).

Two-hourly checks over several days and one or two daily checks over several weeks established that the share of the sexes in incubation was roughly equal (see Table 32), though the male's were longer (average 35.6 against 30.2). In both sexes the spells became slightly shorter as hatching approached, but dropped suddenly after hatching. Dorward found exactly the same for S. dactylatra.

Change-over. (Plate 19, Fig. 42) Arrival of the partner during incubation is followed by mutual fencing and change-over. An odd fact is that before the incoming bird relieves its mate it usually sky-points and moves slightly away from the nest before returning and taking over (see p. 250). Departing birds very often elicit mutual fencing intention movements from the partner, as though trying to influence it to remain on the site. Once the incubating bird rises the incomer pushes directly onto the egg (Fig. 42) and settles down, usually ignoring the mate, who repeatedly sky-points before leaving. Table 46 shows the time taken to change-over. This is calculated from the time of arrival at the nest to stepping onto the egg. It is clear from these results that females are significantly less willing to vacate the egg than are males, which may possibly indicate a stronger incubation tendency.

TABLE 46. Time taken to change over.

Sex arriving	Av. length of change-over		Longest time		Shortest time		No. of cases
	Min.	Sec.	Min.	Sec.	Min.	Sec.	
Male	7	58	22	0	1	30	31
Female	2	49	10	35	0	5	23

Plate 19 Change-over.

A.

Departing bird sky-points after mutual fencing.

B.

Turns in sky-pointing position.

C.

Takes off, still in sky-pointing position.
In this position take-off is accompanied
by a special note.

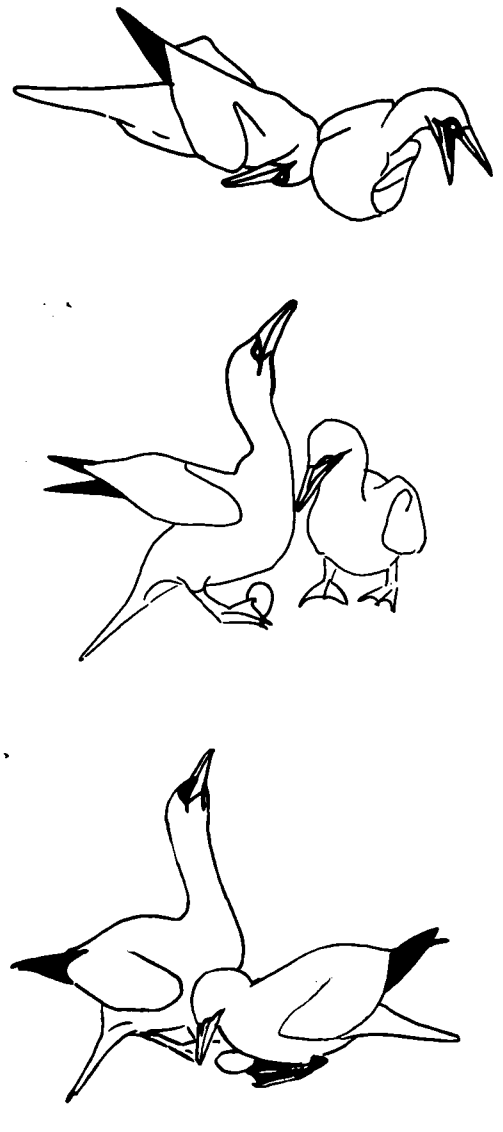


Figure 42.

Change-over procedure.

A. Pushing of incomer.

B. & C. Sky-pointing of relieved bird, incomer moves onto egg.

Note : A. and B. & C. are from different sequencies.

Although change-over times (G.M.T.) are scattered throughout the daylight hours, Table 47 shows that there is a tendency for most arrivals to occur between dawn and mid-day, probably representing birds which departed late the previous day, fished in the early hours and returned between then and mid-day.

After change-over some time usually elapses before the outgoing partner leaves the vicinity of the nest, but once away it usually does not return until the next relief though I have records of birds flying over and inspecting their nests several times from the air before finally departing. Significantly these were usually birds involved in competition for mate or site. Occasionally a relieved bird brings nest material and may then spend further time sleeping beside the nest.

TABLE 47. Proportions of arrivals (male and female) at different periods of the day, throughout the season.

	05.00 to 09.00		09.01 to 12.00		12.01 to 15.00		15.01 to 18.00		18.01 to 22.00	
	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.
April	6	9	25	7	12	4	14	11	6	6
May	10	10	19	19	20	3	3	10	4	2
June	20	16	16	16	3	15	6	3	3	2
July	5	38	10	12	3	1	1	2	18	10
August	20	16	22	15	2	2	1	0	11	11
September	25	18	16	14	14	5	1	1	5	1
October	24	30	10	20	0	4	12	4	0	0
Average	16	19	17	15	8	5	5	4	7	4

Hatching. Once the egg begins to chip it is transferred to the top of the webs; incubation underfoot would crush the weakened shell. In three instances this transference was seen when the egg had developed only a small hole, by which time the chick is cheeping. The stimulus to which the adults respond could therefore be either visual or auditory. It should be recalled that transference of the egg to the top of the webs may also be caused by warm weather. Thus two entirely different stimuli elicit the same response.

The newly-hatched chick is also brooded in this position and in four observed cases aberrant behaviour at this stage resulted in its death, the adult continuing to incubate either the hatching egg or the new chick underfoot. Of 13 other cases eight eggs disappeared around their due hatching date, and five chicks disappeared at less than five days, possibly also due to trampling underfoot, or perhaps to faulty feeding (Snow 1960, says Shags sometimes experience great difficulty in feeding small young). Of these 17 cases seven were first-time breeders - a disproportionately high number.

In a further case the small chick almost died during a spell of female attendance in which she trod on it, subsequently recovered, but at three weeks died during bad weather. This is probably another instance of death due to parental inadequacy. Nevertheless, even experienced adults sometimes stand on their newly-hatched chicks, which must be highly resistent to such treatment. The presence of more feathers than usual in the nest at this stage may help to protect the chick.

One female was seen to prise half an eggshell off the hatching chick. This was a precisely performed piece of behaviour and not merely accidental due to the female mandibulating the eggshell with the chick inside. However, it is not, apparently, necessary and chicks are certainly capable of freeing themselves, though they may take over 36 hours to emerge after chipping (cf. two days in the Manx Shearwater, Lockley 1942; three days in the Royal Albatross, Richdale 1942; and four days in the Sooty Shearwater Richdale 1945).

Treatment of eggshell. Gannets leave the eggshell lying around the nest for some time after hatching (four days noted) and may eventually drop it over the side or place it on the rim, though sometimes it is merely trampled into the nest. Occasionally it is mandibulated like nest material and pieces flung away with a quick sideways head shake. This disposal is not practised systematically. Non-removal may be connected with lack of predators which could be guided to the nest by the shell (cf. Greenshank Tringa nebularia C. & D. Nethersole Thompson 1941; Black-headed Gull, Tinbergen et al (1962) and terns, Cullen). The other possible reasons for eggshell removal discussed by these authors (lacerating young, nest hygiene, etc.) could, of course, account for the Gannet's eventual disposal, though this seems unlikely.

- 13 -

THE CHICK

Feeding. See Chapter 4.

Care of Chick.

Gannets brood their chicks on top of or between the webs for some time after hatching (Plate 20A). To move the chick the adult sometimes opens its bill very widely (in contrast to the movement used for shifting the egg) and trembles its mandibles (possibly partly released feeding behaviour) one on each side of the chick, meanwhile making small tucking movements. This (like handling nest material) is often followed by sideways head shaking and occasionally mandible vibrating.

The adult habit of removing hard objects from the floor of the nest by deep probing (nest-digging) becomes more common when the chick is tiny. It may help to prevent injury to the egg or chick.

After about three to four weeks the chick is no longer brooded and must endure all weathers, which it survives extremely well, although a combination of prolonged rain and cold proved fatal in five cases for chicks between three to five weeks old. Later adults sometimes shade their chicks by standing sunwards of them, but chicks were never seen to seek this deliberately. When (presumably) too hot they pant a lot and sprawl supinely on the drum (Plate 20C). They also stand on their tarsi and expose the under surface of their webs which they also dither, thus aiding heat loss. The sudden onset of rain in cool weather on several occasions caused many adults to attempt to tuck even large young (2-3 weeks) beneath their breasts, so that where practicable these are sheltered.

Chicks are frequently preened from about three days up to losing their down and occasionally when in the juvenile plumage. At this stage mutual preening between chick and

Plate 20 The chick.

A.

Day-old chick being brooded on top of webs.

B.

Four day-old chick.

C.

Sleeping position of chick and adult.

D.

Wing-exercising in five week-old chick.

adult also occurs.

Adults defend their young from attack either by potential predators e.g. Herring Gulls, or from other Gannets. Gannets with eggs or young chicks watch hovering gulls intently, with head retracted and bill vertical and lunge at them if they come near. Even man is liable to be attacked, particularly when the young are newly hatched.

Chicks virtually ignore hostilities between adults and may do to sleep during menacing bouts with, in some cases, the neighbour's threatening beak within an inch or two of their faces. Beak hiding only occurs if they are actually pecked. In the rare absence of the female, chicks direct the aggressive biting of the incoming male, and may also act as the substitute in re-directed aggression.

Adult Recognition of Chick.

Many colonial species distinguish between their own offspring and other young of the same species. Arctic Terns attack strange young if they approach for food (Cullen). Black-headed and Herring Gulls kill strange chicks if these wander into their territory (pers. obs.) and Guillemots apparently recognise their chick on a crowded ledge even if it has moved position slightly (Uspenski 1958), though Tschanz (1959) says that the chick plays a part in the process. King Penguins (Stonehouse 1960), Yellow-eyed Penguins (Richdale) and albatrosses (Rice & Kenyon 1962) also recognise their young, and/or are distinguished from strange adults by them. Even when the young of Adelie Penguins have formed creches the adults find and feed only their own (Sladen 1953). This recognising ability gradually matures; substitutes are accepted when chicks are small but not later. Young Shags gather on the sea-rocks after fledging and are fed by their own parents (Snow 1963) although after becoming active and until about a month old, Snow states that chicks "often" go to neighbouring nests and are accepted. Coots Fulica atra will adopt young if they are less than 14 days and resemble their own young,

otherwise they may be killed (Alley & Boyd 1950). Young Coots therefore imprint on their parents. It is seldom possible to know how the distinction between young is achieved, though calls appear to play some part.

In these species it is clearly advantageous to reject strange chicks, since their habits result in many chicks approaching and begging from strange adults. To accept these would clearly result in the inadequate feeding of all. On the other hand, in the Gannet, as also in the Kittiwake, chicks normally stay on the nest and there is usually no danger of feeding strange ones. Wandering chicks, however, are strongly attacked, as they are in S. dactylatra and (probably) S. leucogaster.

The Gannet is clearly well able to distinguish individual adults and not merely its mate (Richdale reports the same ability in Yellow-eyed Penguins) and might be expected to recognise its own chick. A series of substitutions, designed to answer two questions in particular, was therefore carried out :-

(1) Does the adult respond appropriately to prematurely offered newly-hatched chicks, and if so from how early in incubation (i.e. without having hatched one itself). A graded series of substitutions demonstrated that chicks are accepted well in advance of the hatching date. Chicks which hatched as much as 32 days before and 19 days after they 'should' have done fledged successfully at the usual age. The adults therefore reacted appropriately to eggs which hatched out of step with their own internal condition. as determined by the date of their own egg. This does not show that there is no change in responsiveness of the adult as a result of incubation, but that any change within the limits of the experiments were too small to affect the chick's survival. Several other instances of the very variable relationship between physiological condition and external situation

have already been mentioned in this account. Hormonal state is the coarse adjustment and reflex neural response to external stimuli the fine one.

(2) Do adults, having experienced their own chick, thereafter distinguish between it and any other, either of similar or dissimilar age ?. If so at what age of chick does this discrimination occur ?. Also, does the adult need to experience hatching?.

The substitutions fell into three categories, eggs for chicks, chicks for eggs, and chicks for chicks of differing ages.

Eggs for chicks. In four out of five cases the adult accepted eggs in place of chicks varying from 3 - 17 days. In the fifth case the chick was 23 days old, and the adult treated the egg as nest material.

One may conclude that, at least for the first two weeks after hatching, adults will often return to incubating, though they may lose this reversibility after about the third week. In view of the fact that infertile eggs may be incubated for at least eight weeks beyond the normal hatching date (which shows what a large part external stimuli play in terminating incubation), whilst three weeks after hatching its chick a bird will then reject an egg, it may be concluded that experiencing the chick, as such, over a prolonged period, reduces readiness to incubate an egg. Here, as shown also in the substitution of chicks for eggs, there is clearly no sudden switch in behaviour as the result of external stimuli, but rather a slow internal change to which externally received stimuli (e.g. chick,etc.) contribute cumulatively.

Chicks for eggs. In all of six cases, chicks ranging from 3 - 23 days were accepted instead of eggs. Chicks were thus provided 0 - 16 days earlier and 3 and 9 days later than the 'expected' hatching date. Adults therefore, do not require each year the experience of hatching

an egg to enable them to react appropriately to a chick. Of course, their method of feeding probably does not require any particular physiological state to accompany hatching (cf. pigeons, in which the production of crop milk is necessary and incubation behaviour ceases automatically a few days after the egg is due to hatch).

Chicks of differing ages. Six exchanges were made involving chicks differing from 0 - 7 days, covering an age range of 2 - 36 days. All were accepted, showing that up to this age at least, a Gannet will accept a substituted chick differing considerably in age from its own.

In fact, observations of 'natural' situations showed that occasionally 10 - 11 week-old chicks wandered onto a nest during the adults' absence as a result of disturbance, and were accepted in addition to the rightful chick. In one case the rightful chick was smaller and died competing with the intruder, but usually, if both chicks were large, both survived despite an age difference. Also, adults whose own chicks had fledged occasionally accepted and preened chicks which paused at their nest on the way to the edge.

"Chick 5029 fledged on September 3rd. 1961 and on September 7th. another chick arrived at the nest, was accepted and remained for 24 hours. Chick 5038 fledged September 4th. 1961 and a stranger was accepted from 8th. to 12th. September."

To balance this picture it is necessary to add that in the presence of their own chick adults usually discriminate against a stranger if they see it arrive. Under such conditions it is, of course, a 'wandering' chick and as such attacked.

It would be a disadvantageous division of labour if some pairs reared their own as well as a neighbour's chick. The aggression of the adults towards wandering chicks and the cliff position of many sites, to which the young respond innately by staying strictly on the nest, make it unlikely that a Gannet chick will find its way on to a strange nest. There

has therefore been no need for adults to develop the ability to distinguish their own chick from others. By contrast, a Herring Gull (and probably all the species mentioned above as able to recognise their own young) may easily be faced with a chick which wandered undetected into their territory and must either be fed or rejected.

Some observations revealed puzzling variation in parent reaction to their own chick off the site, sometimes attacking them and at others not. In one instance a female who was attached to two nests, one empty, attacked her own chick fiercely when it tried to join her on the second nest but accepted it when it (and later she) returned to the proper one. However, adults also tend and defend their chicks slightly off the nest. Therefore one cannot say that parents accept a chick (their own or another) only at their own nest; however chicks are more likely to be attacked away from it.

Summary. Gannets accept chicks of widely differing ages for eggs. They do not require either the experience of the full incubation period or of hatching to respond appropriately to the chick. Their reaction is reversible for some time. They also accept substituted chicks widely different in age from their own. However, they fiercely attack wandering chicks. This, together with the chick's innate tendency to remain strictly on the nest means that parents are rarely, if ever, called upon to discriminate. The goal of feeding only their own offspring is therefore usually achieved without discrimination on the nest.

Adult Aggression Towards Chicks in the Colony.

Adults (even non-breeders on the fringe) are conspicuously aggressive towards unattended or wandering chicks of any age, and several females were seen to wander round attacking unattended chicks indiscriminately. Even a small, downy chick releases violent attack. One such chick, already almost dead from previous attacks, crept up to a nest, con-

taining a chick of similar age and lay there. The adult on duty attacked it violently and killed it. When change-over took place the incomer did not apparently notice the dead chick for a time, but later launched the most extreme form of attack for several minutes, calling stridently and striking repeatedly at the chick.

It is rare for Gannets to leave their chicks unguarded, even for a moment, unless one parent dies, a spell of bad weather occurs during the later stages of chick growth, or it is very late in the season. But when it happens the results may be fatal : I have five records of unguarded chicks killed by neighbouring adults, even though the chicks remained quietly on their nests.

This aggression warrants special emphasis, particularly in view of adult aggression towards newly-fledged juveniles (p.225). It may be an effective method of discouraging chicks from wandering and therefore advantageous, but the habit of attacking non-trespassing chicks seems, so far as the species is concerned, to be a dysgenic extension of a functional behaviour pattern. Non-selective and apparently of no advantage to the performer, it has persisted perhaps because there has been no selection pressure capable of eliminating it without incurring other disadvantages. If adults did not attack unattended chicks in this way, members of a pair could then fish simultaneously, thus increasing their food-gathering capacity (see p.65) which could be important in a less constant feeding environment.

When (rarely) a number of chicks were simultaneously left unattended they wandered about and indulged in playful behaviour, showing that it is apparently adult aggression which chains them to their nests.

In summary, wandering chicks are strongly attacked by adults, even though the chicks, as individuals, would be accepted as substitutes for their own. The tendency to attack

off-site or unguarded chicks effectively discourages wandering or the absence of both parents together.

Adult Aggression Towards Fledged Chicks on the Sea.

Newly-fledged young, unable to rise from the water, are often attacked by adults and immatures near the Colony. The following extract is taken from a field note book for 26th. August, 1961 : "of six juvenile Gannets on the sea four were seen to be attacked by adults and immatures, from 1 - 20 taking part in the attack on any one chick. In three cases the attacks persisted for over an hour, and involved 2nd., 3rd., & 4th. summer and adult birds. A constant stream of newcomers, attracted by the commotion, replaced leaving birds. The attacks (biting of the head) were launched either from the air or from the water nearby. The juveniles often faced-away or submerged their bills and foreheads. They also attempted to thresh their way clear by pounding the water with their wings and dragging the attendant adults yards through the sea. Even if the attacks themselves did little damage, the exhausting effect of dragging two or three adults for an hour, plus the inevitable waterlogging, must have an adverse effect on the juveniles (Plate 21) and could easily reduce its chances of successful fledging". I have several records of juveniles forced to return to the Rock after such attacks - one with adults attacking all the way.

The attacks occur most commonly during the first two to three weeks of the fledging season. This apparently is also true of the Arctic Tern, which tends to attack the first chicks on the wing rather more than later ones (Cullen); the Black-headed Gull (H. Kruuk pers. comm.); the Shag(Snow 1963) and it is also suspected in the Guillemot; Rice & Kenyon (1962) record that Laysan and Black-footed Albatross chicks on their way to the sea are attacked by adults. In none of these cases, however, are the attacks comparable in severity to the Gannets'. In the Gannet at least, there is as yet no convincing suggestion for the adaptiveness of this behaviour. Gannets react to a dead, wounded or in some way abnormal adult and sometimes to a pair fighting on the water, by circling over them in a dense cloud which could be suggested, though perhaps rather unconvincingly, as an anti-predator device. They react similarly to almost any strange object (e.g. a canoe, a boat new to the area, a swimmer, etc.).

Plate 21. The juvenile.

A.

Juvenile of twelve weeks, about to be fed.

B.

Juvenile wing-exercising. Note dark ventral surface and absence of lines on webs.

C.

Juvenile (on left) is 'sea-gazing'. This behaviour becomes common a few days before departure. Note variation in plumage between different juveniles.

D.

Waterlogged juvenile returning to Rock after attack by adults.

The reaction to chicks, however, cannot sustain even this explanation and it seems possible that it is an extension of the habit, perhaps advantageous in the colony, of attacking unguarded chicks. If so, it is another example of aggression 'outcropping' outside its functional context. The adults practising this aggression would not be reproductively penalised as a direct result and the habit of distinguishing between 'chick on the sea' and 'chick in the colony' may therefore not have been selectively favoured.

Chick Behaviour.

The behaviour of the chick will be described in order of its appearance.

Body care or comfort behaviour. During the first few days little is seen of the constantly brooded chick except wobbly head movements beneath the adult. At the age of about eight days (Plate 20B), when the chick is still very sparsely covered with down and has only rudimentary wings, it makes its first attempts at wing-flapping, ordinary head shaking and rotary head shaking. Wing-exercising (Plate 20D) (i.e. sustained bouts of wing-flapping) occur from three weeks onwards, but do not become regular until the flight feathers have erupted. With the freeing of the primaries it becomes frequent and is unfailingly stimulated by a shower of rain. Wing-exercising bouts usually last about 30 - 60 seconds. The whole wing is flapped at first but gradually the action of the proximal part decelerates and only the wing tip moves. Wing-exercising (usually performed facing the wind) is not accompanied by jumping or walking (as it is in Herring Gulls, for example). This would usually be dangerous. Young Kittiwakes, too, jump much less than other gulls (Cullen) probably for the same reason.

Rotary head shaking, however, remains relatively infrequent and even the down-shedding period produces nothing

comparable to the spectacular increase which accompanies the adult moult of body feathers. Sideways wing-stretching and wing-arching, with neck forwards and downwards and head horizontal, occur within the first fortnight.

Chicks begin preening (i.e. nibbling down) at about two weeks, though until the feathers grow, it is relatively perfunctory. Adults preen their chicks from about one week and chicks, from the age of about eleven weeks, begin preening their parents. Mutual preening between parent and chick was recorded from chicks of 70 days onwards (this seems relatively rare in birds). Often chicks preen their parents on the wings and back, which allo-preening adults hardly ever do, indicating that the preoccupation which adults show with each others' head and neck develops later.

'Oiling' (the movement by which birds with an oil gland distribute the secretion over their plumage), including rolling the crown on the oil gland at the base of the tail prior to rubbing the wings and back, was seen from 58 days onwards. By this time the feathers are well grown, though still thickly covered with down in many places.

Yawning, i.e. mouth-opening involving only the lower mandible (not using the naso-frontal hinge as adults occasionally do to raise the upper mandible) occurs within the first ten days. Distension of the inter-ramal skin to dilate the pharanx and accommodate fish occurs early in development (certainly by 10 - 14 days). Gular-fluttering, so characteristic of the Pelecaniformes, also appears in this period and is seen in hot weather or intense food-begging.

Chicks sleep with their heads hanging over the nest rim (Plate 20C) or curled round like a dog, until they are six to eight weeks old, when they begin to adopt the adult posture, standing or sitting with head in scapulars (Plate 20C) Even fully grown chicks (12 weeks or more), however, occasionally sleep prone, with head lying on the ground, a habit never

found among adults. The persistence of juvenile or pre-juvenile habits is an interesting topic. Young Herring Gulls, though perfectly able to fly, will often crouch instead.

Although tiny chicks cannot void clear of the nest, they apparently do not produce faecal sacs, and merely soil the nest. The adults occasionally dig in the nest bottom and fling away bits, but it is usually not possible to note whether soiled material is specially selected. Later, the chicks void clear of the nest cup. Direction of faeces downwards on to the side of the nest as sometimes seen in adults was not observed.

Appeasement postures. Beak-hiding (see Dorward's Plate 8B. for similar posture in S. dactylatra) as in the Kittiwake (Cullen) is the young chick's response to attack, either by strange adult or larger chick, and appears during the first month. The bill is tucked either centrally or to one side beneath the body, and the chick lies flat on the ground. Adults often continue to attack (and sometimes preen) beak-hiding chicks for long periods (e.g. 30 minutes), so that the chick's appeasement posture is not immediately effective. It seems desirable, wherever possible, to have some measure of the effectiveness of appeasement behaviour to avoid creating a false impression of their efficacy. Beak-hiding and adult facing-away are two relatively straightforward examples, compared for instance with the Black-headed Gull's head-flagging, and (as one would expect) both have limited effect.

Chicks are noticeably less prone to beak-hide from their own parents, even if (as sometimes happens) these attack them, but will do so. During the excessively boisterous attacks which large young make on their parents, facing-away sometimes occurs spontaneously without the adult having retaliated, the chick apparently associating its own aggressive behaviour with parental retribution.

The pelican posture is rarely seen in chicks, but occasionally a brief form, passing into facing-away, can be detected. It is interesting that this posture (argued, p. 163 to be partly aggressive) should be lacking in the chick.

From about nine weeks chicks show facing-away (which also results in the beak being hidden, but is different from beak-hiding as defined here), in the form used by adult females. They still continue the infantile beak-hiding, however. Chicks face away from each other, but only beak-hide when subjected to severe attack from a much larger chick.

Handling nest material. Chicks show an interest in nest material from about two weeks, picking up straws, feathers, etc. and mandibulating them. Later they attempt to snatch grass or seaweed from incoming parents, placing it on the rim of the nest with nest-building movements and mandible vibrating.

From about eight weeks they frequently 'play' with nest material, tossing feathers and sticks into the air and catching them. This behaviour could help to perfect the co-ordination necessary for manipulating fish. It is usual for the young of higher vertebrates to 'handle' objects in their environment, thus gaining experience of various kinds. The young Gannet's apparently precocious interest in nest material is therefore not unusual.

Aggressive behaviour. Facing-away, which has already been mentioned, appears with an increasing tendency towards aggression. Chicks menace each other when about a month old, but only perfunctorily. Later they develop adult-type menacing, darting their beaks towards each other, with the final sideways twist. They fiercely attack trespassing chicks, irrespective of size difference, and sometimes maintain attacks, accompanied by yapping, for long periods. This could help to prevent doubling-up of chicks.

Chicks occasionally menace neighbouring adults (who

normally ignore them) and from about seven weeks frequently menace and attack their own parents, so severely that the adult female often faces-away and both sexes, but particularly the male, occasionally retaliate strongly. These attacks are delivered with the unco-ordinated movements typical of young animals; violent and mis-timed jabs, excited yapping, contortions and perfunctory self-preening are all mixed up. The stimulus received by the adult when the chick grabs its beak in an attacking manner never causes regurgitation, whereas the touch of the chick's bill in food-soliciting does.

Wandering chicks (during fledging or as a result of exceptional circumstances already mentioned) are attacked by adults and any other chicks within beak range. Already the aggression which is to characterise so much of their adult life is conspicuous. Since each nest contains only one chick this quarrelsome tendency is not disadvantageous. In the Kittiwake one chick usually becomes dominant (Cullen) and hence obviates dangerous fighting. An interesting difference apparently exists between S. serrator and the Gannet. Wodzicki & Robertson (1953) state that chicks of the former begin to visit each other from about six weeks and during the last two or three weeks before fledging gather in groups, exercise or wander about the gannetry (which is on flattish ground at Cape Kidnappers). If correct (it could conceivably be a result of disturbance by visitors) this represents a very significant difference and it would be interesting to have some objective measure of this race's aggression for comparison with the Gannet (see also p. 86).

Bowing and mutual fencing. Bowing, although extremely rare, does occur in chicks of 11 weeks or more. The bows observed were ill-defined, but clearly incorporated the head shake and an incipient dip, with wings partly open and were accompanied by shrill yapping (cf. adult calling). Equivalent aggressive territorial behaviour

(long calling) occurs in Herring Gulls no more than eight weeks old.

I also twice saw fully grown chicks performing a short bout of low-intensity mutual fencing with the female parent following aggressive action by a neighbouring pair. This is exactly the situation in which the female would have fenced with the male had he been present.

By the time the chick fledges it may have shown all adult behaviour patterns (though it is unlikely to have bowed or mutual fenced) except copulation, aggressive nest-biting nest-digging, gathering nest material, sky-pointing and behaviour associated with incubation and care of the chick. It is striking that even when chicks leave the nest they never sky-point. This only develops in social behaviour (e.g. clubs) later.

Leaving the Nest.

Pre-leaving behaviour. From the age of about six weeks chicks begin to wing-exercise regularly. As the primaries free themselves from the sheaths the exercise becomes more vigorous and from about ten weeks the Gannet can fly but would probably not survive if it did. There is no tendency to exercise facing the sea, but rather into the wind, from whatever quarter. Rain induces a terrific outburst of wing-exercising which may continue steadily for minutes on end, producing a highly unusual effect when myriads of black wings sprout from a mainly white colony (see Film).

From about mid-September, the flatter parts of the colony tend to be temporarily deserted by large numbers of parents during bad weather (e.g. gale force winds with rain). This permits the 10 - 13 week-old young to wander more freely and exercise vigorously, indulging in play such as tossing nest material about and tussling with other chicks.

One to four days before departure the chick shows distinct behaviour patterns associated with leaving. The

following account is generalised from many immediate pre-departure observations. The chick assumes a characteristic long-necked position and leans slightly forward, gazing intently out to sea for perhaps two or three minutes before relaxing and turning to face inland again. Individuals watched continuously for up to 13 hours, repeated this process 20 - 30 times. After facing the sea for some time the chick often wing-exercises (Plate 21), a sign that it will almost certainly not leave then. The sea-gazing becomes rather more continuous and concentrated in the final few minutes prior to leaving, though even then it is not always possible to predict the moment of departure. Clearly the chick is subject to conflicting tendencies at this time and these show in the spasmodic alternations between various activities.

When sea-gazing the chick is oblivious to nearby happenings which would normally have attracted its attention. It peers down, thrusting its neck forward as though to get a better view. The wings are often flicked up from the back in a flight intention movement (adults do this before taking off from an awkward position) often followed by wing-flapping. The transition from a tense pre-flight attitude in which the wings are suddenly jerked open, to a more relaxed wing-flapping position is conspicuous. After an interval of seconds or minutes, the chick resumes its sea-gazing, often suddenly reverting to biting and tossing nest material or preening, usually perfunctorily and for a short time, but occasionally earnestly for two or three minutes. The entire pre-leaving process gives one the strong impression that the chick is approaching some 'climax'. In the final few minutes before leaving it may turn inland several times, but always turns back to face the sea. It swallows convulsively prior to a real or abortive take-off, and often makes feet-pattering movements and head shakes.

The take-off occurs after two or three preparatory wing-flicks, when the chick simply jumps into the air. If it is denied all these preparatory movements (e.g. when accidently knocked over the edge by an adult) it can still make a successful recovery. These fixation and orientation movements, though highly characteristic, are not indispensible. If the nest is situated on the cliff edge the chick quickly becomes airborne. Chicks from nests in the flatter part of the colony, unable to clear the nesting ranks, flounder to the edge, violently attacked by adults and other chicks. In a worse predicament, however, are those chicks from nests which are not only inland, but without a jumping off point. Under these circumstances they either work their way gradually to some more favourable spot between existing nests or blunder blindly through, frequently making two or three abortive attempts. After attacks by adults they may return to their own nest from a considerable distance, by a devious route that they have certainly never before travelled, thus showing an ability to appreciate the topographical relations of the nests from a place they have never been before. Some unfortunate individuals are hounded unmercifully and seem to become bemused, and unable to force their way through when opportunity arises. One chick was treated in this way for five days, by the end of which it was so exhausted that its chances of successful fledging were slight. Yet, as recorded earlier, some chicks are accepted, preened (and, once, even fed) on their way to the edge.

The parents do not participate in any way in the chicks' departure. Curiously enough (as Perry 1948 noted) they do not seem to notice the chick's take-off. If it goes, they show no interest and if it returns after an abortive attempt they accept it back without demur. Both adults continue to frequent the nest-site for weeks after the main departure period, and certainly do not feed their chick at

sea. Both parents may be continuously at the site for up to two days after the chick leaves and it could not seriously be suggested that they could then fly out and find their chick on the open sea. The time spent on the site becomes more, not less, which could hardly be the case if they were having to fly ever-increasing distances to feed their chick. There may be odd records of adults at sea responding to food- begging by a juvenile, but these must be highly exceptional.

First flight. Once airborne, the chick usually flies strongly after a shaky start. It often falls 50 or more feet before levelling out, but if the wind is fresh and onshore, it may rise from the moment it jumps off the nest. Wing movements are at first wobbly and uncoordinated and the chick yaws and side-slips erratically, making too-vigorous compensating strokes. Then, its wing-beats, though shallow, become more regular, and it flies strongly for a quarter to two or more miles, often soaring much higher than the cliffs it left, banking and gliding in an accomplished manner. The flight to sea is not in a straight line but often in a wide curving sweep. There is little doubt that, especially under certain wind conditions, the chick could fly for a considerable distance. Several have been lost to sight when still flying strongly.

Post-leaving behaviour. Once on the sea, the juvenile Gannet cannot rise again for some time. (Kay 1949, in a survey from a boat, found that young from Noss, several miles out at sea, were incapable of taking flight even in a gale force wind.) Ducking and bathing movements are shown very soon after alighting, coupled with vigorous wing-flapping. The bathing is occasionally extensive and the bird becomes very wet, the tail especially becoming water-logged. (Adult Gannets usually ride on the water with tail lifted well clear; young birds often trail their tails in the water) In these cases it is associated with preening, in

which the bird may roll, diving-duck fashion, exposing the lower flanks and ventral surface. Several juveniles attempted, unsuccessfully, to rise from the surface soon after alighting. Under ideal conditions, however, it might sometimes be possible. They usually swim quickly out to sea. By 14th. September I have seen, round the Bass, definite juveniles on the wing and performing the shallow dive with which Gannets usually alight on the water. These may have been southward-moving juveniles from St. Kilda or the Faroes.

The juvenile's dispersal has been well followed from ringing results, but one can only speculate about questions concerning the way in which it starts to fish, how long it fasts before it can raise itself from the surface, etc..

- 14 -

'COMFORT' BEHAVIOUR

Rotary Head Shake. (Plate 22)

Most birds shake and settle their plumage after bathing, dust-bathing, preening or other disturbance of their plumage, as being handled. Gannets, however, rotary head shake frequently and regularly, not merely after cleaning activity, both in the breeding colony and in clubs, and frequently on the sea after alighting and bathing. It is also almost invariably performed in the air just after take-off - the bird shakes itself strongly and waggles its tail.

When rotary head shaking the neck is stretched forwards and upwards at about 45° and the hyoid may be depressed, imparting a peculiar facial expression. The wings are flapped vigorously with increasing speed, the neck and head feathers ruffed out (Fig. 43) and the head rotated vigorously several times around the horizontal axis, turning the crown until it almost faces the ground. The wings are then closed, neck retracted, tail waggled sideways and wings shuffled on the back. The forward thrust of the head with elongated neck, and the vigorous flapping make this behaviour particularly conspicuous in the Gannet. In a common variation of this behaviour the body feathers are loosened and shaken with loosely held wings and head rotations - like a dog shaking. Apart from this and other slight variations, e.g. the amount of wing-flapping, etc., the Gannet does not apparently use any other movement to shake its plumage, although the ordinary head shaking is almost always elicited by a soiled bill.

Rotary head shakes are clearly concerned with resettling the plumage as part of the bird's regular body maintenance behaviour. They occur whenever the plumage is disarranged e.g. in the female after copulation, after preening, fighting, etc.. The period of body feather moult, marked on

Plate 22 Body maintenance activity.

A.

Rotary head shake

B.

Panting and 'gular fluttering' in adult.
Note wings held loosely.

C.

Panting in chick. Note wings held loosely.

Figure 44, coincides with a peak in rotary head shaking activity, and the behaviour can be seen to dislodge old feathers.

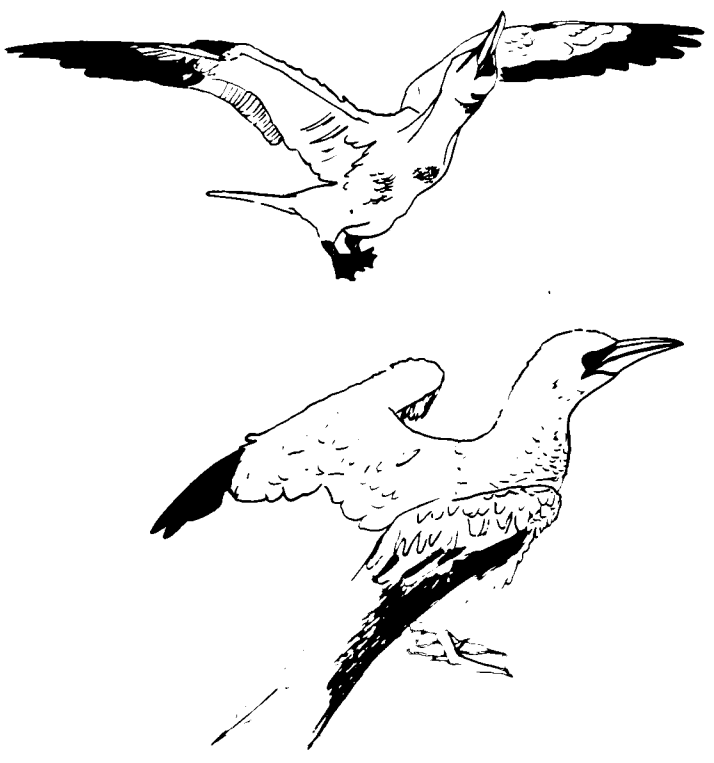


Figure 43. Positions in the rotary head shake. Note ruffled feathers and marked rotation of the head.

Tactile stimulation often causes rotary head shaking. The onset of rain immediately stimulates an outburst, which may be compared with the chick's response of violent wing-exercising, which they do without the rotary head shake. The voiding of excreta elicits it from one or several neighbours - even if it is only the foot which is soiled or the excreta is

merely seen to fall nearby, the association between seeing excretion and the threat of soiled plumage eliciting it perhaps as a conditioned reflex. This kind of linkage may offer a mechanism by which rotary head shaking could become associated with alarm (see below).

Rotary head shaking and alarm. Figure 44 shows the seasonal pattern of rotary head shaking activity which is high during moult and also towards the beginning and end of the season. At both these times the birds are uneasy on land and subject to sudden frights, and rotary head shaking is correlated with alarm. Birds leaving the colony in alarm cause an outburst of this behaviour among the remainder.

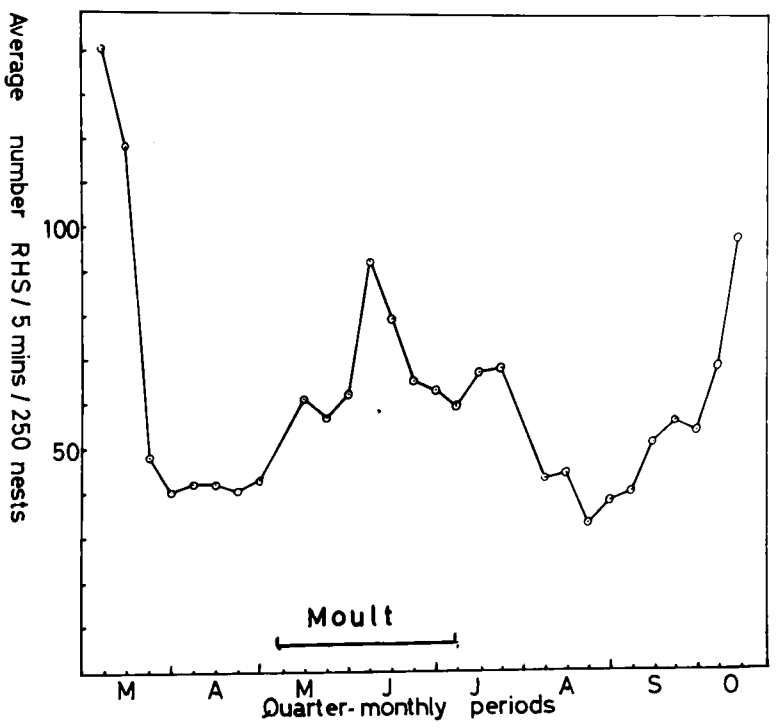


Figure 44.

Frequency of rotary head shakes in a group of 250 nests throughout season. (261 5-min. counts)

The effect of alarm was demonstrated by counting the frequency of rotary head shakes within a group and then flushing nearby gulls, without allowing the Gannets to see what had disturbed the gulls. The clamour alarms the Gannets (and early in the season would cause some birds to leave the colony) and rotary head shaking shoots up to many times the previous level (Table 49) before gradually waning again. The conflict situation arising from the tendency to flee induced by alarm, and the attraction exercised by the site, could

result in rotary head shaking as a displacement reaction. This however does not suggest why rotary head shaking alone should be selected and invites the suggestion that it may prepare the plumage for flight, when the behaviour would be functional and hence no longer a displacement reaction in the classical sense. Some geese, for example, incorporate a similar movement with their pre-flight neck-stretching (Johnsgard 1961). However the Gannet normally performs a vigorous rotary head shake in the air after take-off (even if it has previously done so on land) and this should make any feather adjustment necessary for flight. It might be suggested that rotary head shaking results from feather sleeking, itself a pre-flight phenomenon, and likely to occur in alarmed birds. The rotary head shake might then be a response to tactile stimulation from 'tightened' feathers in birds which didn't fly and needed to restore their plumage to the normal condition by loosening and adjusting them. However Gannets do not sleek before rotary head shaking in the alarm situation - they merely suddenly perform the rotary head shake. In view of these points any functional link between rotary head shaking and take-off remains undemonstrated.

TABLE 48. The change in frequency of rotary head shakes per 5 mins., in a sample of 250 birds before and after gull alarm.

Before alarm	37	40	48	29	75	32	28	50	43	49
After alarm	79	93	83	89	120	73	57	67	111	131

Since rotary head shaking is correlated with the tendency to fly it is not surprising to find that it is also strongly correlated with sky-pointing (Table 49) which itself precedes movement including flight. Sky-pointing birds tend to flatten their plumage, which could provide peripheral stimulation thereby causing rotary head shaking in the way proposed above. But their is no evidence that birds about to fly

rotary head shake more when sky-pointing than when not. However, since sky-pointing is so strongly linked with flight preparation the correlation between flight and rotary head shake will generally occur through this link.

TABLE 49. Correlation between sky-pointing and rotary head shaking.

No. out of 10 birds seen to sky-point, which rotary head shook within 1 minute.	6, 6, 9, 8, 7, 10.	Av. 7.6
No. out of 10 birds, randomly chosen (not sky-pointing) which rotary head shook within 1 minute.	1, 0, 2, 1, 1, 3, 2.	Av. 1.4

It seems justifiable to regard rotary head shaking in all cases (except , perhaps, its occurrence as a possible displacement reaction to alarm) as a response to some form of peripheral stimulation probably acting via the feather follicles. Thus whether it occurs in response to rain, excreta soiled or disarranged plumage or simply feather tightening, it may be referred to the same general causal situation. It need not be functional in the alarm situation in the sense of preparing the feathers for flight.

Sideways Head Shake.

The side to side head shake, one of the commonest movements the Gannet performs, is of interest because it has been incorporated into several functionally distinct displays. Unlike the rotary head shake, the head is not aligned with the neck, so that the movement appears to be articulated between the occipital condyle and axis rather than between cervical vertebrae as in the rotary head shake. In the sideways head shake the head moves; in the rotary head shake the head and neck move.

A similar head shake occurs in Herring Gulls, Kittiwakes, Guillemots and Shags, and doubtless many other birds. It displaces water from the head, the secretion of the salt

gland from the bill, etc.. In the Gannet it is much commoner than in the above species and occurs in several social situations, alone, or as part of more complex behaviour (e.g. the bow).

The following summary shows the occurrence of the head shake in all its modified forms.

(1) Violent head-flinging is used to dispel strongly-adhering matter from the beak. With mandibles widely parted it is also used to dislodge fish bones, etc. from the throat. Spilt fish, eggshell remnants, stones from the nest cup, etc. are all dispelled with this movement.

(2) As a probably non-signal part of threat behaviour vigorous head shakes are interspersed throughout menacing matches, together with pelican postures and nest touching movements.

(3) The sideways head shake is 'locked' in the bow and ocurs after each dip. In the male's advertising display (resembling an inhibited bow) the head shake component is very conspicuous whilst the dip is suppressed. Head shaking is one of the main components of mutual fencing, but differs in form from ordinary head shaking and resembles rather more an attempt to maintain contact with the others' bill during irregular side to side movements, though its resemblance to head shaking can be seen when the partner's bill is momentarily out of reach.

(4) Females use a very inhibited head shake when reacting to the presence of a nearby male which they want to attract. They also react to the voice of their incoming mate by rapid head shaking and facing-away. An exaggerated form of head shaking is also used by the female as a ritualised signal in soliciting copulation. The head is held loosely and flung violently from side to side. The female usually squats, with head held low, and continues the movement intermittently during copulation.

By contrast to the wide occurrence of ordinary head shaking, rotary head shaking is confined entirely to few situations. In none of the situations described above, with the possible exception of number 1, does the Gannet use a rotary head shake.

Why should the one form have been selected for incorporation into signal displays whilst the other occurs mainly in one context (soiled wetted or disarranged plumage) and not as a signal. Possibly because in some contexts (e.g. menacing) a rotary head shake would temporarily obscure vision, and in others (e.g. copulation or mutual fencing) would be physically inconvenient. Also the sideways head shake is a simpler movement and therefore more likely to be 'preferred', other things being equal. It may be that the ordinary head shake was more suitable for exaggeration and change.

Clearly one can say little about the function of the head shake in its emancipated form, since it usually occurs as part of a complex behaviour pattern. I have the strong impression, however, that it has non-hostile overtones in many situations. A head shaking bird is very likely to be slightly afraid or friendly, rather than aggressive (cf. head waving of S. dactylatra).

In summary, the sideways head shake in the Gannet is a good example of the wide variation in form, context and function of a simple basic movement.

Preening.

Gannets preen thoroughly for much of their long periods of site-attendance. Their toilet seems more extensive than gulls for example, which may be due to the demands of their oceanic life. After bathing the complete preening procedure, including oiling, is performed on the water. The ventral surface is exposed by rolling onto one side. Gannets also occasionally preen in flight. They do not wing-dry

like Shags, Cormorants and Pelicans, nor adopt special sunning positions like S. dactylatra (Dorward).

Whilst a detailed study might reveal a pattern of preening different parts of the body, it is not apparent. Gannets switch abruptly from one part of the body to another. The remiges and rectrices are drawn separately between the mandibles and the tail is sometimes bent sideways at right angles to the body to help this. The thick quilt-like body plumage is nibbled with the points of the mandibles, and the lower breast and flanks are 'stropped' with a sideways motion of the bill. In a thorough preening session, which may last for over an hour, the oil gland at the base of the tail is erected (the feathers surrounding it can be displaced to uncover the gland), oil is rubbed on to the nape and back of the head and then rolled onto the back and wings from the head.

Preening is occasionally followed by direct head-scratching, in which the pectinated middle claw is certainly used, though perhaps other claws too.

Perfunctory preening often follows other activities. The area preened is often decided by postural facilitation. Following bowing the bill tip rests on the upper breast and this region is most frequently preened after bowing. Also preening occurs at a specific point in the behaviour sequence following a fight or a bout of menacing. As the tension gradually relaxes, the first non-hostile behaviour, apart from head shaking, is invariably a rotary head shake and then short preening bouts. The preening can be seen to arrange the plumage which is often soiled and disordered.

The seasonal incidence of preening was followed, as for other behaviour patterns, in two groups of 20 nests and is presented, together with sleeping on Figure 45.

Sleeping.

Adult Gannets, including incubating birds, sleep

with heads tucked in scapulars (see Plate 20C). The bill is dexterously inserted between the feathers and the head is almost entirely covered. Much of the time on the site is spent sleeping, particularly during wind and rain. They occasionally doze with bill forward, but never sleep properly in this way.

The seasonal incidence of sleeping is plotted in Figure 45, taking into account the number of birds present during each count. The level is fairly constant. Diurnally there is a peak in the last hour of daylight (and presumably also at night), but otherwise no periodicity. Unlike Shags, Gannets do not usually rest side by side on the nest; if one stands the other sits. There is no precise point in time at which the female 'takes over' the centre of the nest, though she does so before egg laying.

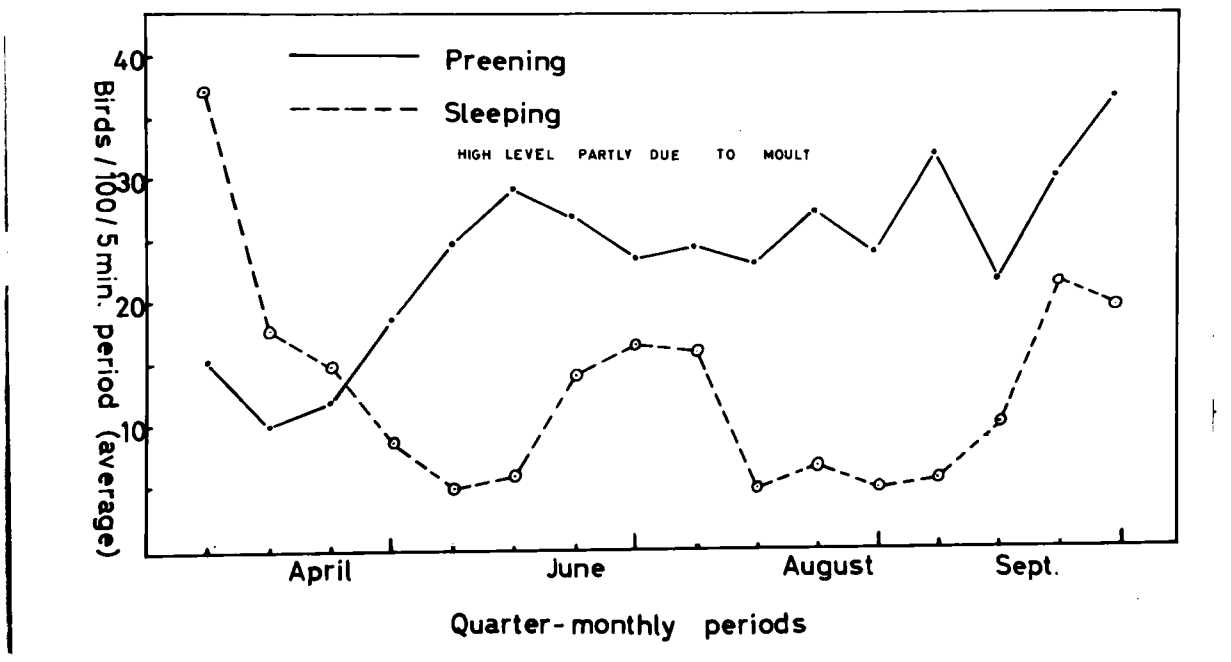


Figure 45. Frequency of preening and sleeping throughout the season, measured by regular five-minute checks on two groups of twenty nests.

After an exhausting fight Gannets invariably fall into a deep and prolonged sleep, no doubt part of the necessary recuperative process and possibly comparable to battle fatigue in soldiers. I have several times caught by hand Gannets sleeping on the fringe of the colony following a fight, and have records of such birds sleeping almost continuously for three days.

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SOCIAL BEHAVIOUR AND CLIFF NESTING

In this final chapter I will briefly discuss some wider aspects of the Gannet's sociality (most of this account has directly involved the pair) and bring together as much as possible of its breeding biology by relating it to the habit of cliff nesting.

The chapter begins with a discussion of sky-pointing, the last remaining major posture in the Gannet's repertoire which finds a place here mainly because it does not belong in the main stream of agonistic displays already described.

Sky-pointing.

Whereas for some Gannet displays described in this account a function and a highly characteristic context are readily given (e.g. bowing, mutual fencing, facing-away in response to male advertising) sky-pointing occurs in a wider variety of situations and its function is less plain.

Form. (Plate 23, Figure 46) In sky-pointing the neck is stretched vertically to its fullest extent and held stiffly. The bill points sky-wards (sometimes even backwards of vertical) and the eyes look forwards - a combination made possible by the Gannet's binocular vision. These features prompted the descriptive name but in the discussion of sky-pointing the movements associated with it are also included. The wings are raised upwards, not outwards, by rotating the humerus in the glenoid cavity and lifting the distal end of the radio-ulna ('wing busking'), a movement performed to some extent during ordinary walking (Plate 23A).

In this posture the bird begins slow foot-raising 'on the spot' revealing the striking digital lines, prepatory to turning and walking or flying away from the nest (see Plate 19) often with a special 'groan'. Gannets move slowly in the full sky-pointing position with a characteristic rolling gait

Plate 23 Sky-pointing and leaving behaviour.

A.

Ordinary walking position, wings slightly raised, neck curved, bill slightly upwards.

B.

Full sky-pointing position in group of fringe nests. Note swaying of body.

C.

Walking in full sky-pointing position into completely empty area.

(Plate 23B) lifting and lowering the feet deliberately and seemingly oblivious to surrounding activity. They may be threatened or even jabbed without abandonning the posture, although their swivelling eye movements show that they are taking in the local situation.

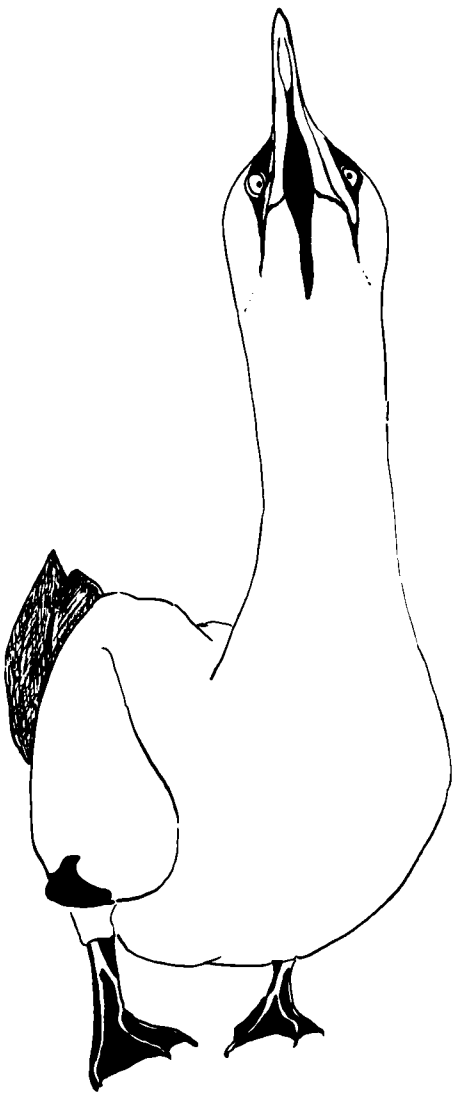


Figure 46.

The sky-pointing position. The black facial soft parts and inter-ramal skin form a conspisuous pattern against the white head and throat. Both head and feet are thus strikingly obvious.

After the first few careful steps the Gannet sheds its caution and dashes for the fringe (Plate 23E) or some convenient stopping place (Plate 23D). It aids progress by wing-beating as though rowing over the ground, and is clearly distressed by the hostile reception as shown by its gaping and swallowing movements.

Motivation. See p. 250. Occurrence and function are best considered together and, in this case, before motivation.

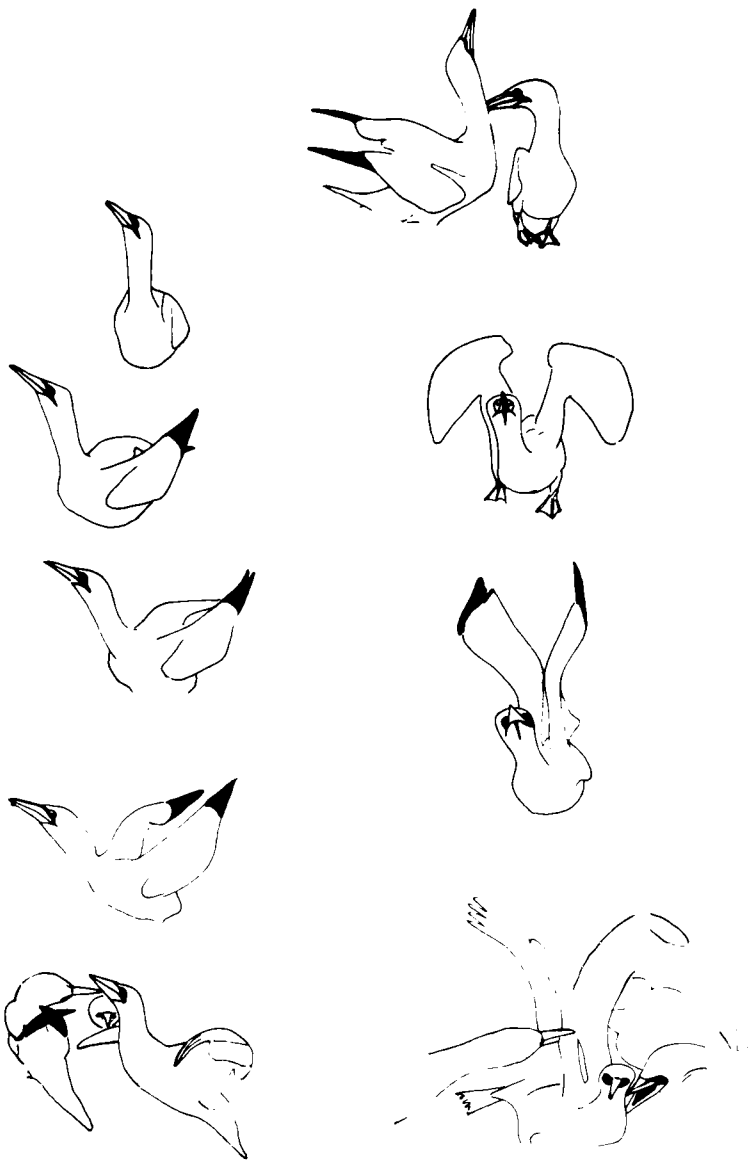
Occurrence and function. The best description of the sky-pointing context is that it occurs before and during movement, usually on foot and particularly away from the nest-site. Since sky-pointing is such an elaborately exaggerated and common behaviour pattern,

occurring often outside the pair relationship, one suspects a signal function in a wider social sphere. It will be shown that sky-pointing clearly elicits reaction from the mate and neighbours, although reaction from the latter is probably not beneficial to the sky-pointing bird.

Sky-pointing usually begins on the nest, typically during change-over by the relieved bird (but also by the incomer) just before the former flies or walks off, and may last for two minutes without a break. Usually the bird is surrounded by others (on flattish ground) but may sky-point when completely isolated (Plate 23C), the bird moving a step or two in the full sky-pointing position, then running or hopping with the 'take-off' groan. Even then, however, the bird is usually en route from the nest to a take-off point. Birds moving about in the fringe prospecting, collecting nest material, etc. usually do not sky-point.

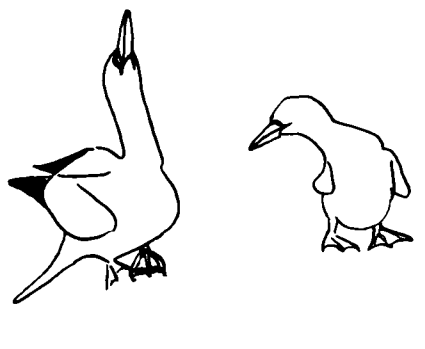
When directly preceding flight the full behaviour sequence is :- sky-point with wings busked, wings flicked (intention of flight), intention movement of jump, actual take-off, with tail depressed to increase lift still in sky-pointing position (see Plate 19). When preceded by sky-pointing, take-off is also accompanied by a groan in about 60% of cases. Take-off without sky-pointing is only accompanied by a groan in some 20%.

The form of the movement, in which the bill is so obviously removed from the attacking position, clearly suggests appeasement, and in fact this function has been stated or implied (Tinbergen 1953b; Fisher & Lockley 1954; the most committed statement being Barlee's 1956). In addition, the situations in which it typically occurs would seem to require an appeasement posture, which no doubt influenced previous interpretations. The only way (short of model experiments which were impracticable) to gather evidence relevant to the function of sky-pointing seemed to be to observe (a) when, precisely, it occurred and (b) what effect



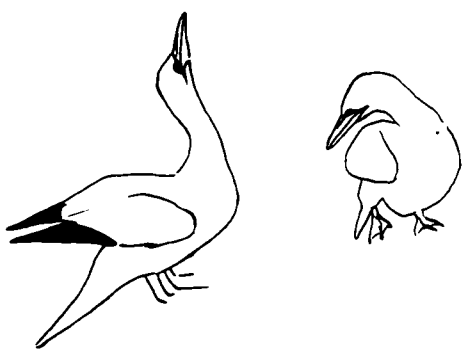
A.

Sky-pointing bird leaving the site (top right) and 'dashing' to fringe. Note (left column) how position of head and neck alters and wings used as 'oars'. Right column shows wings held vertically to minimise risk of being seized. Nevertheless he is attacked.



B.

Effect of sky-pointing bird on mate. Bird on right about to leave, but mate sky-points, so right bird turns and begins slight mutual fencing.



C.

Effect on neighbours of sky-pointing in group of fringe birds. Far bird bows slightly, two on left menace and bird on right remains in relaxed position.

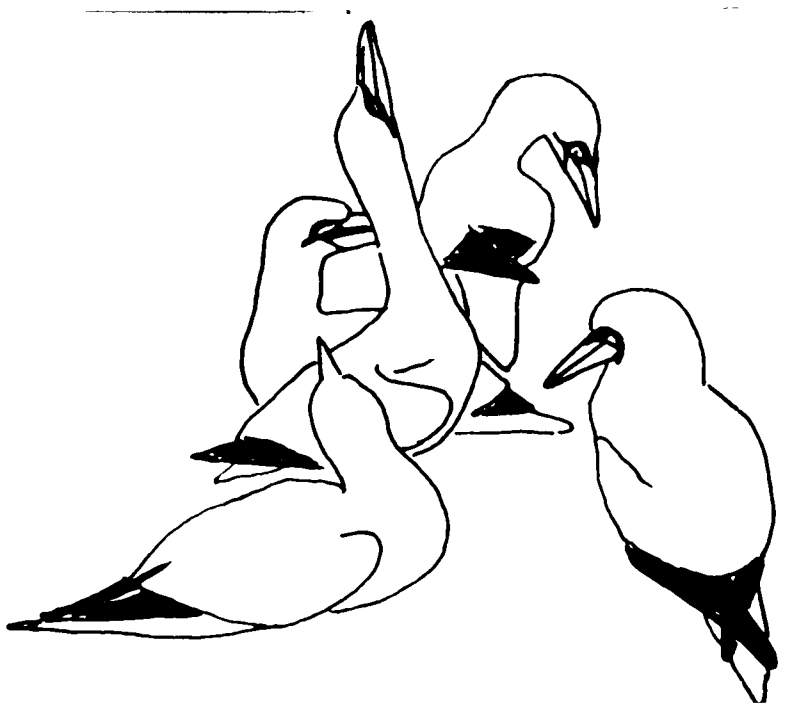


Figure 47.

it had on other individuals. Systematic notes were therefore made of 557 occasions on which it occurred, where there were no additional complications of attack, stealing nest material, disturbance, etc.. These fell into seven classes :-

(1) Birds leaving their nests to move through the colony sky-pointed and then dashed in 60/83 (72%) cases and merely dashed in the remainder.

(2) Birds moving some distance from their nests butwwithout having to pass through others sky-pointed in 69/76 (91%) cases. The difference between categories (1) and (2) suggests that the prospect between passing through hostile neighbours decreases, rather than increases, the tendency to sky-point.

(3) Birds moving only slightly off their sites - a foot or two - sky-pointed in all of 19 cases.

(4) The few records of birds approaching their sites on foot indicate that where they have to pass through others they do not sky-point (0/14), but where they can approach without they may do so (4/11, 36%).

(5) Prior to flying from their nests after change-over birds sky-pointed in all cases, but, taking into account departure after short visits only, in 47/130 (36%).

(6) Although sky-pointing never occurs prior to take-off with nest material, birds occasionally walk in this position holding nest material. Birds taking off without nest material other than from their nests sky-pointed in about 16/132 (12%) of cases. Many of these had left the nest on foot and were taking off from some vantage point. In a literal sense, therefore, they were still 'leaving the nest'.

(7) Movement on foot along the fringe of the colony involved sky-pointing in 58/118 (49%) of cases. Many of the sky-pointing birds had just left the colony, but precise proportions cannot be given, since a bird's behaviour prior to its arrival in the fringe was often missed.

The preceding analysis reveals a posture which,

though highly predictable in a few situations, is far from an invariable response to the pre-movement situation. Further it does not effectively prevent attack (see below) and is not adopted when attack is likely; instead the bird dashes. Sky-pointing usually occurs before the bird has been attacked. When attack appears imminent a bird may 'freeze' in a non-sky-pointing position (Plate 23D) for over five minutes before dashing.

To see whether sky-pointing reduced the probability of attack, counts were made of its effect on the behaviour of neighbours (it should be remembered that sky-pointing here includes associated foot and wing movements; it would be inaccurate to interpret the observations as showing anything about the head and neck part of sky-pointing dissociated from movement).

In 78 cases of sky-pointing to which the reaction of previously quiescent neighbours was noted 60% elicited a menace. This is to be compared with the effect on other birds of alternative movements of roughly similar magnitude. Thus 33/432 (8%) rotary head shakes and 0/56 bows drew menaces. It appears that sky-pointing is more likely than these other behaviour patterns (both of which involve vigorous movement) to elicit hostile behaviour.

Whilst this may well be due to conditioning, the neighbours recognising sky-pointing as an intention movement of departure, probably involving blundering past their nest, it strongly suggests that the performer is not thereby any more immune to attack, but rather less so. In fact the sky-pointing bird actually makes his departure by dashing through the nesting ranks - a procedure he could equally well carry out without the preliminary posturing, since neighbours attempt to bite him in either case.

If an appeasing function seems unlikely on the above evidence, some other must be found for such a striking

display. Successful site maintenance and breeding is highly dependent, in the Gannet, on efficient change-over. Unattended nests are liable to lose egg or chick. It is therefore important that a conspicuous pre-leaving signal should be given to remove the danger of both adults leaving together. Gannets cannot return quickly enough to prevent mishaps, once having left. The elaborate and prolonged posturing could clearly perform this signal function, which is certainly recognised and responded to by the mate (Fig. 47B). This suggestion makes more sense of sky-pointing in the cliff-ledge situation in which it is usually possible to leave without approaching any neighbour - a particularly cogent point, since it will be argued that Gannets are primarily cliff-nesters.

It may be doubted whether this explanation could account for sky-pointing in situations away from the nest, but it may have become 'frozen' into the pre-moving situation, which in this species usually means departure from the nest.

Motivation. Although sky-pointing sometimes occurs in sexual and hostile situations, it also occurs much more widely as the preceding examples have shown, and it is not a particular balance of fear, aggression or sexual tendencies which forms the common denominator of these occasions. Rather, it is the situation 'about to move', particularly from the site. The motivation of sky-pointing is therefore much less obvious than in the Gannet's agonistic displays, though it probably contains an element of fear.

To sum up, the observations show that sky-pointing does not have a marked appeasing function, but is if anything more attack-provoking than other movements. It is possible (though far from proven) that sky-pointing functions as an intra-pair signal movement, facilitating efficient change-over. Both functions may be involved. It is probably at least partly fear motivated.

Derivation. It seems likely that sky-pointing is a ritualised flight intention movement. Whilst many geese show neck lengthening before flying up, some geese(Johnsgard 1961) have incorporated chin lifting movements and lateral head shakes. It is not difficult to see how progressive elaboration of a simple neck-lengthening could produce the sky-pointing posture. The peculiar rotation of humeri now associated with sky-pointing could be an intention movement of flight adapted to a restricted take-off position, Whilst the Gannet appears to have retained and elaborated sky-pointing in this phylogenetically primitive context, other Sulidae have transferred it to an entirely different context.

This posture has been studied in Leucogaster and dactylatra (Dorward, who called it sky-pointing) and sula Verner 1961, who called it four-pointing) and, perhaps alone among the various displays in the Sulidae, has been described in sufficient detail to permit a comparative discussion. It is very similar in form in the four species. In sula and dactylatra the tail is pointed upwards (almost vertically in the former) whereas in leucogaster and the Gannet it usually is not (in fact it is often markedly depressed in the latter - probably a secondary feature which could result from its association with take-off and the need for lift). In leucogaster active wing movement is absent. In dactylatra sky-pointing is accompanied by a characteristic drawn-out whistle and in sula by a "single rattling drawn-out note". This compares with the special groan in the Gannet.

In sula, four-pointing, the most frequently observed display, is associated with male advertising, but according to Verner, is also used as an ownership display and in maintaining and strengthening the pair-bond. He does not say whether there are differences characterising these various

uses. In leucogaster sky-pointing differs slightly in form from that in dactylatra and also occurs more when a mated pair are together, and alternatively as an aerial display by the male. However it also functions as a male advertising display from the ground. In dactylatra sky-pointing is performed by unmated males as an advertising display towards un-mated females and is usually performed only from the 'site', though this is much less fixed than in the Gannet.

One further point is that whilst ownership, pair bond strengthening and male advertising all employ a similar display in sula (i.e. all are modifications of sky-pointing) the equivalent displays in the Gannet (ownership, mutual fencing and advertising) are also all versions of one display - though a display quite different from sky-pointing. This relationship in the Gannet can be partly explained by considering advertising and mutual fencing to be agonistic displays modified by the presence of the mate.

In summary, sky-pointing is clearly a homologous posture in the four members of the Sulidae under discussion. It has become strongly differentiated in function. In sula it is apparently least well differentiated, serving three purposes (however there may be differences which have not yet been described). In leucogaster sky-pointing is more differentiated, and, although largely a male advertising display, it is also performed in a wider variety of situations. In dactylatra it is almost exclusively a male advertising display. These three apparently form a graded series. The Gannet, however, has apparently ritualised sky-pointing as a posture associated with moving from the site. This could be related to its denser colonies and greater aggression, though the function of the posture, and therefore any possible link with increased aggression and the need for appeasement is uncertain.

Social Behaviour.

Relationship with neighbours. In the Gannet the dense colonial habit has led to extensive interaction between neighbours, who know each other, show some personal preferences, are stimulated by each others' behaviour, etc.. In addition, aggressiveness makes demands on social behaviour. Signal movements are conspicuous and used extremely frequently - indeed, often apparently 'unnecessarily'. Many other colonial sea-birds (e.g. penguins) apparently need less elaborate signal (particularly appeasement) behaviour.

Social facilitation (Crook's 1961 modification of Crawford's original definition is "that phenomenon observed when the performance of an activity by an individual stimulates the immediate performance of the same activity by its neighbours") occurs in the Gannet. In one group bowing activity may be low, whilst in another it is very high, having spread from an original 'nucleus', perhaps of birds stimulated by a departing bird blundering through. Even rotary head shaking seems to be influenced by the sight of others performing it and may occur in 'waves'. Certain areas within a colony are more likely to be disturbed by over-flying birds and therefore show (over the season) more bowing than another apparently equivalent group (see Fig. 34). Such differences probably influence important events like the onset and synchronisation of laying within the groups (see Chapter 3)

Relationships away from the nesting site. Besides nesting in dense colonies, Gannets fish in flocks, fly in skeins from the fishing grounds to the breeding station, collect nest material communally and gather as 'clubs'. They also rest in aggregations on the sea, but are not evenly dispersed in these, and show little evidence of attraction for each other.

I wish here to draw a distinction, at least of degree if not of kind, between the Gannet's social relation-

ships at and away from the breeding group, the latter showing fewer and simpler interactions. This point becomes particularly relevant when considering the evolution of colonial nesting and the more complex forms of social behaviour.

The habit of fishing in flocks might be regarded as social behaviour, but so far as can be seen from their methods of fishing, Gannets act as a group of independent individuals brought together by a shoal of fish and by the attraction which a fishing bird undoubtedly has for others within in sight.

Flying in skeins back to the breeding Colony is such a regular habit that it must have advantages - probably each bird benefits from the updraught of the bird in front. Gannets do not fly from the breeding station in skeins, probably because they are not heading for any fixed point.

Communal gathering of nest material (Plate 16) as in Kittiwakes, is a regular habit, though not necessarily for the same reasons. Wind direction determines the general area, but birds clearly attract each other. However, there is little interaction (and no display) between members of such a group.

The 'clubs' show social behaviour of the complex kind shown by breeding birds - fights, threats, displays, copulation, etc.. The incipient sexual behaviour of both immature and adult club birds has already been commented on. At these gatherings (part of one is shown on Plate 7) even two year-olds (though rarely one year-olds) form temporary pairs, with bowing, menacing, mutual fencing, female-facing-away, etc.. These displays are to some extent incomplete in form, the bows containing few dips etc., the mutual fencing less intense. The individual distance between these temporary pairs is less, and also less regular, than in a breeding colony, so that such gatherings have a dense and uneven appearance from afar. A conspicuous feature is the tendency

for birds of equal age to pair together. Although a sub-adult may form a temporary association with a three year-old it is unusual for an adult or sub-adult to do so with a two year-old bird. The behaviour of club birds, though sometimes aggressive, is altogether more 'tentative' than in birds establishing a site proper. Although young females regularly show the typical appeasement behaviour - facing-away from males - they also show aggression to them, as though their individual aggression, regardless of sex, has not yet been inhibited by sexual and fear tendencies. Furthermore, males do not respond to this by attack, but by reciprocal menacing, or even mild fleeing.

The nest touching movements typical of adults in conflict situations (p. 196) also occur in immature birds even when they are sitting on bare rock. No nest material is required to 'release' or direct this behaviour.

Sky-pointing is comparatively rare among club birds. Three year-old birds may copulate successfully (i.e. as defined on p. 201), though this is rarely seen. I have never seen a two year-old mount. However, sexual behaviour, like aggression, is atypical and disorganised. Females may reach out and mutual fence with one male whilst still part of a temporary pair formed with another. Both sexes wander freely.

In all the above instances (except the clubs which form an intermediate category between the 'complex' social behaviour in the breeding colony and the simpler social relationships away from it) Gannets perform activities in groups. But pair contact is still limited to the nest or site. It seems unlikely that they can ever meet away from it except fortuitously . It seems perhaps useful to de-limit the one category of social behaviour (at the nesting colony) from all the others given above.

The Gannet and its Breeding Habitat.

This section will consider the Gannet's adaptations to cliff-nesting. Many of these have already been mentioned under other headings and will here be drawn together by comparing them, from the viewpoint of convergent evolution, with those of the Kittiwake.

First, however, three distinct questions must be discussed, (1) why do Gannets choose small islands (2) why do they choose cliffs and (3) since at the present time they nest on both cliffs and flat ground, may one of these two habitats be considered 'ancestral' and the other 'derived'. (1) Gannets have a very strong tendency to nest on outlying rocks and small islands. In 1939 of 23 breeding stations 19 were of this kind (Fisher & Vevers 1944). This habit must confer advantages and the avoidance of predators is an obvious possibility. As already mentioned, man is today the Gannet's only predator, but other mammals once inhabiting Britain could easily have prevented Gannets from forming their noisy and conspicuous Colonies on flat mainland ground. However mainland cliffs are often inaccessible and yet today are rarely used. It therefore seems that islands as such offer advantages. They may be more strategically placed for gathering food, being as it were, in the middle of potential fishing grounds, whereas mainland sites are dead ground on all but the seaward side so far as fishing is concerned. Islands will also afford greater help from air currents, being generally windier. These, however, are relatively minor points and the main factor may well be that the Gannet's ~~fear~~ wariness of land makes it strongly favour small islands since these are the nearest approximation to open sea.

(2) Even small islands are usually not inhabited equally on both cliffs and flatter tops, the Gannet obviously preferring the former. This can hardly be an anti-predator device unless evolved in response to man, since most Gannet stations

are inaccessible to other predators and must always have been so. The cliff-nesting habit is therefore a preference distinct from, though associated with, the island preference. (3) The topic of the Gannet's ancestral nesting habit must be considered before comparison with the Kittiwake's cliff-nesting adaptations can be properly made. Thus, Cullen demonstrated that Kittiwakes had diverged from the ground-nesting habit common to ancestral Larids and secondarily adopted cliff-nesting as an anti-predator device. The Gannet, on the other hand, is in my opinion ancestrally a cliff-nester and the utilisation of flatter ground is the more recent habitat extension. This view is supported by much of the following evidence :-

A. Gannets are anatomically unsuited to flat-ground nesting. They are comparatively poor walkers and find take-off difficult except in strong wind; the pectoral muscles are extremely small in relation to the bird's size and weight (flight muscles are 13% of total weight, compared with Guillemot 25%, Mute Swan Cygnus olor 14%, Great Black-backed Gull Larus marinus 16.5%, Fulmar 10%, Snipe Capella gallinago 29%, Barlee 1956). In addition Gannets have the highest aspect ratio wings of any British bird (aspect ratio 16 Barlee loc. cit.).

Most of these features are adaptations for its fishing method (long, fast flights; streamlined power diving, etc.) but it is reasonable to expect that Gannets would use the type of nesting habitat least in conflict with them. These difficulties are mitigated by cliff-ledge nesting.

B. Despite the large number of nesting Gannets on the flatter parts of Grassholm, the great majority breed on the cliffs of small islands or sea-rocks at the present time. Furthermore nearly all gannetries formed or prospected within the last 100 years or more have been on cliffs and almost all on small islands (e.g. Lundy and Isle of May, both prospected

around 1922, Bempton, colonisation begun 1924, Great Saltee 1929 to 1932, Scar Rocks 1942, later defunct, Cape St. Mary 1918, Fisher & Venables 1938, Fisher & Vevers 1951). However the gannetry at Bird's Bay, Anticosti Island was on the coast cliffs of an island more than 100 miles long and 83 miles from the nearest Colony (Wynne-Edwards 1935). Lack (1934) records that in Iceland (on Grimsey) the Gannets took to nesting on the main island when their nearby nesting stack collapsed; the new site was already occupied by a few pairs.

C. If the Bass is typical of gannetries with nests on both cliffs and flatter ground, the cliff-nesters always return first and leave last. It has been shown (Chapter 3) that Gannets are apparently ~~afraid of~~ easily alarmed in their nesting habitat when they first return. Their earlier return to cliff nests may suggest that these sites are less frightening and therefore perhaps less unfamiliar, evolutionarily speaking.

D. Comparative evidence from the Sulidae does not help to decide the issue. According to Murphy nebouxii is often a flat-ground nester, variegata mainly a cliff nester, dactylatra and leucogaster both ground and cliff nesters and sula a tree/shrub nester. Thus cliff-nesting is obviously not any more typical of boobies than is ground nesting - perhaps less so, but it is interesting that Murphy, with no axe to grind, records the boobies are more timid on flat ground than on cliffs.

E. Behaviourally, Gannets seem adapted to cliff-ledge nesting (see the comparison with Kittiwakes for a full list).

Comparison With the Kittiwake.

Despite the very distant relationship between Gannets and Kittiwakes their shared territorial and cliff nesting habits have, convergently, produced many striking similarities. Yet they are also different in many ways, partly due to phylogeny but also, for example, to the Gannet's greater aggressiveness and reduced fear of predators. The

richness of the Kittiwake's adaptations to cliff nesting revealed by E. Cullen's study make it ideal for comparison with the Gannet. In the following I have tried to bring out the characters shared by both and to explain features possessed by either alone in terms of some other aspect of their biology.

Gannet	Kittiwake
SIMILARITIES	
Presumed (at least partial) anti-predator device	Presumed (mainly) anti-predator device
Nests on small islands and mainly on cliffs.	Nests on extremely tiny cliff ledges, etc..
Low adult mortality (partly from safe nesting and partly from oceanic life) and high breeding success.	
Annual adult mortality 6%.	Annual adult mortality 12% (Coulson & White 1959).
Hatched young fledging 92%.	Hatched young fledging 88%.
Deferred maturity. First breed 4/5 years.	Deferred maturity. First breed 3/4 years.
Presumed competition for sites.	
Fierce reproductive fighting (special fighting method),	Reproductive fighting, less fierce due to small bill and body size (special fighting method).
Permanent site attachment.	Permanent site attachment.
Occupy nest on arrival and pairs form on nest.	Occupy nest on arrival and pairs form on nest.
Nest densely.	Nest densely.
Protracted greeting ceremony (presumably to overcome aggression).	Protracted greeting ceremony (presumably to overcome aggression).
Adaptations to cliff habitat.	
Specialised fighting (pushing with beak).	Specialised fighting (twisting with beak).
Beak releases and directs attack.	Beak releases and directs attack.
Excreta sticks nests.	Excreta sticks nests.
Female squats in copulation.	Female squats in copulation.
No (or little) egg retrieving.	Not recorded.
Young remain on nest.	Young remain on nest.
Adults do not 'recognise' young.	Adults do not 'recognise' young.
Young face-away.	Young face-away.
Nest material rare, stealing rife.	Nest material rare, stealing rife.
Nest guarded.	Nest guarded.
Chicks have good clinging ability.	Chicks have good clinging ability.

Gannet	Kittiwake
Lack of predators.	
No special alarm call.	Alarm call rare.
Attack would-be predators.	Remain on nest till predator close. Eggshells and excreta not removed.
Eggshells and excreta not removed.	Young not cryptic.
Young not cryptic.	Noisy and conspicuous displays permissible.
Noisy and conspicuous displays permissible.	
Other similarities.	
Gather nest material communally.	Gather nest material communally.
Rain induces nest building.	Rain induces nest building.
Chick fed by incomplete regurgitation, possibly for nest hygiene.	Chicks fed by incomplete regurgitation, possibly for nest hygiene.
No feeding call.	No feeding call.

DIFFERENCES

Adaptations to cliff nesting in Kittiwake, absent in Gannet	
Males do not show any appeasement posture in fighting.	Males beak-hide in fighting.
Do not bring mud to nest.	Bring mud.
Do not 'trample'.	'Trample'.
Often nest on <u>flat</u> ground.	Very rarely nest on flat ground (cf. Paludin 1951).
Greater aggression in Gannet.	
Male bites female on arrival at site.	Female not bitten.
Female bitten during copulation.	Female not bitten.
Separate site ownership display (aggressive).	No separate display. Ownership and male 'advertising' by 'choking'.
No special alarm call.	Special (rare) alarm call.
Attacks man.	Will not attack man.
Chicks aggressive to adults.	Chicks <u>not</u> aggressive to adults.
Chicks attacked on sea.	Chicks not attacked on sea, (or not as much).
Appeasement posture of chick not very effective.	Appeasement apparently more effective.
Don't raft, (less frightened?)	Congregate in rafts prior to returning to nests.
Other differences.	
Longer breeding season.	Shorter breeding season.
No evidence for food shortage	Indirect evidence for food shortage.
After fledging young do not return and are not fed.	Chicks fed after fledging.
Poor vocabulary.	Richer vocabulary.
Sky-pointing (pre-movement posture).	No equivalent.

Conclusion. Many of the similarities between the two species are clearly adaptations in both to cliff nesting. Many of the differences are due to the Gannet's larger size and aggressiveness. To place alongside the above evidence for convergent evolution it would be desirable to compare the Gannet with other Sulidae. It is hoped to do this in the future.

GENERAL DISCUSSION.

To save repetition the detailed discussions are in the relevant chapters (particularly chapters 4 and 7). Here, the aim is to assemble some points which seem to me important, and briefly discuss their possible implications in an attempt to add perspective to the account.

A convenient starting point is the Gannet's marked territorial behaviour, observed particularly in its extreme aggressiveness but also in its strong site attachment. It is not altogether obvious why the site should be so important. It would be satisfying to demonstrate site shortage and hence the need for fierce competition. The present British Gannet population, nesting in part on flatter ground, is clearly not limited by site shortage, although if cliffs formed the main original nesting habitat (for which some evidence has been given) direct site competition may have been more important in the past.

Territorial competition, however, is real enough and breeding success goes to the most aggressive members of both sexes so long as their relations with each other are not thereby jeopardised. Within limits therefore aggression should confer survival value. Two main lines of thought may be followed from this point.

The Gannet's strong site attachment is partly expressed by long seasonal attendance (two thirds of the year) - much more than needed for incubation and chick rearing. This extended season makes possible a comparatively widespread laying period (whether this can be considered an advantage has already been discussed) . In turn chicks can be reared with about equal facility (extreme limits excepted) at any period of the breeding season, suggesting that Gannets enjoy a dependable food supply. We may even wonder why the process has not extended further; why Gannets do restrict

laying to about six weeks of a strictly annual cycle. Despite lack of evidence for a seasonal 'tailing-off' of food supply, however, they probably could not feed chicks in winter.

A long breeding season with 'spare time' at both ends makes replacement laying feasible. This is rather an unexpected feature in a single-egg laying species with a protracted nestling period. Further, Gannets are long-lived and have a high reproductive success. These features tend to enhance the value of the site.

Despite the above advantages, several factors lower the Gannet's recruitment rate (Chapter 7). These must be density dependent effects and the most plausible suggestion for a possible mechanism (Ashmole in press) is direct food competition around the breeding Colony. However, the available evidence, though relatively slight, suggests that this might be inadequate to explain the situation in the Gannet. It seems, nevertheless, that some mechanism is at present restraining the Gannet's reproductive 'effort' (though it is increasing in numbers). One of the most valuable future Gannet studies would be a systematic investigation of this general problem.

The second line of thought pursues the dominant effect of aggression in pair relations and social behaviour. Because males are so aggressive females have evolved a specially high tolerance of attack, without fleeing or retaliating. Upon meeting and in copulation they accept fierce biting and have developed an appeasement posture restricted to this situation. Yet they are themselves aggressive to other females, and in site defence, and the pair perform a meeting ceremony which is probably a modified aggressive display. So, also, is the male's advertising. Another appeasement posture (the pelican posture) is performed by both sexes in ambivalent fear/aggression situations. Yet a third posture (sky-pointing) appears to be associated with the difficulty, among aggressive neighbours, of leaving the site, though evidence for its

function is still lacking. Finally an extreme form of appeasment, capable of immobilising it for hours, is shown by the chick. Aggression seems to have required a set of appeasment postures appropriate to several different situations. In addition, it appears to have required constant guarding of the chick. We may also recall attacks by adults on fledged juveniles, the key to whose dark plumage, apparently disadvantageous in one respect, may lie in the need to reduce adult aggression. Thus the effects of aggression stand out clearly in the Gannet and it becomes of special interest to consider other members of the Sulidae in this respect.

Apparently, they all show less obvious signs of aggression. Sula sula, leucogaster, and dactylatra at least, show more normal pair and social relations. Fights are not excessively severe; males do not bite their mates, either on meeting or in copulation; pairs have no special meeting ceremony; males show no specific ownership display; appeasment postures are less well-developed (females do not face-away); chicks are not constantly guarded and can 'afford' light ventral plumage. If the many ecological differences between the members of this small family can be related to behavioural differences, an investigation of aggressive behaviour may provide a useful starting point.

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APPENDIX A

Function of Head Colour.

The slight sexual dimorphism in the colour of the head is difficult to understand. In several terns (Cullen) and the hooded gulls (Tinbergen 1959) the black cap or dark hood is used in agonistic and pair-formation displays and clearly possesses threat valence, hence the tilting of the cap away from each other in tern pairs, and the head-flagging in Black-headed Gull courtship. In these cases, however, there is no difference between the sexes in the character concerned, which is definite and clear-cut. Also both sexes perform the appropriate movement to remove it as a visual stimulus. In the Gannet, on the other hand, a slight sex difference in head colour does exist, the character is not definite and clear-cut (one would have expected a more striking colour and colour-pattern if it were associated with a signal function) and in the meeting ceremony the head is not turned away at all in the male and only briefly in the female, and in any case can hardly be said to conceal the colour very effectively.

Where a clear-cut sex difference in head adornment occurs, as in the King Penguin, it may have a definite function in courtship, and help the male to obtain a mate (Stonehouse 1953), though Richdale (1951) says this is not true for the Yellow-eyed Penguin. Murphy suggests that head patterns in penguins function in facilitating species-recognition at sea. Neither of these suggestions could apply to the Gannet.

If the head colour seems unlikely to be important as a social signal it might be suggested that it reduces the Gannet's conspicuousness to fish. This is unconvincing since the female often loses the colour entirely in the later stages of chick growth, just when the young require most food. Also there is great variation in the age at which it develops

unlike the pale ventral plumage, which Phillips (1962) has shown probably to be of advantage in fishing.

In the absence of any positive value in the yellow head colour, there is the suggestion that it is merely an incidental result of metabolic waste products. This is unhelpful in accounting for a plumage character of this magnitude. Nevertheless distinctive plumage features in other species have sometimes been held 'functionless' (Lack 1947 in discussing rufous wing bars in some Geospiza).

The fading and disintegration of female head colour is difficult to explain, since in both sexes the carotenoid pigment within the non-metabolising feather is exposed to the same external factors (insolation, halogenation, etc.), though the female is subject to biting from the male. However, even unmated females turn pale and spotty and in any case the fading could not be explained in this way. Nor could fading be explained by withdrawal of pigment for yolk formation (if such a process were possible) since it also occurs in non-laying females. The function and physiology of head colour in the Gannet clearly provides several problems for future work.

APPENDIX B

Distribution of Breeding Population on the Bass Rock.

Here the general distribution is described and the populations of selected small areas given more accurately. Most of these can be located on Fig. 2.

1. Main distribution. The two main masses breed on the east and west faces of the Bass (see Plate 1 and Fig. 2). The north face holds a pocket under the foghorn but is, in general, thinly populated due to lack of suitable ledges. The south face holds the Lighthouse establishment and the old chapel (see Fig. 2). Apart from a group of some 50 nests on the headland, a group on the cliff below

it and a small group just above the Lighthouse it is devoid of Gannets, although apparently this was not always so. Old accounts indicate Gannets above the landing place (probably the equivalent of the present 'west landing').

On the east side they breed right up to the top of the cliffs and the uppermost groups are on gently sloping slabs, easily accessible, though here they do not spill over on to flat ground. The rookery above the middle of the east cliffs is one of the very first to be repopulated early in the year and is probably one of the oldest established on the entire Rock. To the north of east the cliffs become thinly populated and south of east swing round into the landings area and battlements.

The great west cliffs, actually facing S.W. and W., hold a dense population and above the cliff top proper continue onto the broken ground with some large, flattish plateaux, and many outcrops and small faces which make ideal nesting terrain. About its upper limits the spread of this group is difficult to follow since it suffers most from disturbance by man. A number of birds in this region have probably held sites for three or more years without breeding successfully. The topography of the Rock is here quite different from the east side and it is on the steep, bare slopes above the west face that the great mass of immatures and non-breeders settle, wind permitting.

Above the sheer N.W. cliffs (Plate 1) which hold pockets of Gannets on the broader ledges the ground slopes steeply to the grassy summit. The Gannets have colonised the lower part of this slope and a group of some 400 nests and sites (the observation colony) push right up to the grass line (Plate 2).

The population increase may also be followed by counting several separate groups each year. Counts for 7 such groups are given in the table. Details of location

have been prepared (Nelson in press) to allow subsequent identification by others.

TABLE. Population changes in seven discrete groups.

Area	Approximate number of nests and sites 1961	1962	1963
Headland	11 sites 48 nests	61 sites nests	75 sites nests
Lighthouse colony	6 sites 20 nests	6 sites 20 nests	10 sites 25 nests
Needle colony	35 sites 35 nests	35 sites 35 nests	24 sites 35 nests
Upper east face group 1	No record	7 sites 16 nests	12 sites 13 nests
Upper east face group 2	No record	4 sites 2 nests	5 sites 2 nests
Upper east face group 3	No record	2 sites 17 nests	4 sites 16 nests
Base of east face	No record	13 sites 17 nests	4 sites 24 nests

APPENDIX C

Seasonal Arrival and Build-up.

1961 First seen near Bass Jan. 7th.. 1-30 flying near Bass between Jan. 8th-12th.. Several landed Jan. 13th.. On March 17th. more than 80% of nests in old parts of Colony occupied.

1962 A very few birds seen near Bass between Jan. 4th.-13th. Several landed Jan. 14th.. By Jan. 24th. many hundreds back. By Feb. 19th. hardly any (about 6 on lower east cliffs). Feb. 20th. none on Rock, though several hundreds flying off west side. Feb. 21st. a few on Rock and over a 1000 on the sea and flying round. Feb. 24th. 'Needle' full, virtually all east side occupied, several back in observation colony for first time. Feb. 26th. appalling conditions but many birds remain, including new arrivals. Feb. 28th. east side still thickly populated, but west side very thin, (wind N.E. force 5-6). March 3rd. wind west but west side thinly populated, east side also much thinner, Needle deserted. March 5th. 1,000- on sea, but cliffs almost empty, slight increase by midday on east side, snow lying on Rock. March 7th. snow still lying; very few on cliffs and virtually all males. March 8th. an increase. March 9th. a calm day; dramatic increase, fullest yet. Increase continued

March 10th.. March 12th. marked decrease, strong north west wind. Between March 10th. and April 9th. attendance continued thin, with large empty areas even in established groups. April 10th. an increase. April 12th. considerable increase. April 13th. observation colony full. Until April 25th. the fringe of the observation colony was largely unoccupied in the early morning, but a dramatic increase occurred in the evenings.

1963 Jan. 1-17th. a few birds within sight of the Bass every day. Jan. 18th. many more and several landed. Jan. 19-22nd. a few near the Bass but none landed (contrast this with Jan. 24th. 1962). From Jan. 27th.-30th. there were a 'lot' round the Bass and probably several on the cliffs (but no observations were made). By Feb. 9th. the lower east cliffs were well filled, but none higher. From Feb. 10-17th. there were few Gannets on the Rock and none in the areas near the cliff tops. On Feb. 21st. some birds returned to the observation colony (cf. Feb. 24th. 1962). There are no further observations between Feb. 22nd. and March 25th. (my arrival date) by which time all the established areas were well filled, including the observation colony. There were very few fringe birds returned by this date. Between March 26th. and April 17th. the fringe remained thinly populated. From then on birds established late in 1962 and newcomers of the current year began to arrive. The first club gathering was seen on April 20th. about 200-300 birds, including a few three year-olds.

APPENDIX D

Seasonal Departure.

The final departure of Gannets from the Rock in Autumn is not a clear-cut process and birds may return in force after preliminary absences.

1960 Oct. 27th. most birds away, most back again the next day, only to leave again by Oct. 29th. Rock clear of adults Nov. 1st., though a few were flying round. On Nov. 7th. a few returned to the Rock for the last time, but some were seen in flight nearby until the end of November. After mid-December 3 or 4 daily were around the Rock until the end of the year.

1961 On Oct. 16th. an estimated 30% of nests were occupied. From Oct. 30th. to the end of the year none were recorded on the Rock, but several in the vicinity (date records not kept).

1962 By Oct. 1st. over 60% of birds were absent from the Rock (there had previously been noticeable absences since Aug. 11th. and on September 9th. the observation colony was very thinly attended). By Oct. 5th. most were back again, but on Oct. 6th. the Rock emptied drastically and was the real date of departure. Nevertheless late birds were recorded. 'A few' were present on Nov. 17th. (and most days before this). Between Nov. 18th. and Dec. 28th. none on the Rock but some, on several days, nearby. On Dec. 29th. 12 birds landed on the Rock.