The behaviour of the Gannet

By J. B. Nelson

(Plates 41-47)

INTRODUCTION

Gannets *Sula bassana* were studied from 1960 to 1963 on the Bass Rock (plate 41a), which is situated at 56°04′N, 2°38′W in the Firth of Forth. This paper aims to give a full description of their main behaviour patterns (excluding chick care and the development of behaviour in chicks, which will be treated separately) with an analysis of the situations in which they occur. Beyond this the causation, adaptiveness (or function) and evolutionary aspects of Gannet behaviour at the breeding colony are of great interest and will be kept constantly in mind. Some of the ecological findings have already been published elsewhere (Nelson 1964a, b). A review paper containing an outline of some of the Gannet behaviour here described in detail has also appeared (1964c), though pre-dated in writing by the present account.

Previous accounts of Gannet behaviour are fragmentary (Armstrong 1942, Gibson-Hill 1948, Perry 1948, Fisher and Lockley 1954 and Barlee 1956), although Warham (1958) has well described some behaviour in the Australasian Gannet *S. serrator*. Several Gannet behaviour patterns (e.g. male advertising, female facing-away, the sideways head shake in its many contexts) have not previously been described and virtually nothing has been written about the causation and function of the remainder.

Several recent studies have related diverse features of a bird’s ecology, behaviour and structure to some major adaptive theme. Von Haartman (1957) demonstrated the relationship between hole nesting and the behaviour of the Pied Flycatcher *Muscicapa hypoleuca*; E. Cullen (1957) related Kittiwake *Rissa tridactyla* behaviour to cliff nesting;
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Phillips (1962), in experimental work with gulls (though the findings may have wider applications), connected plunge-diving with the presence of white on the head and under-parts, which reduces conspicuousness to fish; and Crook (1962) showed how the process of contact and pair bond development in weaver-birds may be related to their feeding habits, dispersion and sexual or seasonal dimorphism. Tinbergen and co-workers are gradually uncovering the entire anti-predator system in the Black-headed Gull *Larus ridibundus*, which affects many features of its behaviour such as spacing out of nests, egg-shell removal (Tinbergen et al. 1962) and roosting habits. In the present study the implications of dense colonial nesting (mainly on cliffs) coupled with strong site attachment and aggression gradually emerged as central aspects of the Gannet's breeding biology and behaviour. Correspondingly, these will be discussed in detail; they have an important bearing on the wider topics of population dynamics, including recruitment rate (deferred maturity, non-breeding adults, clutch size). Site acquisition and defence involves violent and persistent aggression and seasonally prolonged and concentrated site attendance. Both these have associated disadvantages. I hope to show that Gannet behaviour often represents an adaptive compromise between conflicting selection pressures.

A convenient framework for the description of behaviour is the succession of events in the annual breeding cycle. Before this a brief account of voice and some morphological characters involved in display is relevant.

**STUDY AREA AND METHODS**

I was fortunate enough to live on the Bass Rock for part of 1960, followed by continuous spells (February to October or November) in each of the three seasons following; my wife joined me for most of this time. In the main observation colony—some 300 nests and sites* on sloping ground at the top of the north-west face—171 adults were ringed with individual combinations of coloured, spiral chicken rings and B.T.O. rings. This group had a clear inland boundary which facilitated the plotting of each new nest or site in the 'fringe'. A rapid extension of this boundary occurred in three annual 'waves' and some 90 new nests or sites were added. Behaviour involved in site establishment and pair formation could therefore be watched closely; both are among the more difficult processes to observe in most birds.

Two hides were used and the birds soon ignored them. A portable tape-recorder was used to detail rapid and complicated interactions and a ciné-film of the main behaviour patterns was used for drawing certain

*A nest is defined as a small, fixed area which is defended and contains nest material. A site is a small, fixed area which is defended but contains no nest material.
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sequences. Since most of the Bass Gannet population* nests on cliffs or steep ground near the top of cliffs, behaviour recorded from the observation group was checked by observations on cliff birds.

MORPHOLOGY AND VOICE

This aspect has been treated previously (Nelson 1964c), but is included with additional comment here because of its relevance to Gannet displays. The North Atlantic Gannet is given specific rank along with the Australasian Gannet and the South African or Cape Gannet S. capensis, though the differences in morphology are very slight. Many authors place all three in the genus Morus to distinguish this group of true temperate-water Gannets from the pan-tropical booby genus Sula. In the Gannet the sexes are much alike in voice and appearance. Reversing the situation in all other members of the Sulidae, male Gannets are slightly larger and heavier than females, with bigger beaks (male culmen average 100.2 mm., range 93.5-110, 33 measured; female average 98.9 mm., range 94-104, 31 measured). This difference may be connected with aggression, which is stronger in Gannets than in other Sulidae and also greater in the male than in the female.

The whole family shows facial patterns of highly coloured soft parts and bills. Gannets have yellowish (ranging from pale yellow to deep orange-buff) heads and necks, pale blue beaks with conspicuous black lines running horizontally along them, and black skin extending above the ice-blue eyes to the corners of the gape and also as an extensible black strip on the gular pouch and throat. Since the head is a focal point in many displays involving its presentation and withdrawal, the conspicuous lines may aid the communication value of these movements. There are many well-known examples of such ‘markers’: for instance, the black cap of the Arctic Tern Sterna m.acerura is tilted differently in movements with different signal values (J. M. Cullen 1956), the hood of the Black-headed Gull is used in ‘head-flagging’ (Tinbergen and Moynihan 1952), and the specula of ducks are touched in stylised manner (Lorenz 1941).

The Gannet’s yellow head colour shows a sex difference, being usually paler and (particularly late in the season) spotted with white in the female. Since there is much variation in this character and in different years the same individual may be lighter or darker than its mate, it cannot safely be used to sex birds, though the darker of a pair will probably be the male. Whereas the greater spottiness of the female is due to a moult difference (not, as has been suggested, to the biting of the female by the male; unmated females become spotty too) the paler colour is clearly a pigment intensity difference.

*In June 1962 we counted the Gannets and found some 5,500-5,700 breeding pairs; 1,300-1,500 pairs with nests or sites but no eggs or chicks; and 2,000-2,500 non-breeding birds, including adults and immatures, without nests or sites.
Unlike other members of the family, Gannets have conspicuous greenish lines on the toes and fusing on the tarsus, providing a fairly reliable means of sexing. In males the green tends to yellow and in females to blue. Again there is overlap, but when a pair are together the sexes can usually be recognised. In extreme cases solitary individuals can be sexed. The function of lines standing out so clearly against the blackish webs is probably to emphasise the movement of the feet in the Gannet’s pre-flight posture. Similarly, the Blue-footed Booby *S. nebouxii* uses its astonishingly conspicuous blue feet in an exaggerated ‘parading’ movement, and also flings them upwards and slightly outwards, fully spread and showing the soles, when it flies in to the nest site in the early stages of pair formation.

Like most sea-birds the Gannet has extremely few calls. It relies for communication mainly on visual signals. The voice shows no sex dimorphism, in contrast to some boobies in which, due to a sex difference in the structure of the syrinx (Murphy 1936), males whistle and females shout harshly. Nevertheless, individual differences in voice enable the Gannet to recognise mate and neighbours as they fly in. Chicks also recognise the voices of their parents. The main call, usually associated with aggression, is a strident *urrah rah rah*, given by both sexes about four times per second when flying in to the site (we shall see later that this involves some aggression). The pace of the syllables accelerates, their loudness increases and a final ‘shout’ is given just before touch-down. Much the same call is given by both sexes when fighting, in threat behaviour, during attacks on chicks and in some displays. The alarm version is loud and staccato, repeated three or four times on a descending scale.

During take-off and often after a hop or run a soft *ooah*, attenuated and sometimes disyllabic, is uttered. Just before or during take-off from a ledge this call often resembles a low groan, and is usually accompanied by a special posture (plates 46b, 47a and 47b) preceding movement. Because it is often given from a strained position, neck stretched and tail acutely depressed, it has been suggested to result involuntarily from physical contortion. However, it is produced by birds in all sorts of normal positions, including flight, and may be absent from the contorted ones: it is almost certainly produced ‘voluntarily’.

A call resembling the soft *crok* of a Raven *Corvus corax*, and apparently not previously recorded, was sometimes heard from Gannets in fast, level flight.

**Background Information**

The reader may wish to relate the following points to some part of the detailed account, even though they fall outside the scope of the present paper: Gannet nests and pairs are more or less permanent; adult life
expectation is about 16 years; they usually breed first at five years after holding a site for all or part of the previous season; eggs are laid mainly between mid-April and mid-May, exceptionally in March and June; breeding success is high (in terms of fledged young from eggs laid it averaged 73% over three years). There are plenty of new sites available on the Bass which are in no way topographically unsuitable unless Gannets require features so subtle as to be unrecognisable by detailed comparison with sites already in use. There are many adults among the immature birds gathering in 'clubs' at various points on the Rock, and these are probably non-breeders rather than off-duty breeders.

SITE ESTABLISHMENT

It seems probable that Gannets, although now often nesting on flattish ground, were originally and are still primarily cliff-nesters, as indicated by their many adaptations to cliff nesting (e.g. fighting method described on page 242, ability to 'cement' nests, behaviour of young, and many others).

Gannets strongly tend to nest in the colony of their birth, often close to the nest from which they fledged or, in any case, close to other nesting birds of the same species. Particularly large numbers of Gannets in the observation colony were ringed by other people between 1955 and 1959 and the high proportion of ringed birds (41%) establishing sites on the fringe of this group during the present study showed that many of the birds ringed there as chicks returned to breed for the first time within a few score yards of the area of their birth. Had they scattered over the entire Rock, such a concentration, in one small section, of ringed four- to five-year-olds could not have ensued.

There is a strong tendency to nest within about three feet (the pecking distance) of birds already established, which leads to the typical compact structure and expansion of Gannet colonies (plate 44). Dense nesting is often 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 respect it has often been remarked that suitable areas are neglected in favour of others nearer existing nests. Wynne-Edwards (1962) suggested that dense colonial nesting is also part of the social machinery limiting breeding areas and partly regulating the admittance of new breeders. However this may be, it seems that the dense colonial breeding so characteristic of the Gannet is not forced upon it solely by the shortage of nest sites at present. There must also be other advantages whose nature remains to be demonstrated. Synchronisation of breeding to take advantage of seasonally abundant food may be one.

During winter Gannets apparently range over the sea without aggressive interaction (e.g. in feeding). The acquisition and defence of
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a breeding site, however, seems to have required the evolution of intensely competitive behaviour. Tinbergen (1936) 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 breeding. In the Gannet aggression in the site context is so important that it has been favoured even though its effects are not confined to the situation for which it was selected, but ‘out-crop’ in ways which seem less adaptive but inevitable. A male which, due to outstanding aggression against other males, easily acquires and defends its site, may also be more aggressive towards its mate and chick. The responses of these will be influenced (as indeed they have been) and the raw material provided for the development of progressively more efficient appeasing behaviour (page 267). In this way one important behaviour system can influence much of a species’ biology, as aggression has done in the Gannet. The development of any one trait is eventually limited by the general requirements of the species. Thus, the relationship between Gannet mates is, at one stage, already so fine that the slightest ‘false move’ by the female may release violent aggression in the male. Still more aggressive males might well attack too often and too strongly and so reduce their chances of pair formation. Similarly, the fear tendency must be adequately developed so that aggression is expressed only in the ‘right’ situations. Males which always fought and never fled would quickly be eliminated.

Male Gannets usually establish and maintain a precise site for all or part of the season prior to that in which they first breed, in contrast, so far as known, to other British seabirds except the Cormorant Phalacrocormorant Phalacrocorax carbo (Kortlandt 1942) and possibly the Fulmar Fulmarus glacialis. Arctic Terns, at the other extreme, may choose the nest site only a few hours before the first egg is laid (J. M. Cullen 1936).

Period over which sites established
Table 1 shows the dates on which sites were established. In 52 out of 53 cases breeding did not occur until the season after establishment. Sites established relatively early in the season were attended more than were later ones, where attendance was often sporadic. Birds late in establishing a site but regular in attendance usually bred the following year. Other late males either abandoned the site or held it for a full subsequent season before breeding. ‘Squeezed in’ sites (page 240) were more consistently guarded in the early stages than fringe ones and also returned to earlier in the following year, possibly due to the greater social stimulation experienced there (cf. Kittiwakes: Coulson and White 1960).

Method of site establishment
The following details refer to birds newly establishing sites. Experi-
Table 1. Dates of site establishment by Gannets *Sula bassana* on the Bass Rock in 1961 and 1962, shown in half-monthly periods

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enced breeders simply return and occupy their old nest (or site if the drum has disintegrated) performing the ownership display (page 248) when stimulated by intruders.

Site establishment is preceded by aerial reconnaissance mainly over a particular area. It is impossible to keep an individual in sight for long but hundreds of fragmentary observations, supported by the behaviour of a dyed male, indicated that regular flight reconnaissance preceded the first tentative attempts to obtain a site. To avoid unnecessary fighting, it is essential that, in the later stages, they should be able to pitch hesitantly on to the exact site, perhaps in the midst of a nesting mass. However, the assertion (Palmer 1962) that accidental trespass of this kind can lead to severe fighting and even deaths seems quite wrong; such birds are only too willing to escape and hardly ever retaliate except to aid their getaway. Only intruders with territorial ‘intentions’ fight back.

Prolonged scanning of the nesting group is followed by ground reconnaissance from an unoccupied nest or vantage point, or from the fringe. I recorded five different males successively occupying a vacant nest in two to three hours, each being displaced by the owner who had joined a widowed female near-by. This shows the constant pressure exerted by young males attempting to take over empty nests and the premium on guarding them. Before a male will fight in defence of a site he must have occupied it for at least a few hours and probably two or three days or more. Owning males returning from foraging, which often takes two or three days, thus usually re-assert themselves without serious fighting. The tendency of young males to return to the breeding colony only after most of the old males are back in residence may be a further adaptation to this end.

Males establish sites by taking over existing nests, squeezing in between them or (as in the fringe of the observation colony) establishing themselves in a new area, usually very close to an existing group.

*Taking over existing nests.* The low adult mortality rate of 6% (calculated from the annual return of colour-ringed individuals) and the female’s continued attachment to the site if the male dies means that each year few nests are vacated by both owners. Within the group of ringed birds only four such cases were recorded, although the ‘taking over’ process is responsible for maintaining the stability of Gannet
colonies. In cases where one partner dies it is usually replaced appropriately: in other words, the male continues to hold the site and finds a new mate, or the female accepts a new male who may have taken over in her absence. In some cases established females returning late were unable to oust 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. The converse rarely occurred.

Lockley (in Fisher and Lockley 1954) has stated that young Gannets take up the outer edges of a colony and that the inner section consists of older birds. This is true only of an expanding group. Since in a stable population there is no reduction in density in the old-established (supposedly central) parts it follows that the first-time breeders take over nests scattered throughout, and are not concentrated on the outer fringes. Such nests will occur evenly in a group unless the edge suffers more from predation. Where, however, a general or local increase is taking place, newcomers will, as in the observation colony, establish sites on the fringes. Without knowing whether the population is stable or expanding one cannot deduce that the age of the birds in the centre of the colony is on average greater than at the fringe.

'Squeezing in' between existing nests. The density and regularity of old-established groups is greater than newer ones, due partly to the initial tendency of new birds to defend a larger area than they later maintain, leaving gaps which are only gradually filled. Slight adjustments of nest positions also occur after winter disintegration of drums and help to achieve even dispersion. Nevertheless, it sometimes happens that a spot which, because of its smallness or difficult position, has remained empty for years, is suddenly adopted by a male who clings to it despite fierce hostility from neighbours. It is tempting to speculate that such males were born near-by and are for some reason, possibly a conspicuous landmark, particularly stimulated to return there (page 237).

On average only one male chick would survive to breeding from the offspring of such an area over many years, so possibly explaining the sudden and tenacious adoption of these unlikely spots.

Establishing a site in a new area. The pattern of site establishment in the fringe of the observation colony (where most of the observations were made) was revealed by twice-daily checks and large-scale mapping. Newcomers were wary and no attempt was made to ring them. However, the return of birds colour-ringed as chicks (over 600 were marked in the observation colony during 1960-63) will eventually provide recognisable individuals. The dyed male mentioned earlier confirmed points deduced from unmarked birds.

Site establishment involves readily recognisable behaviour which, together with the length of time spent on the site, shows whether birds are in earnest or mere casual visitors. A male laying claim to a spot,
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which in the early stages may be simply a patch of grass without distinctive features, flies in calling and makes a characteristic nest-biting movement after landing there. If there is no nest material he bites the ground or makes intention movements of doing so, still calling loudly. This (or equivalent) aggressive behaviour is widespread in the Sulidae. In its primitive form it is simply a nest-biting or touching movement, often with widespread wings, but in the Gannet it has also given rise to a more elaborate site-ownership display, bowing (page 248). Males bent on establishing a site threaten other males wandering nearby, bow frequently and when relatively idle stand in a relaxed manner with retracted neck, preen or sleep. By contrast, an intruder or casual visitor lands without calling or nest-biting and stands in the anxiety posture with long neck and sleeked feathers, scanning the neighbourhood. He does not bow or show marked aggression towards birds near-by, but is, on the contrary, easily displaced by challengers. Since individuals later establishing themselves first come to sites as casual visitors it follows that the transition stages are difficult to recognise. Some immatures spend most of a season in the preliminary stages, showing only weak attachment to a particular spot. The longer a bird spends on a site the more bitterly he will fight to retain it.

Aggression and the site

The site is the Gannet’s only territory and is used for pair contact, copulation and breeding. In the male three forms of aggressive behaviour—fighting, threat and ritualised (aggressively motivated) display—are connected solely with the site. Gannets, though highly gregarious when fishing, gathering nest material or resting on the sea, are not in these circumstances aggressive. During communal gathering of nest material they may snatch grass from each others’ beaks, but I never saw even the mildest fighting. Even when crowded together devouring trawler offal they rarely squabble, in strong contrast to Herring Gulls *Larus argentatus*. When breeding birds meet on the fringe of the colony (perhaps en route to a take-off point) they are not aggressive. Yet on their sites they become fiercely hostile.

Tinbergen (1936) emphasised the balanced nature of agonistic behaviour and Lack (1954) similarly stated that in territorial behaviour the avoidance response of non-owners is as important (or more) as the aggression of the owner. Nevertheless, though it is true that in the Gannet all except serious contenders for the site either avoid males guarding their sites or flee when menaced, severe fighting is common. All references to aggressive behaviour in sea-birds which I have found indicate that Gannet fighting is quite exceptional in frequency and severity, although Tuck (1960) recorded ‘severe mortality’ due to fighting among Razorbills *Alca torda* at Akpatok Island.

**Fighting** (fig. 1, plate 45c). Male fighting functions as part of the
process of site establishment and maintenance. Of 53 sites whose establishment was followed in detail 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.

Fighting often begins in earnest after high intensity threat behaviour (plate 45a) but does not require this as a necessary first stage; often one bird lands and dashes straight against the other. The combatants interlock bills (fig. 1) and attempt to drive each other from the nest or site; strong pushing movements of the legs, with feet curved for better grip, are transmitted to the opponent through straining body and extended neck. The wings are threshed around and the tail spread and depressed against the ground for increased leverage. Although the beak is the focal point for attack, other parts of the face, head and neck are also seized; the birds shift grip with amazing speed and intersperse slashes, stabs and worrying or shaking movements with the main, tense pushing.

During fights damage is inflicted on both combatants by surrounding birds, particularly where the head of one is held as it were on the chopping block of the opponent’s beak, and the pecks of neighbours are powerfully effective. It might therefore be inferred that the pushing with extended neck enables one to thrust away the opponent whilst itself remaining on the site and so escaping attacks from neighbours. In fact, the winning bird makes no attempt to remain on the site during a fight; on the contrary, he drives his opponent before him, ignoring the bites of enraged neighbours.

It is worth emphasising that this method of pushing with extended neck (made possibly only because of the Gannet’s extremely strong neck developed for plunge-diving) is well-suited for displacing an opponent from a cliff ledge. Gannet fighting has probably evolved its present characteristics in the context of cliff nesting, to which it is functionally best adapted (cf. the Kittiwake’s method of ‘twisting’ an opponent off the ledge: E. Cullen 1957). The apparently dysgenic severity of fights in flatter parts of the colony may have resulted from
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the application here of a fighting method evolved in a different context in which an important factor was the tendency of one or both birds to fall or be pushed off the ledge, so ending the struggle unless it is renewed in the sea below. This would partly explain such severe fighting which runs counter to the general situation in birds, where displays replace it; if fighting did not evolve under flat conditions, no wonder it is poorly adapted to them. Further, Gannets sometimes attempt to displace opponents by diving on to them in a typical shallow fish-hunting dive. Whereas this is effective against a ledge opponent it is, of course, futile on flat ground. In its use of a behaviour pattern primarily evolved in an entirely different context, here fishing, the Gannet may be compared to the Sparrowhawk *Accipiter nisus* which uses hunting behaviour to break off twigs for its nest (Bal 1950).

The length of extreme Gannet fights is partly due to the surroundings and also to a strong tendency shown by dominant rivals to deny escape to the opponent. Even when the latter tries to pull loose and flee the other hangs on or pursues him and renews the struggle. This may be to inflict a sound defeat and lessen the chance of further challenge from that rival.

The eyelids do not protect the eyes during fighting but the semi-transparent nictitating membrane is drawn across as a reflex response to any anticipated contact. The lens can withstand fierce jabs and must somehow be exceptionally well-protected. Gannets, unlike Shags *Phalacrocorax aristotelis* (Snow 1963), do not avoid each others' eyes when mutual preening and certainly not when fighting. Birds caught whilst sleeping off the effects of a severe fight (which they sometimes do for three full days) often bore nasty wounds; in one most of the eye tissue was hanging out of the socket (plate 45b), another had the eye socket filled with blood and a third had an opaque eye. Others had deep cuts in the facial soft parts and one had a deep peck wound near the oil gland. The head is often pock-marked and bleeding where neighbours have stabbed it hard. One bird died from a peck wound in the abdomen. Extreme exhaustion and filthy, tattered wing and tail feathers caused by the wild threshing are further consequences underlining the severity of these struggles which may last up to two hours virtually non-stop. Yet it should also be said that adult mortality due to fighting is, despite its ferocity, totally insignificant.

Males use a different method when attacking females, which they seize by the scruff of the neck and force away. This is partly due to the female's appeasement behaviour in which she faces away, thus hiding her beak from the male.

Females fighting in the presence of the male (but not vice versa) are unwilling to carry the fight off the site, not to avoid punishment from neighbours, but to remain as close as possible to the male who, rather
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than the site, is usually the object of dispute. Such females always attempt to push against the male and will quietly endure sustained attack from the rival so long as they occupy this coveted position. Once dislodged they renew the struggle with great bitterness. When the male is absent, however, females show the male pattern of fighting, pursuing the opponent some distance from the site.

In fights between females the one willing to accept the greatest punishment usually wins, though not necessarily the rightful owner or the most aggressive (by vigour of attack). The male tends to switch his attack to whichever female is losing at the time. He is obviously puzzled and shows conflict behaviour throughout (nest building movements, comfort movements and so on). Occasionally in the heat of the struggle both females mistake the male for the opponent and by the fury of their combined attack drive him ignominiously from the site.

In summary, fighting in the Gannet is uncommonly severe; it is an effective method of settling site disputes, and is probably adapted to cliff nesting, which would explain some of its features, including biologically undesirable severity on flat ground. There are sex differences in fighting procedure.

Fighting and the morphology of the sexes. Although females do not establish the site they quickly form a strong attachment to it and will then share in its defence. In birds, shared defence of territory is usually associated with similar plumage in the sexes, just as in territorial species showing unequal aggression, the more aggressive, usually the male, is more conspicuously coloured. In most colonial sea-birds the sexes look alike, but defence of territory is by no means always (if ever) equally shared. Male Kittiwakes, for example, usually do most of the fighting (E. Cullen 1957). It is not completely satisfactory to suggest that the similar appearance of the sexes confers equal valence as a deterrent to intruders through common possession of threat characters, since, despite this, the sexes readily recognise each other (e.g. Black-headed Gull: Tinbergen 1956; Kittiwake: Cullen 1957; and Gannet). Therefore a female's resemblance to a male may not in itself add to her intrinsic deterrent value. In any case, since she is herself aggressive such resemblance would be of slight advantage here. In fact on occasions it would benefit the female to differ conspicuously since during fights between two females the male is sometimes mistakenly attacked by one of them and his subsequent retaliation may decide the issue against her. Nevertheless, at this stage it may be assumed that the close morphological similarity is connected with shared defence of territory; general features such as the pale ventral surface in both could, of course, possess survival value in quite different contexts such as fishing (see Phillips 1962). In the Woodpigeon *Columba palumbus*, where the sexes are similar and defence of territory is shared, the male does *not* seem to recognise a female
except by her behaviour, particularly the way in which she reacts to aggression (Cramp 1958).

Threat behaviour (fig. 2, plate 45a). Obvious threat behaviour between neighbours consists of incipient overt aggression with jabbing and an extremely common stereotyped behaviour pattern here called 'menacing' and interpreted as a ritualised form of threat behaviour (see below). It is an interesting fact that all four boobies with which I am familiar (S. sula, S. dactylatra, S. nebouxii and S. variegata) lack the ritualised menace, which one might well have expected to occur throughout the family as the 'normal' expression of hostility. S. variegata has the most comparable threat behaviour; it too is a dense and primarily cliff nesting species.

Incipient aggression is intermediate between fighting and stylised menacing and mostly occurs as high intensity agonistic behaviour between newly-established pairs or strong rivals, often when more serious aggression is likely to follow. The rival is threatened by thrusting towards him a widely-opened bill, whose lower mandible often twitches spasmodically. It is accompanied by strident aggressive/fright calling, and unlike the stereotyped menacing frequently results in beak gripping.

Gannets menace from standing, sitting and incubating positions. In encounters between equals the beak is opened and thrust with a marked sideways twist of the head towards the opponent and then withdrawn. The withdrawal is clearly a 'pre-set' part of the behaviour and does not depend on aggressive reaction from the opponent. Insofar as the sideways twist and withdrawal are exaggerations of menacing, and probably enhance its signal value, they are evidence for its ritualised nature. Although one bird initiates the menacing bout, the movements of the participants often synchronise. Although near enough to bite, established birds rarely do so in these encounters—hardly surprising when one realises that during the nesting season each bird menaces and is menaced thousands of times. To give an idea of the frequency of menaces the data in fig. 3 can be arranged to show that

Fig. 2. Threat behaviour. Two menace each other in site dispute. Note the turning of the left-hand bird's head and the withdrawn position of the other's
every bird, during the time spent singly on the nest throughout the season, menaces a neighbour more than once per hour in the hours of daylight. The value of ritualisation is evident here, since it would be extremely wasteful and inefficient if even a small proportion led to real fighting.

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.

Menacing between hostile birds, when judged from knowledge of the situation to be intensive, is associated with head shaking, frequent touching of nest material, repeated pelican postures (to be described in part 2) and bowing.

The form of menacing, the situations which elicit it and the actual attack to which it may lead show that it is at least partly aggressively motivated. Although clearly hostile (all stages between ritualised menacing and fierce fighting occur), it acquires certain overtones during the course of co-existence with neighbours. Whilst even slight intrusion immediately elicits full threat behaviour, perfunctory menacing occurs on countless occasions, sometimes without visible cause, at very low intensity and without calling. Fig. 3 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 corresponds with a similar trend in bowing and may be partly due to the relatively high level of external stimuli eliciting aggression at these times (wandering birds, prospectors and so on).

![Fig. 3. Frequency of menacing (threat behaviour) throughout the season. Counts from two separate groups are shown by continuous and broken lines.](image-url)
Menacing helps to ensure the characteristically regular spacing-out within the colony. The most intense and prolonged (half an hour or more) bouts occur when site boundaries are least well-defined, soon after establishment. Such behaviour may even prevent 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. Although in breeding groups on flatter ground each nest is normally just beyond practicable jabbing distance of the neighbours, inserted pairs once accepted may be tolerated even when the wing tip or tail actually touches a neighbour. Again, even stereotyped reaction shows modifications which could lead to important changes in habit (e.g. denser nesting).

**Bowing** (fig. 4, plate 42a). As in most birds and despite the fighting and menacing, Gannet aggression on the site mainly takes the form of displays. The commonest and most conspicuous of these may be descriptively termed 'bowing' (the 'wing bow' of Perry 1948 and the 'curtsy' of Lockley 1954 and Warham 1958). Since this movement plays an important part in the Gannet's social behaviour and also well illustrates several general points concerning displays it will be described in detail.

**Description.** A full male bow is a stereotyped movement taking four to twelve 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, starting slowly and increasing in speed and amplitude. The bill is inclined slightly downwards, or sometimes held horizontally. After one to five head shakes the head and thorax are bowed forwards and downwards in a smooth sweep alongside either wing or foot* (occasionally between the feet). This gives the bow its distinctive character, the whole forepart of the body moving, not just the head. Often the tail is raised or even cocked vertically, probably for balance. 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 ‘wing-drying’, or merely hung loosely. Commonly, 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 fig. 14b in part 2).

After the final dip the wings are folded and the bill tip pressed tightly

*Out of 669 recorded, 44% dipped to the right and 56% to the left. This difference is statistically highly significant and completely puzzling. Warham (1958) also noticed this tendency, though he did not give actual figures.

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FIG. 4. Bowing. This aggressively-motivated display signals site-ownership. In (a) the bird is performing the 'dip' (each bow contains one to five) and in (b) the sideways head shake which occurs between dips against the upper breast in a 'pelican position' (65% of all bows were followed by this posture—see plate 46a—to be analysed in part 2). Usually the bill tip lies to the same side of the median line as the dips 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 *urrah* loudly 10 to 30 times.

Certain individuals showed consistent and permanent peculiarities in their bows. One male had a high-flinging, rapid head shake. Another bowed lazily with the wings only a little open and with never more than two dips. Others were distinguished by stance; speed, direction and extent of dip; movement of wings; and silent bowing. Thus even within a stylised display 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.

To analyse the intensity of bowing I counted the number of dips, classified four positions of extent of wing-opening, timed the duration of the pelican posture and divided performances into 'co-ordinated' and 'unco-ordinated' (a measure of muscular control in terms of jerkiness or smoothness, hesitancy or assurance, which was useful in distinguishing between the bows of males varying in status). Finally, it was usually possible to classify bows as 'stimulated' when evoked by some external stimulus, such as a threat or a neighbour's bow, or 'endogenous' when performed without any obvious external stimuli. 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 bow for no obvious reason. Admittedly distant flying birds are always in view, but nesting Gannets ignore these. Further evidence for spontaneous bowing was that sleeping birds awoke, bowed and went back to sleep.

The measures of intensity given above were, in fact, linked in both sexes and bows with most dips also showed greater opening of the wings, longer pelican postures and more co-ordination. These well-marked differences were actually measured in many hundreds of bows from both sexes, though it seems unnecessary here to give a statistical analysis of the results.

Besides the above correlations a marked sex difference was found: male bows were more intense by all measures (i.e. more dips, wings further out, longer pelican posture and more co-ordinated) and also three and a half times as frequent in a sample of 1,068 bows excluding all possible factors which could influence one sex more than the other. Such sex differences in the same display provide a further objective measure of differences between the sexes in site attachment. Males establish the site, spend more time on it and are more faithful to it from year to year. Correspondingly, their site ownership display shows measurably higher intensity. Similarly, the analysis of bowing components and the measure of its frequency are quantitative assessments of intensity and with enough refinements could eventually enable things like the strength of bowing tendency in different categories of site owners (new, old, fringe, central, cliff nesting, flat ground nesting) to be more accurately assessed. A beginning was made in this study, and it was shown that newly-established males bowed more frequently than old ones; that experienced birds with no egg bowed more frequently than the same class of birds with egg and that the presence of the female greatly reduced bowing frequency in all classes of males. Also, club males showed only a female-type bow of low intensity; since the sexual and territorial behaviour of these males is highly transitory it is not surprising to find a territorial display less intense than in established birds.

Frequency. Fig. 5 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 continues to decline during incubation. By comparing the incidence of bowing among birds with and without egg, though otherwise similar, it was shown that broodiness inhibits bowing. 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 despite the continued presence of the egg.

The gradual increase in bowing frequency following the incubation-lay corresponds with a comparable increase in threat behaviour and
the length of mutual fencing bouts (page 269). These latter measures possibly suggest a rise in aggression which, towards the end of the season, could be correlated with both a change in the external stimulus situation (presence of large chicks or increased trespassing of some adults) and also with a rise in the internal (e.g. gonadal) contribution to aggressive behaviour. Oddly enough, however, the increase in bowing towards the end of the season takes it beyond its early season level. This late flowering of territorial behaviour seems an 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. On the other hand many passerines show an autumnal resumption of song, connected with a recrudescence of gonad activity. In the Gannet this late peak cannot be fully accounted for by external stimuli. The prolonged post-breeding stay at the site is not a quiescent period but a very active one.

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, high counts being usually correlated with a marked increase in such traffic; certain early and late counts were very high. 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. Hot weather reduces the mid-day level of activity.

Motivation. The form of a movement may indicate its motivation, as when obviously related to attack, fleeing and so on. Other criteria include the kind of behaviour with which it is associated in time, either long-term or closely (Tinbergen 1959). Evidence will be given here for considering bowing to be an aggressively motivated display in which a fear component and a 'site effect' are also involved.

Although bowing is not obviously a hostile act, it closely resembles nest-biting which is certainly aggressive (probably re-directed aggression). It is elicited by all acts of territorial infringement or the threat of such. The frequency of bowing increases about tenfold when non-breeding birds fly time and again over a nesting group. A veritable frenzy of bowing results if some crash in down-draughts. Even birds landing legitimately on their own site cause increased bowing locally. The approach of an unmated female to a receptive male elicits an inhibited form of bowing, which is in fact his advertising display, whilst in established pairs the arrival of the mate immediately gives rise to a prolonged meeting ceremony which is also a modified form of bowing. In all these different circumstances, therefore, the approach of another individual elicits bowing or related behaviour.

There is a long-term association between the frequency of bowing and other manifestations of aggression. First, the seasonal pattern of bowing follows that for menacing and where two (or more) behaviour patterns vary in the same way throughout a season parallel long-term changes in motivation are probably involved. Second, when bowing is most frequent (seasonally) mutual fencing bouts are longest (see page 271 and table 8) and their length depends on the amount of aggression between the sexes, though it may also be correlated with differences in sexual tendency. Hence again aggression and increased bowing are apparently correlated. Cross checks like these are some test of the accuracy of interpretations about any single behaviour pattern. Thus the frequency of bowing, menacing and mutual fencing all rise together, but independently of, say, comfort behaviour—a phenomenon which can be relatively simply explained if these three behaviour patterns do, in fact, have aggression as a common causal factor.

One cannot necessarily conclude that when the frequency of bowing is low (e.g. during incubation) aggression has declined. The actual expression of hunger, fear, aggression, sex and so on reflects both the strength of the readiness to respond and the external stimulus situation (perhaps further complicated by whatever other drive systems happen

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to be interacting with these at the time). For example, Sevenster (1961) 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 contributing to bowing, thus simplifying further analysis of this display.

Bowing and aggression are also linked during short periods of time, since bowing is highly predictable in certain situations associated closely with overt aggression which it accompanies or follows rather than precedes. After intense fights the winner bows frequently; bowing is interspersed between bouts of jabbing and also in menacing matches; it often accompanies attacks on chicks; it is often performed by males alighting on their unguarded nest sites, a situation in which they commonly first show aggressive nest-biting. Also, if the female is on guard the male bites her fiercely before taking part in the meeting ceremony, which as noted above, is a modified form of bowing. In all the above cases aggression and bowing are closely linked.

After a fight only the winner, now occupying the site, bows, but if the contestants are neighbours, both owning sites and ready to continue the fight (i.e. still aggressive), *both* bow. Occasionally two males fight to exhaustion and both leave the disputed site, in which case *neither* bows. Thus without aggression and the nest site with which it is associated Gannets do not bow. The theory of the motivation of displays which regards them as derived from fear, aggression or sex motivation in varying balance may be inadequate to explain the site-factor in bowing, unless site and aggression are indissolubly linked in the Gannet. The increased frequency of bowing 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 then absent and re-appear only as bowing wanes.

In many animals aggressive displays are also thought necessarily to 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. Many fights are started or renewed in response to the challenge of disputed ownership, signalled by bowing, and it would be hardly surprising if, in that situation, a fear element should form part of the motivation of bowing. We might therefore look for a component most exaggerated when occurring in response to some 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 fits with expectation, since at that point the bowing bird might be attacked. This view accords with the observation that 'stimulated' bows incorporate pelican postures more often than do 'endogenous' bows (70% as against 57% in males, 34% as against 21% in females) and 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. Further, the pelican postures were of longer duration when following stimulated bows.

It must be admitted that there are inconsistencies about this fear component as a usual part of bowing. It may be remembered that one of the characteristics of high-intensity bows (e.g. from secure, old males) is that they are particularly likely to be followed by a pelican posture and, furthermore, one of relatively long duration although there is no sign that such birds are frightened and every reason to think them aggressive. Possibly the pelican posture has become 'frozen' into the bows of secure birds and ceased in them to be quite as sensitive an indication of motivational state. Also (as will be shown in part 2) the pelican posture is itself an ambivalent aggression/fear motivated posture and may partly depend on a rate of change between these two tendencies rather than an absolute value of either.

In summary, the pelican posture varies with situation and those situations most likely to involve the bowing bird in overt aggression elicit 'stress-type' bowing with the most marked pelican postures.

Function. Direct proof of the function of complex displays is seldom possible and few authors demonstrate the accuracy of their functional interpretations of bird displays. Some (e.g. obviously aggressive but nonetheless ritualised behaviour such as menacing) hardly need demonstration.

Bowing in the Gannet is a predictable response to certain recurrent situations already mentioned, and all the evidence suggests that it functions as an ownership display of the 'distance evoking' type to repel potential intruders. Indeed (apart from obvious exceptions) bowing is the only behaviour pattern entirely restricted to the site. The chance observation of an unusual incident strikingly confirmed site and bowing relationship. An adult alighted on a piece of floating driftwood and bowed several times. Two or three others attempted to displace it; one succeeded and immediately bowed. He, in turn, was deposed and the new 'owner' bowed. Yet the usual behaviour after alighting at sea is a comfort movement, never bowing. The piece of wood was clearly treated as a temporary territory.

Bowing is most marked when there are strong ownership ties plus the need to display ownership. Males do it more than females, and especially males establishing a site, when there is more likelihood 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 (e.g. during periods of increased ‘site interest’ 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 practice. All birds within the breeding colony, bowing or otherwise, 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 territory. In this respect it is equivalent to the agonistic displays of many passerines, gulls, waders and so on. A difference of note, however, is that in many passerines and gulls (the Kittiwake is particularly comparable because of its colonial and cliff nesting habits) the ‘song’ or ownership display is also the advertising display by which females are attracted, whereas in the Gannet the two displays are quite distinct although the advertising display is a modified form of bowing.

To sum up, the situations 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.

Derivation. Daanje, in a well known paper (1950), showed how locomotion intention movements can give rise to displays and Tinbergen (1952, 1959) has discussed in detail the ways in which displays may (or possibly must) be derived from simple behaviour patterns (such as intention movements and displacement reactions) which may then be so greatly exaggerated or changed that their origin becomes difficult to trace. Two parts of the bow may be traced back to such simple behaviour. First, the head shake is very similar to, and probably derived from, the sideways head shake (to be discussed in part 2) used to dispel water, dirt and the secretion of the salt gland from the head. After displacement of an intruder, when the dip grades into aggressive nest-biting, the head shake is often far more vigorous,
becoming a head-flinging movement like that used to dispose of nest debris. This is partly because the bill often becomes dirtied in nest-biting. Thus the situation determines the type of dip and the resulting stimuli determine the type of head shake. This interaction of stimuli (in which postural facilitation may play a part) 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 and emancipation of a movement later to become fully stylised as part of a complex display.

Second, the dip in bowing is probably derived from nest-touching or biting, which is found in many Pelecaniformes as an after-landing behaviour pattern. After landing on its empty site a Gannet performs either a nest-touching or a nest-biting movement passing without interruption into normal bowing except that subsequent dips may also, for a time, include nest-biting. There seems little doubt that this primitive behaviour pattern has given rise to bowing by progressive stylisation and the inclusion of the sideways head shake. The transition from nest-biting to dipping with nest-biting and to ordinary bowing in which the bill normally no longer actually touches the nest material, now seen within a minute or two of the bird’s landing at the site, gives a telescoped idea of the process which may have occurred in evolution. Bowing after landing (announcing ownership) and bowing after evicting a rival are the most predictable and probably the phylogenetically oldest bowing situations; both involve the touching or biting of nest material. Although normal bowing includes dipping without touching nest material, it seems justifiable to conclude that the dips are homologous with those of the primary situations. In fact, birds bowing on bare rock sometimes go through the motions of biting or handling nest material.

The form of the pelican posture resembles chick beak hiding—an appeasement posture in which the attacked chick tucks its bill medianally beneath its body or to one side, whilst crouching or lying. The adult pelican posture (plate 46a), which is very probably derived from this infantile appeasement behaviour, differs mainly in degree and is performed in an upright position. The adult female Gannet also shows at least one other appeasement posture (facing away: page 267, plate 43c) closely related to chick beak hiding.

In summary, the important behaviour pattern, bowing, is a complex, stereotyped and mainly aggressive agonistic display. It signifies site ownership and is performed by both sexes, though mainly and more intensively by the male. It repels potential intruders. It consists of movements which no longer fully require their original context and are in that sense emancipated. On these criteria it may be considered to be a ritualised display, derived from simpler behaviour patterns.
BRITISH BIRDS

Table 2. Seasonal dates of first return of Gannets *Sula bassana* to the Bass Rock during 1961-63

<table>
<thead>
<tr>
<th>Year</th>
<th>First seen near Rock</th>
<th>First seen on Rock</th>
<th>First date 1,000+ present</th>
<th>Last date 50% or more un-guarded nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>1961</td>
<td>7th January</td>
<td>13th January</td>
<td>22nd January</td>
<td>8th April</td>
</tr>
<tr>
<td>1962</td>
<td>No record</td>
<td>14th January</td>
<td>24th January</td>
<td>17th April</td>
</tr>
<tr>
<td>1963</td>
<td>1st January</td>
<td>18th January</td>
<td>27th January</td>
<td>7th April</td>
</tr>
</tbody>
</table>

Site attendance

To complete the account of site establishment and maintenance it remains to consider site attendance under the headings return, seasonal duration and site fidelity. It is convenient, for comparative reasons, not to restrict discussion solely to newly-established birds.

Return. Adult Gannets are usually first seen flying around the Bass at the beginning of January or even the end of December. Unlike Kittiwakes (Coulson and White 1958), Manx Shearwaters *Procellaria puffinus* (Lockley 1942) and some other species, they do not normally gather in dense rafts on the sea before returning to the breeding site. Individuals first landing on the Rock, in mid-January, stay only a few hours and may then be absent for long periods.

The date of return is largely independent of weather; birds returned in the last quarter of January 1963, for example, when the severe weather was at its worst. They remain on their sites for a spell, regardless of conditions (which occasionally are harsh in the extreme, as anyone can testify who has watched Gannets from an exposed position in a north-easterly gale with sleet and snow in February), leave again and gradually build up periods of attendance (table 2). As late as the second week in April areas occupied by established birds, mostly experienced breeders, may be suddenly three-quarters depopulated. Sometimes this was partly due to the simultaneous departure of males who had attended their sites for two or three days without the female appearing.

In several cases the members of a known pair were first seen within 24 hours of each other. Austin (1947), Richdale (1944) and Serventy (1941) considered that Common Terns *Sterna hirundo*, Sooty Shearwaters *Procellaria griseus* and some petrels, respectively, return to their breeding grounds already paired, but did not give supporting details. Whilst it is conceivable (but improbable) that in the Gannet old pairs may meet fortuitously at sea, or even return to the colony together, such a process plays no real part in the coming together of the pair.

Newly-returned Gannets are very wary and occasionally ‘panic’ in the same way as Arctic Terns (J. M. Cullen 1956), whole areas suddenly clearing as the birds fly out in a cloud, apparently without reason.
Table 3. Correlation between the dates of return of Gannets $Sula$ bassana to the Bass Rock and previous breeding experience, shown by the numbers of each category returning in each quarter-monthly period

<table>
<thead>
<tr>
<th>Status</th>
<th>Feb.</th>
<th>March</th>
<th>April</th>
<th>May</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bred at least twice</td>
<td>45</td>
<td>35</td>
<td>34</td>
<td>2</td>
<td>116</td>
</tr>
<tr>
<td>Bred once</td>
<td>4</td>
<td>1</td>
<td>9</td>
<td>5</td>
<td>19</td>
</tr>
<tr>
<td>Established a full season</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Established end of previous season</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>24</td>
</tr>
</tbody>
</table>

Tinbergen has suggested that this behaviour expresses fear of land in oceanic species, which seems to fit the present case. It may be that the parts of the Rock first repopulated (mainly a broad band at mid-cliff level) 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. These are also probably the oldest-established areas on the Rock. Coulson and White (1960) recorded that Kittiwakes returning first belong to the densest colonies and suggested a cumulative effect of social stimulation carried over from year to year. Gannets, however, nest at a fairly uniform density where topography allows, except in fringe areas.

Colour ringing and site mapping begun in 1960 provided four categories of returning Gannets by 1963: experienced birds having bred in at least two successive years; experienced birds having bred once only; birds which established sites early the previous year without breeding; and birds newly-established towards the end of the previous season. Table 3 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 they run little risk of losing their sites since new males do not usually prospect till April.

Seasonal duration. Experienced adult Gannets are present at the Bass from about the end of January to November; much longer than commonly thought (e.g. Wynne-Edwards 1962). In the mild winters of 1934/35 (Robinson 1935) and 1964/65 (F. Marr and the Bass keepers) some were present throughout. The annual period spent at the site, including the more intermittent attendances, is thus, at the longest, 9 to 9½ calendar months, or a third to two-thirds longer than any other British sea-bird (Shags excepted, since they often remain around the breeding area all year). Experienced birds spend about four months on the site in addition to the time required for incubation (44 days) and feeding young (94 days). These details support the remark made
earlier on the centrality of the nest site in Gannet breeding biology. Fig. 6 shows the relationship between the stay at the colony and the extent of the different phases in the breeding cycle.

**Fidelity to site.** Table 4 shows the proportion of colour-ringed males which returned to the same site in successive years. Since pairs generally remain constant it is usually not possible to decide whether the female is mainly faithful to the male or to the site. 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, the female acquired a new male on her old site in ten cases; one moved to another site within two yards; one tried unsuccessfully to pair with a neighbouring male; and one remained alone on the site but was displaced by a pair formed in her absence. Of 16 comparable instances in which males lost their females, 15 remained on the same site and acquired a new female and one moved to the next-door female whose mate had died.

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**Fig. 6.** Seasonal extent of various activities at the breeding colony. The periods refer to an average pair and not to the colony as a whole.
**Table 4. Site fidelity of male Gannets *Sula bassana* on the Bass Rock**

The figures in brackets represent the number of males surviving. The number ringed in 1962 included a higher proportion of younger birds than in other years (see later). A bird unfaithful to the site in one year is not subsequently counted in this table. In the last column a further five may or may not have survived and been faithful in 1963; nests were isolated and observations insufficient.

<table>
<thead>
<tr>
<th>Year ringed</th>
<th>Number ringed</th>
<th>1st year after ringing</th>
<th>1st and 2nd years after ringing</th>
<th>1st, 2nd and 3rd years after ringing</th>
</tr>
</thead>
<tbody>
<tr>
<td>1960</td>
<td>26</td>
<td>26 (26)</td>
<td>22 (23)</td>
<td>14 (16)</td>
</tr>
<tr>
<td>1961</td>
<td>26</td>
<td>25 (25)</td>
<td>22 (23)</td>
<td></td>
</tr>
<tr>
<td>1962</td>
<td>11</td>
<td>5 (8)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>63</td>
<td>56 (59)</td>
<td>44 (46)</td>
<td>14 (16)</td>
</tr>
</tbody>
</table>

**Fig. 7.** Seasonal site attendance by 'experienced' individuals, based on 9,585 observations. Each point has been obtained by averaging, for many nests, the number of times the site was attended by the male, female or both during the quarter-monthly period, and expressing these as percentages of the total number of checks.
Females may continue to defend their old site even after re-mating elsewhere, which indicates their strong attachment to it quite independent of whether there is a male there, and also independent of the location of their new mate. Such attachment is consistent with their normal site defence behaviour, including bowing. Experienced breeders show the strongest site attachment, and males newly-established late in the season show least. Failed breeders are more likely than successful breeders to change sites (13%, involving one or both partners, changed sites the year following failure, where both were known to be alive). On the whole it may well be adaptive for individuals to return to the micro-area in which they have already bred successfully, but to change it after failure.

*Site attachment indicated by seasonal attendance.* Site establishment is followed by a long phase of site attendance, during which a stable pair bond is achieved. In all categories (experienced, successful breeders, failed breeders, newly-established) males spend longer on the site than females, befitting their role as the sex originally establishing the site and showing greater attachment in other ways. Figs. 7, 8 and 9 give

![Graph](image-url)

**Fig. 8.** Seasonal site attendance by newly-established pairs, based on 4,709 observations (see caption to fig. 7)
seasonal details of male, female and pair site attendance in experienced pairs, newly-established pairs and failed breeders respectively.

Experienced birds. Fig. 7 shows that in experienced pairs the male was recorded at the site consistently more frequently than the female throughout the season. On about 45% of all checks the male alone was on duty and on a further 20-25% he was at the nest with the female. There is no significant daily rhythm except early in the season when males and pairs are mainly in attendance later in the day.

Newly-established birds. Fig. 8 also shows a consistently higher male than female attendance, but the males are absent far more frequently than are experienced males at the same period. Nevertheless, attendance persists until October, so that despite the absence of egg and chick the male alone was in attendance on about 30% of all checks and with the female on some further 20% between April and October. This shows that the site is acquired by systematic attendance, which is far from being the expression of incipient territoriality. In fact, the male has shown such territoriality during the two previous years in the
clubs. The decrease in male attendance soon after pair formation may result from his tendency frequently to leave the female in attendance at this stage, perhaps to stabilise her site attachment as such, irrespective of the pair bond. In all four booby species mentioned earlier the males leave and return repeatedly, sometimes every few minutes, in the early stages of pair formation.

Failed breeders. Attendance in this category was calculated from the time of egg loss. Again the male shows a higher attendance than the female and is little affected by egg loss, his attendance comparing favourably with that of experienced males breeding successfully. The female’s attachment, on the other hand, was lower following egg loss, suggesting that for her the site as such has a less strong attraction than it has for the male. Other independent lines of evidence have already suggested the same thing. Failed breeders spend longer at the site as a pair than do successful breeders, doubtless due to the demands of the chick on the latter.

Length of attendance spells
To investigate site attendance in more detail thrice daily checks were made throughout the season on one group of 20 nests and daily checks on a larger number. Table 5 summarises the attendance data for the more frequent checks on experienced birds.

Four main points emerged:

1. The average duration of male attendance spells is greater than those of the female at all stages of the breeding cycle. This suggests a summation of site attachment with other factors (such as the attraction of mate, egg or chick), producing longer spells in males, which are known from evidence already given to have stronger site attachment. The longest continuous spell recorded was eight days.

2. The average number of spells is the same for both sexes at all periods; it is the length which changes.

3. There is a dramatic decrease in duration of attendance during the first half of the chick’s growth, from 35.6 to 18.5 hours in the male and 30.2 to 18.8 in the female, showing the effect of chick feeding. However, during the second half of the fledging period the male’s attendance spells rise to 23.7 hours, whereas the female’s remain at 18.8. This difference could partly reflect factors responsible for certain other phenomenon associated with the site, such as rising aggression and increasing tendency to perform the site ownership display (see figs. 3 and 5).

4. After the chick has fledged attendance spells rise significantly in males continuing the trend shown in the latter half of the fledging period, but rise less in females.
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Table 5. Comparison between male and female Gannets Sula bassana of experienced pairs in duration and number of attendance spells throughout the season on the Bass Rock (639 spells for males, 637 spells for females, from 12 nests)

<table>
<thead>
<tr>
<th>Period</th>
<th>No. of days</th>
<th>Average length of spells (hours)</th>
<th>Range of spells (hours)</th>
<th>Average number of spells</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>3 weeks before egg laying</td>
<td>21</td>
<td>44.6</td>
<td>39.6</td>
<td>197</td>
</tr>
<tr>
<td>Incubation period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First half</td>
<td>22</td>
<td>37.2</td>
<td>30.8</td>
<td>84</td>
</tr>
<tr>
<td>Second half</td>
<td>22</td>
<td>33.2</td>
<td>29.1</td>
<td>62</td>
</tr>
<tr>
<td>Averages</td>
<td></td>
<td>35.6</td>
<td>30.2</td>
<td></td>
</tr>
<tr>
<td>Fledging period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First half</td>
<td>45</td>
<td>18.5</td>
<td>18.8</td>
<td>58</td>
</tr>
<tr>
<td>Second half</td>
<td>45</td>
<td>23.7</td>
<td>18.8</td>
<td>103</td>
</tr>
<tr>
<td>Averages</td>
<td></td>
<td>21.6</td>
<td>18.8</td>
<td></td>
</tr>
<tr>
<td>3 weeks post-fledging</td>
<td>21</td>
<td>33.2</td>
<td>20.8</td>
<td>127</td>
</tr>
</tbody>
</table>

PAIR FORMATION AND RELATIONSHIP

Pair formation in the Gannet takes place only on the site and is preceded by male 'advertising' and female 'prospecting'.

Male advertising (fig. 10)

In many species the same display functions as male ownership display repelling rivals and male advertising to attract females. In the Gannet the two displays are distinct, though linked. Gannet advertising resembles inhibited bowing with the head shake component exaggerated, the wings closed and the dip reduced to a slight movement of...
the head towards the female eliciting the response (fig. 10). The male
does not even take a step towards her, though he makes slight reaching
movements with extended neck.

It has proved useful in the analysis of displays to consider them
produced by particular levels of arousal of fear, aggression or sex
motivation. In particular, the occurrence of hostile displays directed
towards females now seems hardly surprising in territorial species in
which the species look alike. The similarity between aggressive bow­
ing and the male advertising display may be interpreted along these
lines, particularly when it is recalled that in advertising the aggressive
component of bowing (the dip) is deeply inhibited, whilst the 'neutral'
head shake is exaggerated (there is even some evidence that the head
shake when incorporated into displays is 'friendly'). Thus the male's
aggression is inhibited by sex motivation and in many cases the pair in
fact copulate during their first meeting and always perform the friendly
meeting ceremony (page 269).

The effect of male advertising was demonstrated quantitatively; such
evidence for the function of signal behaviour in birds in general is still
much needed. A natural choice situation is often presented to the
female, who has the chance to respond either to an advertising male or
a male, equally near, who is not advertising. In 74 cases in which
females elicited advertising from fringe males 32% approached the
advertising male rather than a passive male near-by, a further 41% display­ed interest in the advertising male but did not approach and 27% ignored the advertising male. None approached a passive male.
These figures show that male advertising has a real effect in attracting
females.

Female prospecting

Female Gannets must perform the initial searching to obtain a mate
since the male cannot (except fortuitously) contact her away from the
site. Guillemots *Uria aalge*, Razorbills, Puffins *Fratercula arctica*,

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**Fig. 10.** (a) Male 'advertising' to female; the head is shaken from side to side and
the wings are closed. (b) Advertising male in typical stance, slightly long-necked,
bill inclined downwards, and resting somewhat back on tarsi; the female approaches
with bill pointing upwards in a low intensity form of 'sky-pointing'
Table 6. Known age of first breeding of Gannets *Sula bassana* on the Bass Rock

<table>
<thead>
<tr>
<th>Age</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 years</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>5 years</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>5-6 years</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

Kittiwakes and terns, for example, all perform aerial flights together at some time before or during pair formation; Black-headed Gulls have special pairing territories (Tinbergen 1956); Shags may lead the female to the nest site after contacting her away from it (Snow 1963) and many passerines also do this. In the Gannet, territorially extremely aggressive, the male remains on the site and the female must come within range.

Male advertising is released mainly by young, unmated females who search or ‘prospect’ for unmated males. Like territory-seeking males prospecting females are mainly at least four to five years old (from plumage characters and more precise, though limited, evidence in table 6), though in new fringe pairs a significantly higher proportion of females than males show immature plumage. Prospecting females 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 one male was known to be visited by several during a few hours.

Before landing in or near a breeding group they often fly over and probably land and take-off repeatedly before approaching a male. Like site-searching males they know the layout of a small area intimately as shown by the certainty with which they return to a site, once acquired, even in the absence of the male (the alternative, that females almost instantly ‘imprint’ on the area at pair formation, seems less probable). This ability is necessary in areas which forbid exploration on foot to correct a wrong landing. Prospecting females land anywhere, not necessarily near an advertising male, then peer around in a typical long-necked anxiety posture which often releases full advertising from nearby unmated males. However, the female’s posture cannot be reliably distinguished by an observer from that of any anxious bird. The male’s advertising is by no means exclusively directed to unmated females and it is doubtful, to say the least, whether males can distinguish mated from unmated females.

An advertising male stimulates the female to approach, which she does often hesitantly and with small-amplitude head shakes (a sign of conflicting emotions) before finally rushing up in the facing-away (appeasement) position (page 267). Sometimes she merely cranes forward and delicately touches his bill before gradually increasing this to the full meeting ceremony with no prior facing-away.
Table 7. The number of different male and female Gannets *Sula bassana* involved in new as against old nest-sites on the Bass Rock

<table>
<thead>
<tr>
<th>Status of site</th>
<th>Number of cases of nest-sites involving</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1M, 1F</td>
</tr>
<tr>
<td>New</td>
<td>1</td>
</tr>
<tr>
<td>Old</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>2M, 4F</td>
</tr>
<tr>
<td>New</td>
<td>3</td>
</tr>
<tr>
<td>Old</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>3M, 5F</td>
</tr>
<tr>
<td>New</td>
<td>-</td>
</tr>
<tr>
<td>Old</td>
<td>1</td>
</tr>
</tbody>
</table>

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) the female is prepared to stay with the new male; one female began the meeting ceremony with a new male whilst her first mate was still at grips with a challenger! Their extreme responsiveness also facilitates pair formation, since males are usually strictly confined to their sites and have only an inconspicuous behaviour pattern to attract females. Initially, prospecting females show little preference for a particular male and may copulate with five in less than two hours. This promiscuous behaviour resembles that shown by club females. In the colony proper it has obvious disadvantages and leads to the formation of both kinds of triangular and multi-lateral associations (table 7). Also the female's tendency to break the first few pair-bonds she forms requires the male to continue advertising after he has obtained a mate. This again leads to severe female conflicts (out of 57 fights concerned with establishing new pairs, 31 were between females for the above reason). However, the advantages of female opportunism and high responsiveness must presumably favour these traits despite attendant disadvantages.

Second, prospecting females show astonishingly high tolerance of punishment from males and extreme reluctance to retaliate—characteristics which sometimes win acceptance from a hostile male. Clearly, the most aggressive males could only breed and perpetuate this trait to the extent that females were prepared to accept the results of such aggression. The two characteristics, male aggression and female
tolerance, must therefore have evolved in linkage. If male aggression is as important as we believe it to be, the extent to which females accept punishment is not surprising.

The female's approach is itself stimulated by sex interest, yet she is clearly afraid, even though the male does not usually threaten her. Her appeasement posture (facing-away) is strictly a response to an aggressive male and indicates some fear, as does the flurried, flinching nature of her behaviour in the meeting ceremony in which she may also face-away repeatedly. Occasionally females show slight aggression, though this is rarely detectable. Correspondingly, I could not recognise male fear in the new pair situation.

At this point it is appropriate to describe two behaviour patterns intimately connected with the pair bond and already mentioned in passing: female facing-away and the meeting ceremony (mutual fencing).

**Female facing-away** (fig. 11 and plate 43c)

The female reacts to male biting in the pair context by turning her head sideways and presenting her nape, at the same time pushing hard against him (fig. 11) or occasionally, and only as a reluctant alternative, by actual fleeing. Facing-away is a good example of appeasement behaviour in which the bill is turned away from the aggressor. It is interesting that the four possible ways of averting the bill all occur in the Gannet, but in different circumstances. Tucking it has already been mentioned as the pelican posture, pointing it vertically upwards will be described under sky-pointing, turning it to one side is facing-away, and withdrawing it completely occurs as withdrawal in menacing.

Facing-away is clearly fear-induced, as shown by its form (avoidance) and context (response to male attack), and was probably originally turning away prior to fleeing. Nevertheless, since it does not occur in
female-to-female fighting, sex motivation resulting from the pair situation may be involved, though a particularly high level of fear and low aggression may be sufficient to account for it.

Since its main function 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 when the male is not too strongly hostile. In new pairs facing away was followed by cessation of male attack in twelve out of 41 cases and failed to stop attack in the remainder. These figures cannot be compared with cases in which females did not face-away since these are so rare. Although a fair representation of the efficacy of facing-away, and a valuable demonstration of the functional value of a signal movement, the figures do not bring out the important point that facing-away functions most effectively in 'borderline' cases. It may be considered highly adaptive appeasement behaviour if it succeeds (as it does) in permitting pair formation in even a proportion of cases which would otherwise have failed.

It is possible to interpret male aggression towards a new mate as territorial behaviour elicited by the female as an intruder, but it becomes a matter for special remark that males continue to show aggression to their mates throughout their attachment (plate 43c). Some Gannets probably mate for life and others certainly for many years, yet in 98% of 294 cases incoming males bit their females and in 75% of 253 cases incoming females were gripped by the male. The difference is probably due to greater difficulty in biting in the latter situation. Among these hundreds of observations there was one record of a male being bitten by his mate, who had been startled by his arrival. Some writers have implied that the incoming bird bites the bird on the site, but the real distinction, as shown above, is one of sex—only males bite. Male biting in this context is severe enough to dislodge some head-feathers but does not result in observable wounds. I had the strong impression, though without measuring it, that biting was more prolonged and severe early and late in the season.

Females respond to incoming males by rapid head-shaking and facing-away before he lands—sometimes lying almost prone in the infantile beak-hiding position. Presentation of the nape does not prevent the male biting, but removes any risk of the female retaliating and releasing serious male aggression. It should be added that pair members clearly recognise each other; there is no question of females being treated as intruders until their response to biting proves them otherwise. The calling of an incoming bird evokes head shaking from the mate only, not from neighbours.

In 87% of cases in which males arrived with nest material in their beaks females did not face-away, whereas males without nest material failed to elicit facing away in only 10%, showing that this reaction is
related not merely to the arrival of the male but to his arrival and biting capacity.

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

**Mutual fencing (fig. 12 and plate 41b)**

Mutual fencing between mates is one of the Gannet’s most conspicuous behaviour patterns and seems to have been considered the ‘main’
display by other authors. It occurs most commonly as a meeting ceremony following the arrival of the partners at the nest, usually from flight, but sometimes on foot. It also regularly follows an aggression-evoking stimulus such as a menace from a neighbour, which would typically elicit bowing from a single bird.

**Description.** Whilst still many yards from the nest the in-flying bird of either sex calls stridently about four times per second, in response to which the mate 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 shouts harshly and 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. This display and bowing are the main sources of the constant background of noise at a Gannet colony. Interspersed with bill-fencing are downward movements of the head, perhaps as far as the nest or only a little to one side, which often results 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.

In form mutual fencing conspicuously resembles bowing, and will be considered as a modified form of it. The differences, however, are not merely imposed by the partners' positions (standing breast to breast). Whereas during the head shake 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, though this is 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.

**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. Table 8 shows, for experienced pairs, the length of bouts resulting from meeting on the site at different periods in the breeding season.

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Table 8. The average length (in seconds) of mutual fencing bouts in experienced Gannets *Sula bassana* on the Bass Rock at different times of the season (from thrice daily checks)

The figures in brackets represent the number of cases involved. 'Long absences' = 6+ hours. 'All absences' include those of unknown length.

<table>
<thead>
<tr>
<th></th>
<th>March to mid April</th>
<th>Mid June to end July</th>
<th>September to mid October</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long absences</td>
<td>208 (30)</td>
<td>30 (38)</td>
<td>88 (11)</td>
</tr>
<tr>
<td>All absences</td>
<td>180 (35)</td>
<td>29 (36)</td>
<td>87 (13)</td>
</tr>
</tbody>
</table>

The differences are significant and show that mutual fencing bouts tend to be shorter in mid-season; it is only at the beginning or end of the season that even very short absences may be followed by long (two minutes or more) mutual fencing bouts. In fact, bouts become shorter soon after egg laying, and during part of the chick stage they may be very short (ten seconds). If a pair lose their egg, 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 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. The rise in mutual fencing towards the end of the season could be correlated with a rise in aggression, described earlier. It is obviously a 'non-personal' matter in the sense that recognition of each other by pair members will be at least as good at the end of the season as at other times.

Sex differences. There are sex differences in the form of mutual fencing. Males tend to dip more (table 9) and this difference is significant.

However, fewer dips are no indication that females mutual fence at a lower intensity than males (contrast their bowing), since in two other measures females mutual fence more vigorously than males (table 10) with wings held out more widely and greater persistence in maintaining the display. Also, their mutual fencing probably shows a higher

Table 9. Sex differences in the dip component of mutual fencing by Gannets *Sula bassana* on the Bass Rock

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.

<table>
<thead>
<tr>
<th></th>
<th>Mean number of dips per bout</th>
<th>Range</th>
<th>Number of cases</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>11.6</td>
<td>3-27</td>
<td>27</td>
</tr>
<tr>
<td>Female</td>
<td>4.6</td>
<td>0-21</td>
<td>27</td>
</tr>
</tbody>
</table>
Table 10. Sex differences in wing position and persistence in mutual fencing by Gannets Sula bassana on the Bass Rock

<table>
<thead>
<tr>
<th></th>
<th>New Male</th>
<th>Female</th>
<th>Experienced Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extent to which wings held out</td>
<td>3</td>
<td>17</td>
<td>13</td>
<td>47</td>
</tr>
<tr>
<td>Persistence in maintaining mutual fencing</td>
<td>6</td>
<td>12</td>
<td>10</td>
<td>24</td>
</tr>
</tbody>
</table>

proportion of head shakes, though due to the variability in the movement I was unable to measure it satisfactorily.

Status differences. New pairs show longer mutual fencing bouts than experienced ones at the same time of year (table 11).

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, requires certain assumptions about motivation and function, 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 have 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 and so on) are all consistent with the above facts if it is assumed that the intensity of mutual fencing 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

Table 11. Status differences in the length of mutual fencing bouts by Gannets Sula bassana on the Bass Rock

These records are mid-seasonal only and length of absence has not been taken into account.

<table>
<thead>
<tr>
<th></th>
<th>Mean duration of bouts (seconds)</th>
<th>Range (seconds)</th>
<th>Number of cases</th>
</tr>
</thead>
<tbody>
<tr>
<td>Established</td>
<td>45</td>
<td>5-150</td>
<td>31</td>
</tr>
<tr>
<td>New</td>
<td>97</td>
<td>10-180</td>
<td>9</td>
</tr>
</tbody>
</table>
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 his tendency to dip more than the female (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. 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.

Since the balance between fear and aggression will be different in male and female, it is reasonable to find that their mutual fencing also shows differences (e.g. in number of dips) 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.

Mutual fencing in the Gannet is only part of the full meeting situation, which also includes male advertising leading to the first meeting of the pair. Male advertising, it may be recalled, resembles the ownership display with the aggressive elements reduced, though no male appeasement posture has been incorporated, nor does the male show any appeasing behaviour in his mutual fencing, as does the female. Considering the whole meeting situation in the Gannet, we find that advertising and mutual fencing are examples of pair formation displays derived from a relatively low intensity or 'more timid' (Tinbergen 1959) threat display (bowing) by more or less suppression of certain aggressive elements. Comparing the pair formation situation in the Black-headed Gull, we find that the coming together involves 'song' by the male (aggressively motivated), approach by the female, agonistic display by the male, appeasement (distance reducing) 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 mainly aggressive display), approach by the female in facing-away (appeasing) posture, aggression by the male, further appeasement by the female and a mutual meeting ceremony which, though it forms an outlet for aggression, does not include appeasement behaviour by the male. 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, as already stressed in other contexts.

*Function.* The discussion of motivation has already suggested that mutual fencing is 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 by 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 so again only in response to stimuli which elicit aggression.

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), the more prolonged and intense are the mutual fencing bouts.

*Summary.* Females clearly elicit aggression when the sexes meet on the site; they are themselves afraid. Their initial appeasement behaviour is followed by a mutual display which expresses sexual attraction mixed with aggression in the male and fear in the female. Variations in form, intensity and seasonal incident, 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.

*Later stages in the pair relationship.*

At first the female is attracted only by the male, but soon after pair formation, and only then in the history of the pair, the male behaves in a way which apparently effectively extends the female’s attachment to include the site; he leaves and returns repeatedly in a short period. In addition to gathering nest material, behaviour common to males of all categories, males of new pairs often move a few feet from the site and then suddenly rush back, bite the female and perform the meeting ceremony. In some situations short aerial excursions are made instead. A dyed male, conspicuous at long range, carried out nine such flights in less than half an hour. Repeated returning and mutual fencing probably both strengthen the pair bond and accustom the female to remain on the site when the male leaves. This is vital,
course, to prevent site usurpation; it is precisely at this stage that most conflicts occur, due to triangular associations and so on.

After the first few prolonged male absences the female begins to take regular spells of attendance, which are necessary to safeguard nest material from thieving neighbours. Eggs are occasionally laid on bare earth but have a lower chance of survival. After the initial phase of interest centred solely on the male, the female thus acquires a strong attachment to the site, fighting, menacing and displaying in its defence. Nevertheless, all measures reveal that her attachment to it is weaker than that of the male.

The aggression shown by males during pair formation continues throughout the relationship (as late as September a male strongly attacked his mate, with whom he had nested in at least two years, for a full two minutes after her return from fishing). Pair relations will be affected by changes in motivation, some independent of the partner, others reflecting personal factors such as the state of the pair bond. Thus males of new pairs are more aggressive than those of old, but this aggression wanes. Within this framework they show a pattern of aggression which is stronger early and late in the season. Late season aggression cannot be due to males becoming less familiar with their mates and must be a ‘non-personal’ change, emphasising the extent to which many birds react automatically and directly to internal changes. One might have supposed that old pairs would have totally overcome violent aggression between themselves, or even developed ‘affection’. Instead (whether or not the latter is true) males still respond to rising aggression by more severe attacks, even on their old and well-known mate.

The highly adaptive female tolerance of male aggression has already been mentioned as part of pair formation. Females were known to absorb male aggression for up to 20 minutes without retaliation. Later in the pair relationship females are not only bitten on meeting but are occasionally attacked by their mates, often as re-directed aggression stimulated by outbursts of activity in the neighbourhood. Their reaction, even under the most severe male attack, is merely to face-away, despite the fact that females can, on occasions, vanquish males (e.g. intruders). Even provoked retaliation is inhibited and they break off successful aggression to resume facing-away. This tolerance contrasts with the situation in many passerines, for example, the Chaffinch *Fringilla coelebs* and Greenfinch *Chloris chloris* in which, after pairing, the male will tolerate female aggression and she can supplant him at food (Hinde 1953). I do not know of any other example of comparable male aggression sustained throughout a life-long partnership as in the Gannet.

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 happened to be off the
site he was occupying whilst mutual fencing with the other. Thus he
was 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 to get close, and then
facing-away (fig. 11). 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.

Despite the permanence of the pair-bond and the strong reaction
against intruders, partners remain remarkably receptive to strangers of
the other sex. Whilst this allows both sexes to respond to a large
number of suitors in the early stages and later also allows partner
replacement, it also encourages triangular associations (see table 7).
In almost all cases where eggs simply disappeared and all obvious
possibilities could be discounted, at least one owner of the nest con­
cerned 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 likelihood of
several abortive pairings before a stable bond is formed.

In the Gannet the receptiveness of one sex for the other is not
entirely predictable and poses interesting questions about individual
preferences. Males have a marked receptive period at the beginning
of each season, become highly selective later and then go through a
second receptive phase towards the end of the season, though within
this framework there is much variability. After pair formation recep­
tivity is substantially lower but may be retained, even in long-estab­
lished birds, towards particular individuals with whom some previous
relationship has existed and who are clearly still recognised. One
male not only accepted back his previous mate after a year in which
both had successfully bred with new mates, but also drove away his
mate of one year's standing in favour of his original one. This case
was the more outstanding since his original mate had been decisively
beaten by the newer one. The male, notwithstanding, drove the latter
violently from the site despite her prolonged facing-away and tolera­
tion of his attack. On the other hand, another male completely
rejected his original mate 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 she was often forcibly ejected 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, though exactly what is the greater attraction of some individuals remains unknown (Snow 1963 correlated preference in the Shag with physical characters such as crest-size).

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 one male and two females, each of which produced an egg, the male incubated both but favoured the first laid, even though not on the site where he had bred the two previous years. The newer female thus inevitably lost her egg. Even then the male continued to visit the site and repelled many site-establishing males with great determination. His dual site 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.

Many long-lived birds apparently breed together in several successive years and possibly for life. 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 can be misleading, though most authors do not distinguish between 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 12 gives the results of observations on 18 pairs for four years, 43 pairs for three years and 23 pairs for two years in terms of infidelity.

Thus over the four-year period eight males and 16 females left their mate and site of the previous year (irrespective of how many years after ringing). Males seem to have a stronger site/mate attachment than females. Looked at the other way round, out of four years in which both survived, 14 out of 18 (78%) of these pairs remained together the whole time, one out of 18 (5%) remained together only three years in succession and three out of 18 (17%) only two years. Equivalent figures for pairs known only three and two years are readily derived from table 12.

However, the difference between male and female has already been shown to exist in 'pure' site attachment (page 258). Can one further gain an idea of whether any of this site/mate figure is due to mate attraction or whether it may all be accounted for in terms of site attraction?
Table 12. Site/mate infidelity in Gannets *Sula bassana* on the Bass Rock

First year = year of ringing (in which no birds were unfaithful); second year = year after ringing; etc. Birds unfaithful in the fourth year, for example, had been together three successive years; unfaithful in the third year together two successive years; etc.

<table>
<thead>
<tr>
<th>Years</th>
<th>Number of pairs</th>
<th>Faithful pairs</th>
<th>Unfaithful in second year</th>
<th>Unfaithful in third year</th>
<th>Unfaithful in fourth year</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male Female</td>
<td>Male Female</td>
<td>Male Female</td>
<td>Male Female</td>
</tr>
<tr>
<td>4</td>
<td>18</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>43</td>
<td>31</td>
<td>0</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>23</td>
<td>15</td>
<td>6</td>
<td>2</td>
<td>-</td>
</tr>
</tbody>
</table>

Total infidelities: male 8, female 16

The 16 cases of female infidelity arose from a possible total of 163 'chances' to be unfaithful \[[(3 \times 18) + (2 \times 43) + (1 \times 23) = 163]\] 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 ten out of 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 to the site (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 out of 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; and that mate attraction plays an additional part in the case of the female, but not in the male. This fits with the rôle of the male as the site-establishing sex and the female as responsive to the attraction (advertising display) of the male.

*Mutual (allo-) preening.* Members of a pair often follow mutual fencing or copulation by mutual preening (plate 43b) in which each delicately nibbles, with the tips of the mandibles, the head, throat and neck 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; Goodwin (1956), on the other hand, believed that caressing in Woodpigeons is effective in removing...
ectoparasites. It is infrequent when compared with ordinary preening, occurring mainly in established pairs. It may possibly be appeasement behaviour, though it usually occurs after mutual fencing has removed tension between the participants, often after long quiet periods; however, its connection with aggression is clearly indicated in unstable pairs when it may alternate, in the male, with overt hostility. 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 happened—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 due to the bill being brought into the 'correct' position. Similarly, adults often alternate attack on strange chicks with preening of them. In the Red-footed Booby there is no mutual preening and it is interesting that this species also lacks a ritualised meeting ceremony equivalent to mutual fencing in the Gannet. It may well be that lacking the means of turning into harmless channels the aggression engendered by close proximity and the pointing of beaks at one another (inherent in mutual preening) the Red-foot accordingly lacks this behaviour pattern.

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 (Harrison 1965), though Cramp (1958) reported caressing in Woodpigeons with no obvious excess by females, despite Goodwin's earlier remark (1956) that in the early stages of pair formation females do seem to do more.

Following the chronological sequence of the breeding cycle, the next topics are copulation, nest building, egg laying and incubation.

**Copulation (plate 43a)**

Copulation occurs only at the nest site and is usually solicited by the squatting female with violent and rapid sideways head shakes, which sometimes become vigorous flinging movements of such amplitude that the bill tip points over the back to the tail. These continue to some extent during copulation. Before mounting, usually from the side, the male points his bill towards the female's head, head shakes slightly, patters his feet and grips the female's head strongly. Copulation takes 15 to 35 seconds (average 24 seconds, 180 measured) from placing one foot on the female's back to dismounting. During copulation the female head-shakes repeatedly and occasionally arranges nest material. The male waves his outspread wings and patters noisily with his feet, which move singly or in unison—in the latter case he rests on his tarsi. This must be a powerful tactile stimulus to the female and
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perhaps helps to synchronise the act. The toti-palmate foot is surprisingly prehensile and by clenching the toes the claws effectively grip the female's plumage. Cloacal contact follows tail raising by the female. 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 male closes his wings and remains immobile for several seconds, afterwards shaking the female's head strongly. The occurrence of these latter stages were my criteria for deciding whether copulation had been successful. Insemination can probably be reliably detected, since abortive efforts do not produce the cloacal contact and final immobile stage characteristic of complete sequences. After copulation the male may let go of the female, sky-point four or five times before dismounting, fly straight from her back or simply step down.

Copulation behaviour varies considerably. Intruding males or males of new pairs may bite the female so fiercely that she shows fear and prevents cloacal contact by lowering her tail. However, judging by the aggression normally present, and the way in which even hostile males are often successful, male copulatory behaviour and aggression (and female copulatory behaviour and fear) are less incompatible than in other species, where hostility must be eliminated before copulation can occur. This again illustrates the incorporation of aggression in to the normal pair relationship and the development of female tolerance to it.

Out of many hundreds of copulations only one reverse copulation was seen, although they are much commoner in the Phalacrocoracidae —cf. Shags (Dr. J. M. Cullen pers. comm.) and Cormorants (Kortlandt 1942).

Copulation (male rôle) with chicks is not uncommon. Between 8th August and 19th September 1961 and 1962 twelve cases were recorded for males, in two of which the female was also present, so that this behaviour occurs even in the presence of the normal releasing stimuli. In nine cases the chicks were ten to eleven weeks old and the youngest was six weeks. The age of the chicks suggests that it may be necessary for them to approximate to adult size and shape. The females did not interfere.

Although reverse adult copulations were so rare, I recorded twelve cases of females copulating with chicks between 9th August and 19th September 1962 and 1962; in eleven cases it involved chicks from nine to eleven weeks, the youngest being eight 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 copulation passed into preening of the chick's head.

Copulations occur over a period of some seven months (earliest and latest dates 10th March and 28th September), 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 when copulations are frequent, there is a high individual rate (probably a 100 or more per pair in the period before egg laying). The individual frequency during short periods (highest rate four copulations in 40 minutes) seems not unduly high for sea-birds, though quantitative comparative evidence is lacking. I have seen Herring Gulls achieve seven cloacal contacts in three minutes, but without dismounting. Dr. Cullen (pers. comm.) found that Shags mount at about the rate of nine to twelve times a day for a period about three weeks before egg laying. This figure includes unsuccessful attempts whereas these are rare in the Gannet. Fig. 13 shows the

![Graph](image-url)

**Fig. 13.** Seasonal frequency of copulations
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 an inhibitory stimulus provided by the egg (see below).

The sharp drop in copulation rate after egg laying is very striking, particularly since copulation reaches a peak some ten to 14 days before 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 would have done had the egg been absent.

Though re-laying can occur six days after loss if the first egg was never incubated, lost eggs are usually replaced in about a fortnight (Nelson 1964a). This about corresponds with a peak in copulation ten 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 was responsible for the abrupt cessation of copulation after laying, not the onset of gonad collapse making secretion of spermatozoa impossible even after some time (although it is possible that apparently successful copulation could occur even though there had been gonad regression). The suddenness of the change does not rule out the possibility of hormonal mechanisms being involved. Lehrman (1959) mentioned the possibility of external stimuli reflexly causing changes in hormonal secretion.

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) stated that the post-nuptial stage involves a regenerative phase (sexual quiescence) during which the testis does not produce spermatozoa and there is no sexual behaviour. In the Gannet it may be the necessity for a prolonged period of site attachment and aggressive display (both of which presumably require a relatively high androgen level) which keeps the gonads active for a much longer period than in short-cycled species, and reduces the period of the regenerative phase. It would be interesting to compare other long-cycled species with respect to seasonal extent of copulation and also sexual and aggressively motivated displays.
The Behaviour of the Gannet

Table 13. Seasonal variation in copulation success among Gannets *Sula bassana* on the Bass Rock

The figures for 'unsuccessful' copulations will be minimum, since a proportion of apparently successful copulations may well be unsuccessful.

<table>
<thead>
<tr>
<th>Period</th>
<th>Number of pairs involved</th>
<th>Percentage unsuccessful</th>
</tr>
</thead>
<tbody>
<tr>
<td>March</td>
<td>49</td>
<td>22%</td>
</tr>
<tr>
<td>April-May</td>
<td>55</td>
<td>12%</td>
</tr>
<tr>
<td>June-July</td>
<td>87</td>
<td>67%</td>
</tr>
<tr>
<td>August-September</td>
<td>29</td>
<td>67%</td>
</tr>
</tbody>
</table>

Later 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 (by the criteria mentioned) 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.

There is seasonal variation in copulation success, which is highest at the functionally optimal time, i.e. some time before egg laying (table 13).

Copulation commonly occurs within ten minutes of the pair coming together on the site after an absence of more than a few (up to three) hours. It almost invariably follows mutual fencing in the pre-laying stage. The copulation soliciting behaviour of the female is extremely stimulating to the male and almost 'forces' him to mount even if he is 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 in the pre-copulation situation. This raises the interesting point of how far the male's hostility to the female is 'pure' aggression and how far it is sexual behaviour, stimulating to the female and selectively encouraged accordingly. Whilst in many situations the male is undoubtedly aggressive and indeed sometimes drives the female away it seems likely that in the later pair relationships, particularly in copulation, the biting will have acquired a sexually stimulating function thus allowing aggressive males to benefit both territorially and in the sexual part of reproduction.

After the male dismounts the female often touches nest material and makes nest building movements (this happened in 60% of all cases in which behaviour was recorded up to ten seconds after the male dismounted, while the male touched nest material 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. Male sky-pointing is correlated with his tendency to
leave the site for nest material soon after copulation. This movement away from the site is the context in which sky-pointing normally occurs (to be discussed in part 2). Post-copulation trips to gather nest-material vary from a few inches to over a mile. Mutual fencing follows copulation 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 (to be discussed in part 2). 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.

Nest building and associated activity
Gannets accumulate large, compacted nests of sea-weed, grass, moulted feathers and flotsam and add to it any earth they can reach around the nest. The drum or pedestal occasionally measures up to six feet from rim to base, 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 sea-weed, and often containing feathers. The finer material in the cup results from removal of larger items rather than a deliberate choice of fine material, much as in Shags (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. This elevation can be highly adaptive under adverse 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 north-east winds and rain in June and July. 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.

Although nests are not systematically added to by the bird’s own excrement, which is usually voided well clear by both adults and well-grown young, adults sometimes 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 liquid faeces being squirted clear. 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—a measure of
the potential value of this habit to the species. Shag 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. Cullen and Ashmole (1963) have suggested that the Black Noddy Anous tenuirostris, because of its ability to attach nests with excreta, can utilise nesting sites denied to its relative the Brown Noddy A. stolidus, and the Kittiwake has an even greater ability to stick nests on small projections. 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 (273 records of grass and 131 of sea-weed in 1961 and 1962, with more grass than sea-weed in both years) from January to the beginning of October, and indeed may be seen carrying sea-weed in every month of the year, though mainly from the end of February to October. 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 also in mid-air.

One hundred and two 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 two, two, three and four 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, since 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. Before laying, nest material is brought by the male only (231 visits by males recorded, none by females), but subsequently, though less frequently, by the female also. 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. In five minutes during rainy weather in August 1962, for example, 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. E. Cullen 1957). The function in the Gannet may be to elevate the nest and keep the egg or chick drier, though even pairs without egg or chick respond in this way.
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*Nest-building movements.* Gannets spend much time arranging nest material throughout the season. They have no complicated method of interweaving the material, merely placing it in front or to one side whilst standing or sitting and, with rhythmic, small-amplitude, sideways head movements and trembling of the mandibles, pushing it into place. In the early stages of nest-building, even on bare earth or rock, material is deposited precisely on the site and perhaps handled briefly. By turning on the site, the Gannet forms a cup and later additions are built in vigorously and for prolonged periods. Stimuli from the cup probably intensify nest-building. I noticed that after shifting the egg and settling to another spell of incubation they seemed particularly prone to arrange nest material around their 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 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 sometimes in high intensity conflict situations.

Nest maintenance involves 'nest digging', in which the mandibles, slightly parted, are thrust into the floor of the nest and used as a probe to dislodge hard lumps. Digging is performed with concentration and vigour, and seems 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 inefficient for this purpose.

Adults and well-grown young sometimes toss or juggle pieces of stick and other objects, 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. It could help chicks to perfect movements which will later be used in dealing with prey. Unemployed birds in the fringe juggle much more frequently than breeders.

Whereas the nest-building movements already discussed play some part in maintaining nest structure, there are two distinct forms of non-functional nest-touching.

*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. Thus, 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, who is then aggressive, usually mixes nest-touching with bowing and an aggressive male trying to repel a female frequently touches nest material. It also occurs in the male during female-to-female fights on his site.

Nest-touching commonly follows menacing, but less often in pairs than singles; pairs usually follow menacing by mutual fencing.

Nest-touching also occurs in the female after copulation (60% of cases), during mutual fencing, particularly in the female, and, on occasions, in bowing. In some other species, such as the Woodpigeon (Goodwin 1956) an aggressive display (here 'nodding') is thought to be derived from nest-touching.

**Aggressive nest-biting.** Immediately after alighting on their empty nest or site, Gannets, particularly males, bite the nest material, ground or even bare rock, at the same time calling aggressively. Of 91 such landings, 29% 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). Frightened birds, after alighting, showed less tendency to touch nest material or bow. 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. Birds landing away from their sites and birds without sites landing in the fringe never showed aggressive nest-touching movements.

Apart from landing, an agitated and conspicuous form of aggressive nest-biting occurs when birds return on foot to their sites after some disturbance in the colony (e.g. landing off-site and being attacked, knocked off by a fight near-by, and so on) 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. 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.

From the viewpoint of causation it may be asked why nest-touching, rather than anything else, should be the irrelevant behaviour performed in the situations described. Possibly because nest material is an effective directing stimulus in these circumstances. If the conflict occurred at sea, for example, bathing could become the irrelevant
action; in fact, fights ending on the sea are invariably followed by excited bathing in both participants, as in many water birds. On this supposition, preening, rotary head shaking, scratching and other comparable actions could all be considered as 'likely' as nest-touching, but may have been excluded because, for example, they would reduce the bird's ability to defend itself in precisely those 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 redirected attack, as may the male's habit of biting the female, since incoming birds are often menaced by neighbours.

(To be concluded in the August issue, when plates 42, 46 and 47 will also be discussed more fully)
PLATE 41. Above, the Bass Rock, Firth of Forth, and some of its Gannets *Sula bassana*; the island is about a mile round and 340 feet high (page 233). Below, a disturbance among the Gannets on the left stimulates mutual fencing (the meeting ceremony of the pair) from three couples near-by (page 269) (photos: J. B. Nelson)
PLATE 42. Above, 'bowing', a common aggressive display of the Gannet Sula bassana, signals site ownership (page 247). Below, the 'rotary head-shake', which shakes and readjusts plumage, is induced by tactile stimuli or alarm (page 288).

PLATE 43 (opposite). Top, in copulation the male grips the female's head (page 279). Centre, mutual preening is frequent between the pair (page 278). Bottom, the arriving male bites his mate who 'faces away' (page 268) (photos: J. B. Nelson)
Despite their aggressiveness, Gannets *Sula bassana* usually nest as densely as possible; therefore colonies show sharp boundaries and the nests are spaced about two and a half feet apart. Here are cliff-ledge sites on the right and a spread to flatter ground nearer the camera (page 237)

*(photo: J. B. Nelson)*
Above, vigorous threat by Gannets *Sula bassana*; the defending and more aggressive male is in a forward posture, while his mate and the opposing male are withdrawn (page 245). Below, vigorous threat leads to real attack in which the opponent is driven away from the disputed site; note the method of fighting with extended neck and strong pushing movements (page 242). Left, a Gannet permanently blinded in one eye through fighting; fights may be extremely severe and serious damage of this kind is a not infrequent result (page 243) (photos: J. B. Nelson)
Plate 46. Above, the ‘pelican posture’ of the Gannet Sula bassana; this is an ambivalent fear/aggression posture used in a wide range of situations (page 248). Below, high-intensity ‘sky-pointing’ in which the bird moves along with a swaying motion and displays its conspicuously lined feet (page 236) (photos: J. B. Nelson)
PLATE 47. Above, ‘sky-pointing’ by a Gannet *Sula bassana* moving to take off, the wings busked but not spread sideways; this bird is drawing a mild threat from one of its neighbours. Below, flight position which often follows sky-pointing; the bird now frequently utters a sepulchral groan (page 236) (photos: J. B. Nelson)