

The behaviour of the Gannet

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(Concluded from page 288)

EGG LAYING

THE ECOLOGY OF the egg laying of the Gannet *Sula bassana* (effect of density, age and nest position on the onset and synchronisation of laying) is discussed elsewhere (Nelson 1964a and in preparation).

The act of deposition was observed on five occasions on all of which the tail was depressed and guided the egg into the nest—important in view of the Gannet's poorly developed retrieving ability. The one accurately timed laying took two minutes. Eggs may be laid at any time of day, and possibly also at night.

INCUBATION

Gannets (and apparently all Sulidae) lack brood patches and incubate their single egg beneath their webs, which become highly vascularised and hot during incubation. Non-breeding birds caught during the breeding season had cool webs, but no known breeders were caught off the nest, so it was not known whether webs remain hot. Howell and Bartholomew (1962) showed that the mean internal temperature of incubated eggs of the Red-footed Booby *S. sula* was 36° C. and the foot temperature 35.8° C., and suggested that the feet do not provide the main source of heat for incubation. They were vague in their alternative and the difference in the temperatures they recorded would seem too small to disprove the conventional view. The egg temperature achieved by this method compares favourably with that of brood-spot incubation (e.g. 36.6° C. for the surface temperature of Herring Gulls' eggs: Baerends 1959).

The egg is relatively small and thick-shelled and the surface area of the webs, about 46 sq. cm., is certainly enough to cover the exposed part. The egg is most frequently brooded lengthwise, though also crosswise, the webs being placed one after the other on either side of the egg and overlapping. The incubating bird then settles, adjusting itself with slight rocking or 'nest settling' movements. Positions are shifted several times an hour and nest settling movements made more than twice as often. During very warm weather the egg is sometimes transferred to the upper side of the webs or the incubating bird stands with the uncovered egg between its webs, presumably to cool it.

Although some single-egg laying species are incapable of hatching two eggs (e.g. the Laysan Albatross *Diomedea immutabilis*: Rice and Kenyon 1962), the Gannet, like most Sulidae, can do so. The hatching success of experimentally doubled clutches was equal to that of singles

(87% and 85% respectively) though the average incubation period was 46 days compared with 44 for singles. This was due to less efficient covering rather than chilling resulting from egg transference; transferred single eggs did not take longer than normal to hatch. The two eggs were incubated in almost any position, provided the long axis was horizontal. The incidence of rising and settling greatly increased after donation of an extra egg (*cf.* Beer 1961). Incubation may be less efficient in first-time breeders, since a lower percentage of their eggs hatched, though figures for respective infertility rates were not obtained. One such female at first incubated the egg on top of her webs and later lost it. However, there is no difference in incubation period between first-time breeders and experienced birds.

Behaviour during incubation

Except when sleeping, Gannets rarely incubate for more than ten successive minutes without also performing numerous other behaviour patterns. Spells of activity alternate with periods of rest. Certain activities are linked (e.g. menacing, touching nest material and bowing) and when one occurs at much higher frequency so do the others. Other activities (e.g. nest digging) occur in concentrated spells at intervals in contrast to rotary head shaking which occurs at a fairly uniform level. The commonest activity is touching nest material, since this occurs as a displacement activity in conflict situations as well as autochthonously. Preening and ordinary head shaking are the two other commonest behaviour patterns.

During incubation, quiet spells are usually ended by a sudden stimulus such as the arrival or departure of a neighbour. The activity resulting (e.g. menacing) then leads to another activity, such as egg shifting as a result of changed position. However, some activities occur without any such observable stimulus.

Part played by external stimuli

The onset of incubation behaviour might conceivably be released by the external stimulus of the egg in the nest and might also require the bird to be in a particular hormonal state, or perhaps, in the female, require the prior act of laying. To test this, 21 eggs were donated to different nests in the pre-laying period and the reaction of the birds recorded. Where the egg was rejected the date on which their own egg was subsequently laid was noted. The substitutions were of fresh Gannet eggs, except for three pot eggs, smaller than a Gannet's, and one Shag egg.

There were 12 outright rejections, involving both male and female, in which the Gannet gripped the egg between its mandibles and either placed it on the rim of the nest with mandible vibrations as in deposition of nest material, jabbed it in the bottom of the nest, pushed it over the

rim or ignored it. Eleven of these nests were subsequently laid in six, nine (four cases), ten (two cases), 14-19, 20, 21 and 27 days later.

The remaining nine eggs were accepted (three by males, two by females and four by birds of unknown sex), but five of them only temporarily. Birds which continued to incubate and hatch the foster eggs failed to lay their own, an inhibitory effect known in many other species. Of the five which accepted the foster eggs only temporarily, one did not lay and the remaining four laid four, five and nine (two cases) days later. In other words, of birds which did lay subsequently, those which accepted the foster eggs were closer to laying their own than those which rejected them. Beer (1963) also found this for the Black-headed Gull. The tendency to incubate, as one would expect, increases with the laying of their own egg. However, the fact that some individuals rejected a donated egg some days before laying, whilst others accepted one at a similar time may suggest, if incubation depends on a specific hormonal state, that this is reached by different birds at different times in their cycles. Incubation tendency increases with seasonal gonad development, but the response to the egg is apparently present for some time before required. This need not have been the case. Certain aspects of female breeding behaviour can develop independently of others, though all under the influence of oestrogens. Alternatively, incubation behaviour might conceivably have depended on reflexly initiated hormone activity, triggered by the sight or 'feel' of the egg.

Whilst such a strong tendency to reject eggs near to the laying date might not be expected, it was even more surprising to find that a female rejected a donated egg nine days before laying her own, which she then lost, then again rejected a donated egg, but re-laid 20 days after this further refusal. She had therefore recently experienced both laying and incubating, and was within three weeks of laying again, yet rejected a substituted egg. This strongly suggests that incubation tendency is closely linked with the deposition and presence of the egg and quickly wanes in its absence. Of three other eggs donated after natural loss, two were accepted (one a Shag's) and one rejected only two days after the recipient's own had been lost.

Egg-shifting and nest-settling movements

The position of the egg beneath the webs is altered, on average, almost twice an hour, using the lower edge of the closed or slightly open bill pointing backwards between the webs. Settling movements, altering the position of the webs on the egg, are common and invariably follow egg-shifting. Only rarely are they followed by leg or wing stretching, so that they seem to concern incubation rather than the relief of muscle cramp. Nest-settling movements occur even before there is an egg in the nest and become commoner just before laying. Like some of the

adjusting movements in terns (Poulsen 1953), the Gannet's settling movements do not seem to alter the position of the egg but, unlike terns, are caused by feet, rather than body, movements.

Egg-retrieving

Poulsen (1953) concluded that, in all ground-nesters with shallow nests and liable to displace their eggs, egg-retrieving is well-developed. The Gannet, only partially a ground-nester, and with a tall, pedestal nest, shows little retrieving ability if the egg is knocked or experimentally placed out of the nest. This may be because recovery is generally impossible; either the egg rolls into a deep valley between nests or falls over the ledge, and in any case there is very little loss due to accidental displacement. However, eggs placed on the rim of the nest are rolled back into the cup and the bird also attempts, usually unsuccessfully, to retrieve those just within reach though a little below the rim. Even with low rims the egg rolls away from the beak; Gannets seem to lack the steering movement of the egg-rolling Grey Lag Goose *Anser anser* and are very quickly discouraged. I have a single record of a male Gannet which had just lost its egg attempting to roll a neighbour's unattended egg into his own nest. Whereas I have recorded Herring Gulls building many separate nests around eggs successively displaced too far to be rolled, until eventually incubating them several yards from the original site, Gannets do not attempt to incubate outside the nest even where this is possible. Such a response would rarely be useful.

Rôle of the sexes in incubation

When the female first vacates the egg, which, if the male is present, she usually does soon after laying, he immediately begins his first incubation spell, the sight of the egg apparently releasing the appropriate behaviour. The early change-over may be partly due to the female having already spent a long pre-laying spell on the nest. A similar procedure occurs in many other species which habitually take long incubation stints.

Two-hourly checks over several days and once or twice daily checks over several weeks established that the number of incubation stints was roughly equal in the sexes, though the male's were longer (average 35.6 hours against 30.2 hours). In both sexes the spells became slightly shorter as hatching approached, then dropped suddenly after hatching.

Change-over

Arrival of the partner during incubation is followed by mutual fencing and change-over. An odd fact is that before the incoming bird relieves its mate it usually sky-points and moves slightly *away* from the nest before returning and taking over. Departing birds very often elicit mutual fencing intention movements from the partner, as though the

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Table 14. Time taken to change-over by Gannets *Sula bassana* on the Bass Rock

Sex arriving	Average time	Longest time	Shortest time	No. of cases
Male	7 min. 58 sec.	22 min. 0 sec.	1 min. 30 sec.	31
Female	2 min. 49 sec.	10 min. 35 sec.	0 min. 5 sec.	23

latter is trying to influence it to remain on the site. Once the incubating bird rises, the incomer pushes directly on to the egg and settles down, usually ignoring the mate, who repeatedly sky-points before leaving. Table 14 shows the time taken to change-over, calculated from the time of arrival at the nest to stepping on to the egg. It is clear from these results that females are significantly less willing than males to vacate the egg, which may possibly indicate a stronger incubation tendency or reflect the fact that males have usually been on duty longer (see table 5).

Although change-over times are scattered throughout daylight hours, table 15 shows that there is a tendency for most arrivals to occur between dawn and mid-day, probably representing birds which departed late the previous day, fished in the early hours and then quickly returned.

After change-over, some time usually elapses before the outgoing partner leaves the vicinity of the nest, but once away it does not usually return until the next relief, though I recorded birds flying over and inspecting their nests several times from the air before finally departing. Significantly, these were usually birds involved in competition for mate or site. Occasionally a relieved bird brings nest material and may then

Table 15. Proportions of arrivals at the nest by male and female Gannets *Sula bassana* on the Bass Rock at different periods of the day throughout the season

M= male; F= female

	05.00 to 09.00		09.01 to 12.00		12.01 to 15.00		15.01 to 18.00		18.01 to 22.00	
	M	F	M	F	M	F	M	F	M	F
April	6	9	25	7	12	4	14	11	6	6
May	10	10	19	19	20	3	3	10	4	2
June	20	16	16	16	3	15	6	3	3	2
July	5	38	10	12	3	1	1	2	18	10
August	20	16	22	15	2	2	1	0	11	11
September	25	18	16	14	14	5	1	1	5	1
October	24	30	10	20	0	4	12	4	0	0
Average	16	19	17	15	8	5	5	4	7	4

spend further time sleeping beside the nest. I had good reason to believe that off duty birds did not usually congregate in 'clubs', which were composed of immature birds and non-breeding adults.

Hatching

Once the egg begins to chip, it is transferred to the top of the webs; incubation underfoot would crush the weakened shell. In three instances this transference was seen when the egg had developed only a small hole, by which time the chick is cheeping. The stimulus to which the adults respond could therefore be either visual or auditory. It may be recalled that transference of the egg to the top of the webs may also be caused by warm weather. Thus two entirely different stimuli elicit the same response.

The newly-hatched chick is also brooded in this position and in four observed cases aberrant behaviour resulted in its death, the adult continuing to incubate the hatching egg or new chick underfoot. Of 13 other cases, eight eggs disappeared around their due hatching date, and five chicks disappeared at less than five days, possibly also due to trampling underfoot or perhaps to faulty feeding; Snow (1960) stated that Shags sometimes experience great difficulty in feeding small young. Of the 17 cases referred to above, seven were first time breeders—a disproportionately high number. In a further case the small chick almost died during a spell of female attendance in which she trod on it; it then subsequently recovered, but at three weeks died during bad weather. This is probably another case of death due to parental inadequacy. Still, even experienced adults sometimes stand on their newly-hatched chicks, which must be highly resistant to rough treatment. The observed presence of more feathers than usual in the nest at this stage may help to protect the chick.

One female was seen to prise half an egg-shell off the hatching chick in a precisely performed action which was not merely due to accidentally mandibulating the egg-shell with the chick inside. However, it is not necessary, apparently, and chicks are certainly capable of freeing themselves, though they may take over 36 hours to emerge after chipping.

Gannets leave the egg-shell lying around the nest for some time after hatching (up to four days noted) and may eventually drop it over the side or place it on the rim, though sometimes it is merely trampled into the nest. Occasionally it is mandibulated like nest material and pieces are flung away with a quick sideways head shake. This disposal is not practised systematically. Non-removal may be connected with lack of predators which could be guided to the nest by the shell (*cf.* Green-shank *Tringa nebularia*: C. and D. Nethersole Thompson 1942; Black-headed Gull: Tinbergen *et al.* 1962; and terns: J. M. Cullen 1956). The other possible reasons for egg-shell removal discussed by these authors

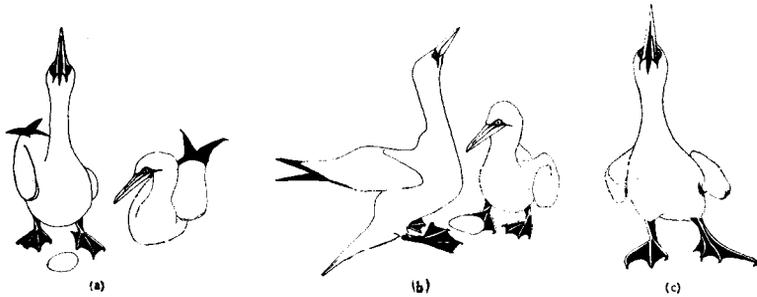


FIG. 14. (a) Sky-pointing at change-over. (b) Note the 'busked' position of the wings in which rotation lifts their distal ends; they are not spread. (c) The sky-pointing bird walks with a marked swaying gait; the striking lines on the webs and the conspicuous pattern of the facial soft parts are both fully exhibited. Sky-pointing is a pre-movement display, given particularly before and during movement away from the nest; it does not, apparently, 'appease' other Gannets between which the sky-pointing individual must pass (see text)

(such as lacerating the young and nest hygiene) could, of course, account for the Gannet's eventual disposal, though in view of the time lag this seems unlikely.

SKY-POINTING (fig. 14, plate 46b*)

Description

This conspicuous posture has already been mentioned in connection with web lines (page 236). In sky-pointing the closed wings are raised upwards, not outwards, by rotating the humerus in the glenoid cavity and lifting the distal end of the radio-ulna. This 'wing-busking' is a movement performed to some extent during ordinary walking and as part of the wing movement involved in taking flight. The neck is stretched vertically to its fullest extent and held stiffly, whilst the bill points skywards (sometimes even backwards of vertical) and the eyes look binocularly forwards. These features prompted the descriptive name used here, but it should be made clear that in the following discussion the associated *movements* (not merely the frozen posture) are included. This is important when interpreting the effects on neighbours; in fact, one cannot dissociate the two and demonstrate the effect merely of sky-pointing.

In this posture the bird begins slow foot-raising 'on the spot', preparatory to turning and flying or walking away from the nest (see fig. 14a, b) often with a special 'groan'. The striking digital lines are conspicuously displayed by holding the feet in a drooping position so that the upper surfaces are visible to the partner. Blue-footed

*The plates referred to in this paper were published with the first part in the July issue.

Boobies, which have no special features on the tops of the webs, parade with their feet fully and rigidly spread out. Gannets move slowly in the full sky-pointing position with a characteristic rolling gait (fig. 14c, plate 46b) lifting and lowering the feet deliberately, seemingly oblivious to surrounding activity. They may be threatened or even jabbed without abandoning the posture, although their swivelling eye movements show that they are registering the local situation. Sometimes, space permitting, the bird runs a few paces in this posture, or even makes a slight jump.

After the first few careful steps, caution is shed and the Gannet, if surrounded by neighbours, dashes for the fringe or some convenient stopping place. It aids progress by wing-beating as though rowing over the ground and is clearly distressed by the hostile reception, as shown by its gaping and swallowing movements once it reaches a safe point.

The best description of sky-pointing context is that it occurs before and during movement, usually on foot and particularly away from the nest site. Since sky-pointing is such an elaborately exaggerated and common behaviour pattern which often occurs outside the pair relationship, one suspects a signal function in a wider social sphere. It will be shown that sky-pointing clearly elicits reaction from the mate and neighbours, although the reaction of the latter is not beneficial to the sky-pointing bird.

Sky-pointing usually begins on the nest, typically by the relieved bird during change-over (but also by the incomer) just before the former flies or walks off, and may last for two minutes without a break. Usually the bird is surrounded by others (on flattish ground) but may sky-point when completely isolated, moving a step or two in the full sky-pointing position, then running or hopping with the take-off groan. Even then, however, the bird is usually en route from the nest to a take-off point. Birds moving about in the fringe, prospecting, collecting nest material and so on, usually do not sky-point.

When directly preceding flight the full behaviour sequence is: sky-point with wings busked, wings flicked (intention of flight), crouch (intention of jump), actual take-off with tail depressed to increase lift still in sky-pointing position (plate 47b). When preceded by sky-pointing, take-off is also accompanied by the groan in about 60% of cases. Take-off without sky-pointing is accompanied by a groan only in some 20%.

Function

The form of the movement, in which the bill is so obviously removed from the attacking position, clearly suggests appeasement and, despite the lack of any other evidence, this function has been stated or implied (Fisher and Lockley 1954, Tinbergen 1959), sometimes in a highly

committed manner (Barlee 1956). The function according to these authors would be to reduce the tendency of other birds to attack the sky-pointing individual as it moved through the colony to a take-off point. The situations in which it typically occurs seem to require such an appeasement posture, which no doubt influenced previous interpretations. The only way (short of model experiments) to gather evidence on the point seemed to be to observe (a) when, precisely, it occurred and (b) what effect it had on other individuals. Systematic notes were therefore made of about 500 occasions on which it occurred, where there were no additional complications of attack, stealing nest material, disturbance and so on. These fell into seven classes:

(1) Birds leaving their nests to move through the colony sky-pointed and then dashed in 60 out of 83 cases (72%) and merely dashed in the remainder.

(2) Birds moving some distance from their nests but without having to pass through others sky-pointed in 69 out of 76 cases (91%). The differences between categories (1) and (2) suggests that the prospect of passing between hostile neighbours decreases, rather than increases, the tendency to sky-point.

(3) Birds moving only slightly off their sites—a foot or two—sky-pointed in all of 19 cases.

(4) The few records of birds approaching their sites on foot indicate that where they have to pass through others they do not sky-point (no cases out of 14), but where they can approach without they may do so (four cases out of 11=36%).

(5) Prior to flying from their nests after change-over, birds sky-pointed in all cases but, taking into account departure after short visits only, in 47 out of 130 cases (36%).

(6) Although sky-pointing never occurs prior to take-off with nest material, birds occasionally walk in this position holding nest material. Birds taking off without nest material other than from their nests sky-pointed in 16 out of 132 cases (12%). Many of these had left the nest on foot and were taking off from some vantage point. In a literal sense, therefore, they were still 'leaving the nest'.

(7) Movement on foot along the fringe of the colony involved sky-pointing in 58 out of 118 cases (49%). Many of the sky-pointing birds had just left the colony, but precise proportions cannot be given, since a bird's behaviour prior to its arrival in the fringe was often missed.

The preceding analysis reveals a posture which, though highly predictable in a few situations, is far from an invariable response to the pre-movement situation. Further it does *not* effectively prevent attack (see below) and is *not* adopted when attack is likely; instead the bird dashes. Sky-pointing usually occurs *before* the bird has been attacked. When attack appears imminent, a bird may 'freeze' in a non-sky-pointing position for over five minutes before dashing.

To see whether sky-pointing reduced the probability of attack, counts were made of its effect on the behaviour of neighbours. In 78 cases of sky-pointing, 60% elicited a menace from previously quiescent neighbours. This should be compared with the effect on neighbours of other movements of roughly similar magnitude. Thus 33 out of 432 rotary head shakes (8%) and none of 56 bows drew menaces. It

appears that sky-pointing is more likely than these other behaviour patterns (both of which involve vigorous movement) to elicit hostile behaviour.

Whilst this may well be due to conditioning, the neighbours recognising sky-pointing as an intention movement of departure probably involving blundering past their nest, it strongly suggests that the performer is not thereby any more immune to attack, but rather less so. In fact the sky-pointing bird actually makes his departure by dashing through the nesting ranks—a procedure he could equally well carry out without the preliminary posturing, since neighbours attempt to bite him in either case.

If an appeasing function seems unlikely on the above evidence, some other must be found for such a striking display. Successful site maintenance and breeding is highly dependent, in the Gannet, on efficient changeover. Unattended nests are liable to lose egg or chick and Gannets cannot return quickly enough to prevent mishaps, once having left. It is therefore important that a conspicuous pre-leaving signal should be given to remove the danger of both adults leaving together. The elaborate and prolonged posturing could clearly perform this signal function; it is certainly recognised and responded to by the mate (fig. 14). This interpretation makes more sense of sky-pointing in the cliff-ledge situation in which it is usually possible to leave without approaching any neighbour—a particularly cogent point since there is much evidence that Gannets are primarily cliff-nesters. The mechanism by which sky-pointing synchronises change-over and induces the non-sky-pointing bird to remain on the site has yet to be worked out.

It may be doubted whether this explanation could account for sky-pointing in situations away from the nest. It may, however, have become 'frozen' into the pre-moving situation, which in this species usually means departure from the nest, and now occurs even when the movement is not merely 'from the nest'.

Although sky-pointing sometimes occurs in sexual and hostile situations, it also occurs much more widely, as the preceding examples have shown, and it is not a particular balance of fear, aggression or sexual tendencies which forms the common denominator on these occasions. Rather it is the situation 'about to move', particularly from the site. The motivation of sky-pointing is therefore much less obvious than that of the Gannet's agonistic displays, though it probably contains an element of fear.

To sum up, the observations show that sky-pointing does not have a marked appeasing function, but is, if anything, more attack-provoking than other movements. It is possible, though not proven, that sky-pointing functions as an intra-pair signal movement facilitating change-over.

Derivation

It seems likely that sky-pointing is a ritualised flight intention movement. Whilst many geese show neck lengthening before flying up, some have incorporated chin lifting movements and lateral head shakes (Johnsgard 1961). It is not difficult to see how progressive elaboration of a simple neck lengthening could produce the sky-pointing posture. The peculiar rotation of humeri now associated with sky-pointing could be an intention movement of flight adapted to a restricted take-off position (it does not occur so markedly in the boobies which correspondingly nest much less densely). Whilst the Gannet appears to have retained and elaborated sky-pointing in this phylogenetically primitive context, all other Sulidae have transferred it to an entirely different one, that of male advertising. In this functionally emancipated context it has undergone great elaboration different in each species.

COMFORT BEHAVIOUR

Two forms of head shaking and preening fall under this heading.

Rotary head shake (fig. 15, plate 42b)

Most birds shake and settle their plumage after bathing, dust bathing, preening or other disturbance of their feathers such as through being handled. Gannets, however, rotary head shake frequently and regularly (not merely after cleaning activity) in the breeding colony, frequently on the sea after alighting and bathing and almost invariably in the air just after take-off, when they shake themselves strongly and waggle their tails.

During rotary head shaking, the neck is stretched forwards and upwards at about 45° and the tongue bone may be depressed, imparting a peculiar facial expression. The wings are flapped vigorously with increasing speed, the neck and head feathers ruffed out (fig. 15a, b, c) and the head rotated vigorously several times around the horizontal axis, turning the crown until it almost faces the ground (hence the name). The wings are then closed, neck retracted, tail waggled sideways and wings shuffled on the back. The forward thrust of the head with elongated neck and the vigorous flapping make this behaviour particularly conspicuous in the Gannet. In a common variation the body feathers are loosened and shaken with loosely held wings and head rotations—like a dog shaking. Apart from this and other slight variations—the amount of wing flapping, etc.—the Gannet does not apparently use any other movement to shake its plumage, although the ordinary head shake is almost always elicited by a soiled bill.

Rotary head shaking is clearly concerned with resettling the plumage as part of the bird's regular feather maintenance behaviour. It occurs whenever the plumage is disarranged—in the female after copulation,

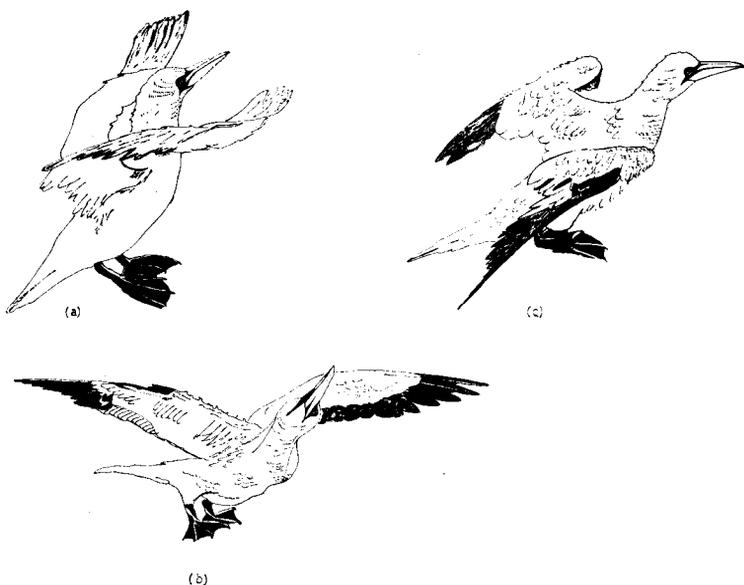


FIG. 15. (a) The wing flapping stage of the rotary head shake, a comfort movement by which plumage is adjusted. (b) The head is rotated vigorously several times. (c) The loosened plumage is shaken strongly

and after preening, fighting and so on. The period of body feather moult, marked on fig. 16, coincides with a peak in rotary head shaking activity; the behaviour can be seen to dislodge old feathers.

Tactile stimulation often causes rotary head shaking. The onset of rain immediately stimulates an outburst comparable to the chick's response of violent wing-exercising which, however, it does without the rotary head shake component. Gannets perform the rotary head shake if soiled by excreta from a neighbour, even if only the foot is dirtied or they merely *see* the excreta fall. The association between seeing excretion and the threat of soiled plumage elicits it perhaps as a conditioned reflex. This kind of linkage may offer a mechanism by which rotary head shaking could become associated with alarm (see below).

Rotary head shaking and alarm. Fig. 16 shows the seasonal pattern of rotary head shaking activity which is high during moult and also towards the beginning and end of the season. At both these latter times the birds are uneasy on land and subject to sudden frights, and rotary head shaking is strongly and positively correlated with alarm. Gannets leaving the colony in alarm cause an outburst of this behaviour among the remainder. The effect of alarm was demonstrated by counting the

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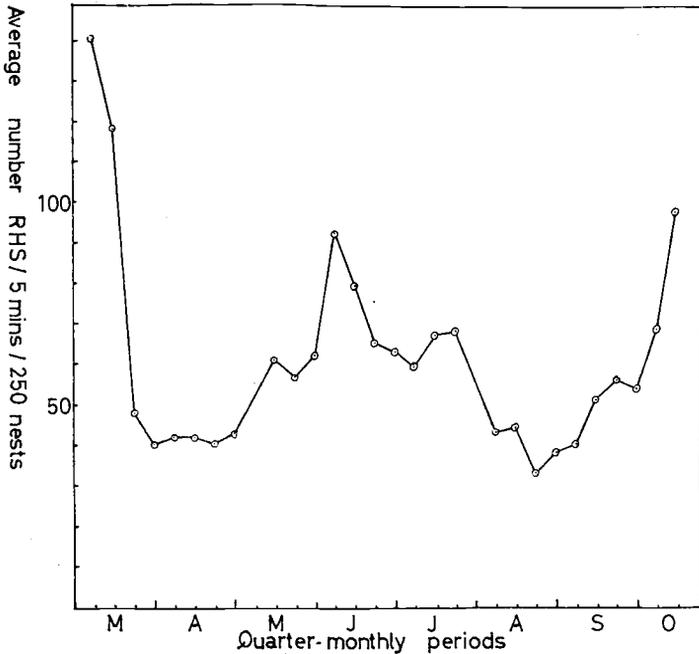


FIG. 16. Seasonal frequency of rotary head shaking, based on 261 five-minute counts in 1962. This behaviour pattern becomes more frequent during moult

frequency of rotary head shakes within a group and then flushing gulls near-by, without allowing the Gannets to see the cause of the disturbance. The clamour alarmed the Gannets and rotary head shaking shot up to many times the previous level before gradually waning. There are at least two possible interpretations of this situation.

First, rotary head shaking following alarm may be necessary to prepare plumage for flight. Some geese, for example, incorporate a similar movement with their pre-flight neck-stretching (Johnsgard 1961). However, the Gannet normally performs a vigorous rotary head shake in the air after take-off (even if it has previously done so on land) and this should make any feather adjustment necessary for flight. It might be suggested that rotary head shaking results from feather sleeking, itself a pre-flight phenomenon and likely to occur in alarmed birds. The rotary head shake might then be a response to tactile stimulation from 'tightened' feathers in birds which did not fly and needed to restore their plumage to the normal condition by loosening and adjusting them. However, any *functional* link between rotary head shaking and take-off remains undemonstrated.

Second, the conflict situation arising from the tendency to flee

induced by alarm and the counter-attraction exercised by the site could result in rotary head shaking as a displacement reaction. This does not suggest why rotary head shaking alone should be the behaviour pattern shown. However, a wing-rattling movement, but without a rotary head shake component occurs in several of the Sulidae as an intention movement of flight. In the Gannet the whole movement has become more elaborate (prolonged and conspicuous flapping) and the entire sequence including the rotary head shake retained apparently both as an alarm or intention movement and as a comfort movement; the boobies use wing-flapping as a comfort movement, but usually without the rotary head shake. The enhanced value in communication achieved by this may again be correlated with the Gannet's dense nesting and aggressive habits, which put a premium on clear social signal behaviour.

Since rotary head shaking is correlated with the tendency to fly, it is not surprising to find that it is also strongly correlated with sky-pointing, which itself precedes movement. Sky-pointing birds tend to flatten their plumage, which could provide peripheral stimulation and thereby cause rotary head shaking in the way proposed above. Since sky-pointing is so strongly linked with flight preparation, the correlation between flight and rotary head shake will generally occur through this link.

It seems justifiable to regard rotary head shaking in all cases (except perhaps its occurrence as a possible displacement reaction to alarm) as a response to some form of peripheral stimulation probably acting via the feather follicles. Thus, whether it occurs in response to rain, excreta, soiled or disarranged plumage or simply feather tightening, it may be referred to the same general causal situation. It *need* not be functional in the alarm situation in the sense of preparing the feathers for flight.

Sideways head shake

The ordinary side to side head shake, one of the commonest movements the Gannet performs, is of interest because it has been incorporated into several functionally distinct displays. Unlike the rotary head shake, the head is held normally and not aligned with the neck, so that the movement seems to be between the base of the skull and the articulating neck vertebra; in the sideways head shake only the head moves, whereas in the rotary head shake the head and neck seem to move as a single unit.

A similar head shake occurs in Herring Gulls, Kittiwakes, Guillemots and Shags, and doubtless many other birds. It displaces water from the head, the secretion of the salt gland from the bill and so on. In the Gannet it is much commoner than in the above species and occurs in several social situations, alone, or as part of more complex behaviour such as the bow.

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The following summary shows the occurrence of the head shake in all its modified forms:

(1) Violent head-flinging is used to dispel strongly-adhering matter from the beak. With mandibles widely parted, it is also used to dislodge fish bones and similar objects from the throat. Spilt fish, egg-shell remnants and stones from the nest cup are all dispelled with this movement.

(2) As a probably non-signal part of threat behaviour, vigorous head shakes are interspersed throughout menacing matches, together with pelican postures and nest touching movements.

(3) The sideways head shake is 'locked' in the bow and occurs after each dip. In the male's advertising display (resembling an inhibited bow), the head shake component is very conspicuous whilst the dip is suppressed. Head shaking is one of the main components of mutual fencing, but differs in form from ordinary head shaking and resembles rather more an attempt to maintain contact with the other's bill during irregular side to side movements, though its resemblance to head shaking can be seen when the partner's bill is momentarily out of reach.

(4) Females use a very inhibited head shake when reacting to the presence of a male near-by which they want to attract. Both sexes also react to the voice of their incoming mate by rapid head shaking. An exaggerated form of head shaking is also used by the female as a ritualised signal in soliciting copulation. The head is held loosely and flung violently from side to side. The female usually squats, with head held low, and continues the movement intermittently during copulation.

By contrast to the wide occurrence of ordinary head shaking, rotary head shaking is confined entirely to a few situations. In none of the situations described above, with the possible exception of the first, does the Gannet use a rotary head shake.

Why should the one form have been selected for incorporation into signal displays whilst the other occurs mainly in one context (soiled, wetted or disarranged plumage) and not as a signal? Possibly because in some contexts (e.g. menacing) a rotary head shake would temporarily obscure vision, and in others (e.g. copulation or mutual fencing) would be physically inconvenient. Also the sideways head shake is a simpler movement and therefore more likely to be 'preferred', other things being equal. It may be that the ordinary head shake was more suitable for exaggeration and change.

Clearly one can say little about the function of the head shake in its emancipated form, since it usually occurs as part of a complex behaviour pattern. I have the strong impression, however, that it has non-hostile overtones in many situations. A head shaking bird is very likely to be slightly afraid or friendly, rather than aggressive.

In summary, the sideways head shake in the Gannet is a good example of a simple basic movement which nevertheless shows wide variation in form, context and function in its incorporation into complex displays.

Preening

Gannets preen thoroughly for much of their long periods of site attendance. After bathing, the complete preening procedure, includ-

ing oiling, is performed on the water. The ventral surface is exposed by rolling on to one side. A curious difference within the family is that, whereas *S. dactylatra* does not roll in this fashion when bathing, both *S. nebovicii* and *S. variegata* invariably do so. Gannets also occasionally preen in flight. They do not wing-dry like Shags, Cormorants and pelicans, nor adopt special sunning positions like other members of the family.

Whilst a detailed study might reveal a pattern of preening different parts of the body, it is not readily apparent. Gannets switch abruptly from one part of the body to another. The remiges and rectrices are drawn separately between the mandibles and the tail is sometimes bent sideways at right angles to the body to help this. The thick quilt-like body plumage is nibbled with the points of the mandibles, and the lower breast and flanks are 'stropped' with a sideways motion of the bill. In a thorough preening session, which may last for over an hour, the oil gland at the base of the tail is erected (the feathers surrounding it can be displaced to uncover the gland), oil is rubbed on to the nape and back of the head and then rolled on to the back and wings from the head.

Preening is occasionally followed by direct head scratching in which the pectinated middle claw is mainly used.

Perfunctory preening often follows other activities. The area preened is often decided by postural facilitation. Following bowing, the bill tip rests on the upper breast and this region is most frequently preened then. Also preening occurs at a specific point in the behaviour sequence following a fight or a bout of menacing. As the tension gradually relaxes the first non-hostile behaviour, apart from head shaking, is invariably a rotary head shake and then short preening bouts. The preening can be seen to arrange the plumage which is often soiled and disordered.

Sleeping

Adult Gannets, including incubating birds, sleep with heads tucked in scapulars. The bill is dexterously inserted between the feathers and the head is almost entirely covered. Much of the time on the site is spent sleeping, particularly during wind and rain. They occasionally doze with bill forward, but never sleep properly in this way. They tend to sleep much more in the last hour of daylight (and presumably also at night), but otherwise show no periodicity. Unlike Shags, Gannets do not usually rest side by side on the nest; if one sits, the other stands. There is no precise point in time at which the female 'takes over' the centre of the nest, though she does so before egg laying.

After an exhausting fight Gannets invariably fall into a deep and prolonged sleep, no doubt part of the necessary recuperative process and possibly comparable to battle fatigue in soldiers. I have several

times caught by hand Gannets sleeping on the fringe of the colony following a fight and have records of such birds sleeping almost continuously for three days.

PELICAN POSTURE (fig. 17, plate 46a)

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

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

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

Pelican postures occur in the aggressive bird during and following aggression of male to female (redirected aggression, aggressive copulation, the new-pair situation, the eviction of unwanted females or adult attacks on chicks) or of either sex to some other species (e.g. Herring Gull whose territory is invaded). In the first-named examples the posturing bird is almost purely aggressive.

Hostile behaviour from neighbours, elicited in a variety of ways

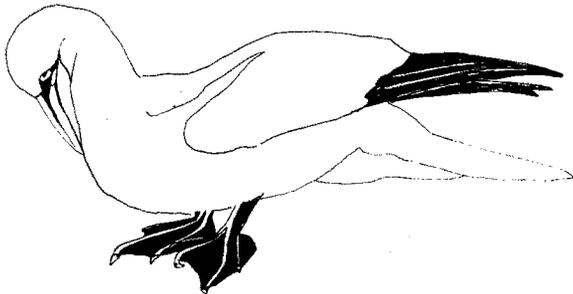


FIG. 17. Pelican posture. This usually follows bowing and also occurs separately in a variety of situations; it is motivated by fear/aggression and probably appeasing in function

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

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

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

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

Since the pelican posture often occurs in situations 'requiring' an appeasement posture (and looks like one), the possibility that this is in fact its function should be considered. Since most bird species fight with their beaks, the pelican posture clearly fulfils one requirement of an appeasement posture—that the weapon of offence should be held in a position markedly different from that used in attack. It is therefore not surprising to find that, for example, the Kittiwake, in which the bill sharply focuses attack (Cullen 1957), has convergently evolved a bill-hiding appeasement posture. Despite the fact that the pelican posture occurs in such a wide variety of situations, and includes aggression beside fear, the most fitting interpretation of function is that it tends to reduce the likelihood of attack or retaliation and is therefore an appeasement posture.

It is difficult to measure the efficacy of the pelican posture; it often fails to prevent attack or retaliation and certainly does not stop attacks already launched, nor does it necessarily inhibit the performer from attacking, though it clearly removes the bill away from an antagonist whilst at the same time maintaining full readiness to retaliate. It seems unlikely to function in protecting the eyes (see page 243) and does not remove the potential attacker from the visual field of the bird performing the pelican posture (*cf.* the 'cut-off' theory of Chance 1962).

It is, however, restricted to the above situations. Appeasement postures elicited in other situations (e.g. male aggression to a female) are different in form. It may be significant that these situations mainly lack the aggressive motivation which may be necessary to evoke the pelican posture.

As already mentioned under bowing, the pelican posture is probably derived from the infantile appeasement behaviour of 'beak-hiding'.

This completes the survey of Gannet behaviour at the breeding colony, with the exception of parental care and the development of chick behaviour, which it is hoped to treat separately; the main emphasis of this paper has been on social communication behaviour in the wider sense.

DISCUSSION

Although the connection between aggression and the site seems clear from the evidence discussed and it has been possible to demonstrate the unity of several different measures of site attraction, including sex differences in the site-ownership display, site attendance and site tenacity, the correlation must be considered seriously incomplete until a convincing reason for the evolution of such intensely competitive behaviour can be suggested.

The supply of suitable nest sites is not strictly limited at present (a) because at many large gannetries there is still room for substantial population increase and (b) because, taking into account the Gannet's ability to use flat ground as well as cliffs, the number of potential gannetries is very large.

Accepting for the moment that Gannets evolved their social behaviour, including violent aggression, under the selective conditions of cliff-nesting, which I believe was the ancestral habit, we may then suppose either that the supply of suitable cliff sites (such as broad ledges and broken cliff faces) was at one time strictly limited in proportion to the Gannet population or that, despite plenty of physiographically suitable sites, there was perhaps a strictly limited number of sites suitable in *all* respects. In other words, that there was some other good reason for crowding closely together and hence adding a new and advantageous dimension to site choice and competition.

It is hard to believe that the British Gannet population could ever

have saturated all suitable stacks and islands. With regard to the second suggestion, since the criterion for full suitability is not whether a site allows simply success or failure, but what *probability* of success it confers compared with other sites, we can imagine social requirements which must be met. Evidence for differential breeding success in birds from sites with different social characters, though comparable with respect to topographical features and age and experience of adults, would help clarify the point. At present my records show an effect of density in advancing the onset and increasing the synchronisation of laying, but not on breeding success *per se*. Also, I have no data on the survival to *breeding age* of young from different times of the same breeding season; perhaps late young survive less well. Such an effect, if present, would provide one factor inhibiting, though by no means preventing, the use of sites lacking in nearness to others and perhaps to many others if a high density is necessary to produce optimal synchronisation and ultimate survival of young. The effect of social factors could well be far more complex, but in the absence of evidence enough may have been said to suggest that, even in the presence of topographically suitable sites, competition for strictly limited, 'totally' suitable sites could conceivably occur and so provide a sufficiently important reason for the evolution of the aggression we observe.

The social stress resulting from fiercely competitive behaviour seems the sort of mechanism which might be interpreted according to Wynne-Edwards's (1962) ideas on the factors controlling the admission of new breeders to a colony. It cannot be doubted that every new would-be breeder in a Gannet colony must survive frequent and often severe challenge and it is conceivable that immature birds are in some way 'inferior' and might be prohibited from breeding under such circumstances. The phenomenon of the adult non-breeders present with immatures on the Bass and yet apparently not prevented from breeding by shortage of sites could then be explained. One of the inadequacies of this interpretation is that (as shown by the three annual extensions of the observation colony) there are no fixed or 'conventional' limits to the colony within which new breeders must find a place or be expelled by older and socially superior members. There is, it seems, nothing to prevent new breeders from settling in the fringes, near to existing nesters but not in direct competition with them. A fuller discussion of this problem turns primarily on ecological factors and is being considered elsewhere. There is no convincing evidence one way or the other for the correlation between strong competition and strictly *limited* nest sites in the Gannet. Yet the competition is indubitably there and if we are to justify its presence in evolutionary terms, remembering its attendant disadvantages, an important function must be found. The site is clearly the object of competition, but the deeper reasons behind site conflicts remain to be found.

THE BEHAVIOUR OF THE GANNET

The dense colonial nesting and strong aggression require clear-cut signal behaviour to ensure adequate communication between members of the community. Correspondingly, Gannet displays are numerous, strongly differentiated and conspicuous. Throughout them all, the determinative influence of aggression can be traced.

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SUMMARY

(1) Gannets *Sula bassana* were studied intensively on the Bass Rock, Scotland, from 1960 to 1963. Particular attention was paid to behaviour in a group of about 250 pairs containing many colour ringed adults. The importance of aggression in Gannet breeding behaviour is stressed in the introduction.

(2) Morphology, including sex differences, and voice are briefly described. Males tend to have yellower web lines and darker buff heads than females.

(3) A brief synopsis is given of some important aspects of Gannet breeding biology outside the scope of this paper.

(4) The process of site establishment in the Gannet is described in detail. Gannets breeding for the first time tend to return not only to the natal colony, but to the local part of this from which they fledged. They usually maintain a site for all or part of the season prior to first breeding. Different types of site acquisition are described. Full details are given of the severe aggression involved in site acquisition; the differences between male-to-male, male-to-female and female-to-female aggression and other forms of aggressive but non-fighting behaviour (menacing and bowing). The latter, an aggressively motivated display signalling site ownership, is analysed in detail. Site attendance in different categories of site owners is described and the sex difference in attendance analysed.

(5) Pair formation and the pair relationship are described. Males advertise by a special display derived from the aggressive site ownership display, bowing. Quantitative figures for its effect are given.

(6) In relation to pair formation and the pair bond, females show appeasing behaviour, 'facing away', and the pair perform a meeting ceremony, 'mutual fencing'. The latter is analysed in some detail, and it is shown that the length and intensity of mutual fencing bouts are correlated with the amount of aggression, particularly in the male, which has to be 'overcome': the more aggression, the longer and more intense the mutual fencing.

(7) Later stages in the pair relationship are described and the male's continued aggression towards his mate stressed. Gannets usually mate for life: 78% of pairs

followed for four years remained together throughout, 5% remained together three successive years and the remaining 17% stayed together two successive years. It was further shown that, irrespective of mate attraction, there is also a strong site attachment in both sexes, though demonstrably stronger in the male, in which, in fact, it could account for *both* site and mate attraction. In other words, site fidelity *alone* was 94%, compared with virtually the same figure (96%) for site-plus-mate fidelity, in which the attraction of the female could have played a part in attracting him back.

(8) Mutual preening frequently occurs in mated pairs and also in temporary associations between 'club' birds; females tend to preen males more than vice versa.

(9) Copulation behaviour is analysed in terms of seasonal frequency and associated behaviour patterns. It reaches a peak about two weeks prior to egg laying and there is a high individual rate. Successful copulations are distinguishable by the male's behaviour. The proportion of successful ones rises prior to egg laying. Reverse copulations are extremely rare, though both sexes attempt copulation with well-grown young. Copulation stops abruptly after egg laying, but restarts within 24 hours of egg loss, even after lengthy (up to 32 days) incubation.

(10) Nest material is gathered assiduously between January and October, but prior to egg laying by the male only. On the Bass more grass than seaweed is used. Rain elicits outbursts of building. The habit of directing the excreta onto the sides of the nest is significant in enabling Gannets to cement their nests on to sites which would otherwise be untenable. Nest building and nest maintenance movements are described.

(11) Incubation behaviour is less efficient in first time than experienced breeders. Egg-donation experiments showed that some Gannets will accept eggs prior to laying their own; others reject them. Of birds which laid subsequently, those which accepted the foster eggs were closer to laying their own than were those which rejected them. Incubation tendency is closely linked with the deposition and presence of an egg and quickly wanes in its absence. Egg retrieving ability is very limited.

(12) The conspicuous behaviour 'sky-pointing', in which the neck is lengthened and the bill pointed skywards, is analysed. It is basically a pre-movement display, used particularly before movement away from the nest. Others have suggested that sky-pointing is appeasing behaviour enabling the bird to make its way unmolested through nesting ranks. The evidence given here refutes this. One important function is probably to synchronise change-over, by signalling impending departure. This interpretation makes more sense of sky-pointing in the cliff habitat, where take-off is easy.

(13) The rotary head shake is a conspicuous and common comfort movement. Basically it is probably a response to tactile stimulation, including soiled or wet plumage or tightened feathers. It is closely linked with sky-pointing and alarm. The reasons for this are discussed.

(14) The simple sideways head shake, a movement which the Gannet has incorporated into many displays, is described in its various contexts.

(15) Preening and sleeping are discussed.

(16) Gannets frequently show a pelican posture, in which the bill is partly hidden by tucking it medianally against the upper breast. Pelican postures are elicited by ambivalent aggression/fear motivation and probably function as appeasing behaviour.

(17) The discussion deals with the evolutionary significance of site competition in the Gannet, in which its outstanding aggression is presumably functional.

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