HEAD FLAGGING IN THE BLACK-HEADED GULL; ITS FUNCTION AND ORIGIN.

BY

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Studies of the reproductive behaviour of various birds and fish have led to the conclusion that many elements of courtship, threat, and other types of display are "derived" movements. Some of these, such as the pecking gestures by which a Domestic Cock calls the hens to food, or the "strutting" postures of courting gallinaceous birds, have doubtless originated as intention movements; that is, incomplete movements caused by low motivation (Daanje, 1951) or, if the motivation is relatively high, by partly inhibited motivation. Other movements are combinations of intention movements of different drives; they are the outcome of low ambivalent motivation. Such is the upright threat posture of the Herring-Gull (Larus argentatus), for example; a combination of the intention movements of attack and withdrawal (Tinbergen, 1952). A third group of derived movements includes displacement activities, due to a strong but thwarted motivation. Thus the "grass-pulling" of the Herring-Gull is actually displacement collecting of nest material, due to strong activation of both the attack drive and the escape drive (Tinbergen, 1952).

Such movements, however, often show certain characteristic differences when compared with the original movements from which they are derived. In many cases these differences are caused by ritualization; a secondary evolutionary adaptation to the signal function of the activity. Ritualization tends to make the movement more conspicuous. This may be effected by simplification and exaggeration of the movement itself (Daanje, 1951), or by the use of conspicuously coloured structures which are displayed in the movement, or by both. For instance, the strutting movements of gallinaceous birds are supported by the spreading of beautifully coloured fans, formed by tail, tail-coverts, or wings. The threat movements of Coots (Fulica atra) demonstrate the white frontal plate. The displacement preening of courting ducks is made more conspicuous by the use of brightly coloured parts of the wings (Lorenz, 1941), etc. So many similar examples are known that an observer of courting or fighting birds expects their "ceremonies" to display the conspicuous parts of the plumage.

During our recent field studies of the reproductive behaviour of the Black-headed Gull (Larus ridibundus) we paid particular attention to one specific courtship movement: the Head Flagging. This, like the examples cited above, seems to be a derived movement. Unlike theirs, its ultimate derivation is obscure, as it could have originated either as an intention movement or a displacement activity, or perhaps even as something else. Whatever the original
movement may once have been, it is now thoroughly ritualized in connexion with its function. It is precisely in this function that the interest and significance of the Head Flagging lies: it seems to negate or nullify a different and entirely distinct behaviour pattern: the Forward Display. It seems, therefore, obvious that the evolution of Head Flagging has been dependent on the evolution of the pattern it serves to nullify. We believe that such a clear and complete case of evolutionary dependence of one distinct behaviour pattern on an entirely different pattern has not previously been described. Perhaps the above might be more easily understood if we describe the courtship of the Black-headed Gull in a little more detail.

Contrary to reports in the literature (Kirkman, 1937; Lack, 1940) we found that not all members of a breeding colony of Black-headed Gulls are mated when they arrive in spring. Pair formation takes place in or near the colony, on "pre-territories" taken up by single males. These are visited by single females; such visits eventually lead to pair formation. After the pair has been formed, the pre-territory is abandoned and the pair select a nesting territory together.

When male and female meet, either before pair formation or after they have become mutually attached, they go through various courtship movements. The male, standing in his pre-territory, first reacts to an approaching flying bird of either sex by uttering a loud long call (Plate 10, upper). We may provisionally write this as "kreeooo." We consider it an expression of aggressiveness, with threat function, as it is often uttered in obviously aggressive situations, such as fights between neighbouring males. Moreover, intruding males are strongly repelled by it. When the approaching bird alights (which only females do) both birds adopt the Forward Display attitude (Kirkman). Since this posture is even more common during hostile encounters between neighbours than in encounters of (prospective) mates, we consider it a threat posture. This is also indicated by the form of the display itself: the bill is pointed forward, suggesting preparedness to fight (Plate 9, upper and lower; Plate 10, lower). As an element of the behaviour of sex partners it is commonest in the beginning of the season, although it may also occur later. We believe that it indicates a certain degree of hostility towards the sex partner. Hostile behaviour in similar situations has been reported in several other birds (Heron (Ardea cinerea), Verwey, 1930; Snow-Bunting (Plectrophenax nivalis), Tinbergen, 1939) and in fish (Cichlids, Baerends and Baerends, 1949; Three-spined Stickleback, Van Iersel and Tinbergen, unpubl.). After the Forward Display, both birds usually adopt another attitude which is, in several respects, the exact opposite of it. They stretch the neck vertically upward, and, with a sudden movement, jerk the head to the side, pointing the bill away from the partner when they do so (Plate 11). The neck
feathers are ruffled at this time, making the neck appear very thick. A similar movement has been observed by Noble and Wurm (1943) in the Laughing Gull (Larus atricilla); they named it "Head Flagging." Kirkman mentions the movement in passing, as an occasional sequel to the "upward display." We are convinced that he includes more than one posture under the term "upward display," and that he failed to recognise the importance of Head Flagging because he appears to have missed the pair-forming ceremonies entirely. Unlike the Forward Display, Head Flagging is never seen during hostile encounters. It is done exclusively by partners or prospective partners.

As it is known that many displays which are oriented to another individual serve to demonstrate conspicuously coloured structures, we naturally wondered whether the Head Flagging made a gull more conspicuous to its partner. We soon realised, however, that a head-flagging bird shows nothing but the white neck to the partner. This can hardly be considered a very conspicuous feature in a predominantly white bird like the Black-headed Gull. At the same time we noticed that the Head Flagging, in complete form, usually had the effect of concealing the brown face from the partner. This concealment of a conspicuous feature gave us a clue in our attempt to understand the function of Head Flagging. In the Forward Display, the birds direct their bill more or less toward the opponent. This orientation is not perfect; a bird may even stand at right angles to another bird, but it very rarely faces away from it. The threat function of the Forward Display, undoubtedly based originally on the aiming of the bill, is enhanced by the brown face. It seems very probable that the latter has evolved primarily to emphasise the threat gesture. In this connexion it might be significant that Huxley and Fisher (1940) found that attacks of Black-headed Gulls on stuffed gulls are directed at the head or nape.

We are, therefore, led to suppose that Head Flagging has evolved as a friendly gesture because it is the opposite, or negative, of the threat movement. It means something like "no offence meant."

Other types of "display" may have evolved in rather similar manner. A male Coot, for instance, threatens other Coots by facing them with the head pointing forward and downward. This movement displays the white frontal plate (which is larger in males than in females, and is largest in spring). The Coot also has a friendly gesture; it bends the head down to such an extent that the front is parallel to, and almost touching, the water's surface. This movement does not display any conspicuous structure; rather it serves to hide the conspicuous bill and white frontal plate. Again it seems plausible to consider the threat gesture as the "primary" movement, and the other as a "secondary" movement, developed to offset the effects of the threat.

It seems to us that the many "inferiority gestures" in which, as Lorenz has repeatedly emphasized, the occiput is turned towards
the opponent, may not be a "demonstration of a vulnerable spot" inhibiting attack (Lorenz). Their effect would seem to be due instead to the fact that the main weapon (the bill, or in mammals such as the Dog, the teeth), and also such structural releasers as support the demonstration of the weapon, are turned away.

**SUMMARY.**

The Head Flagging of the Black-headed Gull, and probably also other gestures of appeasement in different species, seem to have the function of nullifying the effect of threatening gestures and structures. Whatever the origin of such appeasing movements may have been, ritualization seems to have followed the opposite course from that which it usually does. In such cases conspicuous structures are concealed rather than displayed. Therefore, the process of ritualization of these movements has been dictated by the concomitant ritualization of their opposites, the threat movements.

**References.**


Tinbergen, N. (1952a). "Derived movements; their causes, functions, origin and evolution." *Quarterly Rev. of Biol.* (in press).

Black-headed Gull (Larus ridibundus).

Upper: Forward display. Schouwen, Holland, 1926.

(Photographed by N. Tinbergen).
BLACK-HEADED GULL (*Larus ridibundus*).

*Upper*: The trumpeting call, uttered by a male; female (right) about to settle on nest. Texel, 1928.

*Lower*: Forward display as seen by opponent. Scolt head Island, 1951.

(Photographed by N. Tinbergen).
Black-headed Gull (*larus ridibundus*).

Head flagging by pair at nest relief. (The egg models in the centre are lying on the nest rim to test the egg-rolling response.)

Scoit Head Island, 1951.

(Photographed by N. Tinhergen).