

## REMARKS ON THE ORIGINAL SOURCES OF DISPLAYS

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THERE have been many attempts, within the last few years, to trace the evolution of individual behavior patterns and groups of patterns. This is particularly true of the "ritualized" activities or "displays"; i.e. those peculiarly standardized and often exaggerated performances, including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers. Comparative studies of such performances have yielded results of interest to both ethologists and systematists; and the stage has now been reached when it is possible to begin to generalize these results, to draw some tentative conclusions about the sources from which some of the displays have been derived.

Tinbergen has already discussed these sources in an earlier review, (1952), and some problematic aspects of their evolution have been also noted elsewhere, (e.g. in Bastock, Morris, and Moynihan, 1953); but the whole subject might, perhaps, be usefully reviewed and reassessed once again, as briefly as possible, in the critical light of some more recent information and conjecture.

The origin of vocalizations remains obscure (although the suggestions of Spurway and Haldane, 1953, are very interesting in this connection); but a good deal is now known about the nature of the elements that have been most frequently incorporated into ritualized movements and postures.

The commonest of these elements are "autochthonous" intention or low-intensity behavior patterns.

An "autochthonous" activity is one that is caused by its usual drive (see Kortlandt, 1940). Thus, for instance, an attack movement is said to be autochthonous when it is produced by attack motivation. The terms "motivation" and "drive" are used interchangeably here; as short-hand for "the complex of internal and external states and stimuli (usually or normally) leading to a given behaviour." This usage follows Thorpe, 1951, in a somewhat altered form.

Many displays seem to have been derived from autochthonous intention movements alone. The "Agressive Upright" threat display of many gulls is a good example of this type (see Moynihan, 1955). It is motivated by attack and escape drives; and it includes indications of advance and pecking (attack intention movements) plus indications of retreat or avoidance (escape intention movements), combined in a particularly standardized arrangement. Further examples, in other species, are described in detail by Tinbergen (1952).

Other displays have been derived from autochthonous movements of higher intensity. The "Swoop" and "Soar" displays of the Black-headed Gull, for instance, include attack and escape elements of much greater vigor and elaboration (Moynihan, 1955).

The most interesting displays, however, are those that would appear to have been derived, in part at least, from an "extraneous" or superficially "irrelevant" source, i.e. from the so-called "displacement activities" and some other behavior patterns that are sometimes confused with displacement.

The generally accepted definition of a displacement activity, as ethologists use the term, is "an activity belonging to the executive motor patterns of an instinct other than the instinct(s) activated" (Tinbergen, 1952). Such a reaction is supposed to occur, in most cases, when an instinct or drive is thwarted, when it is prevented from finding its usual expression. The "energy" of the blocked motivation is then supposed to "spark-over" somewhere in the central nervous system, in a peculiar and as yet unexplained fashion, to find an alternative outlet in the performance of some apparently irrelevant act (see Bastock *et al.*, 1953). These apparently irrelevant acts, being caused by some drive other than their usual or normal one, are called "allochthonous."

The most plausible examples of displacement or displacement-like reactions, in this sense, are provided by certain "nervous" movements in man. It is well known that human beings may show unexpected "out of context" activities (e.g. yawning, scratching, playing with keys or other objects, etc.), under various conditions of stress and conflict.

It is also probable that similar reactions do sometimes occur in other animals. Thus, for instance, a male Three-spined Stickleback will show "fanning" (usually a parental activity) when its sex drive is thwarted during "courtship" (Tinbergen and van Iersel, 1947), and a Black-headed Gull will show preening and/or nest-building when its brooding drive is thwarted during the incubation period (Moynihan, 1953).

Many apparently irrelevant or "extraneous" movements of birds, therefore, have been interpreted as displacement activities of this sort. Such interpretations, however, are often obviously unwarranted. There is every reason to believe, in fact, that the great majority of the so-called "displacement activities" reported in the ornithological and ethological literature can be adequately explained without assuming the existence of any exceptional "spark-overs" in internal motivation. (It is true that any change in behavior of

any sort, "normal" as well as "abnormal," may involve some type of internal switch; but this is usually much slighter, and/or less transitory, than the "spark-over" posited to explain most of the presumed displacements.) Of the many apparently irrelevant acts cited by Tinbergen (1952), for instance, it is probable that no more than a third, at best, are really displacement activities in the conventional ethological sense.

A few examples, from his list, should make this clear.

Many of the cited activities seem to be purely autochthonous, direct and usual reactions to internal and external stimuli, with only the most superficial and misleading appearance of unexpectedness or irrelevance. Thus, for instance, the "courtship" behavior of caged Willow Warblers, "when showing the inhibited migratory movements called 'migratory restlessness,'" can hardly be a typical displacement. These birds must almost certainly possess some activated "courtship" motivation. Similarly, the "song" of Skylarks after escaping from a Duck Hawk or Hobby is most unlikely to be allochthonous. The "songs" of many birds are hostile (i.e. produced by attack and escape motivation), and this situation is certainly one in which autochthonous hostility might even be expected as a general rule.

Other activities have been misinterpreted because of their peculiar orientation. These are the "redirection activities."

Redirection movements, like displacement, seem to occur when an instinct or drive is thwarted, and their physical form may be very similar to that of some displacement reactions; but the two types of activity are quite fundamentally and definitely different in nature, i.e. in internal causation.

Redirection movements can be defined as autochthonous activities of a drive directed toward an object or animal other than the one releasing and usually directing them (although the releasing object or animal remains available, or partly available, as a potential goal at the time) (see Bastock *et al.*, 1953). An example is provided by the behavior of a Prairie Falcon (cited by Bent, 1938), when disturbed at the nest by a human intruder. Both the attack and escape drives of this falcon were immediately activated; but they were largely incompatible, and the escape drive was strong enough to prevent the bird from venting its attack drive upon the real offending object, the actual disturber. The falcon then found an outlet for its thwarted attack motivation by pouncing upon some other birds, a Barn Owl and a Raven, which happened to pass by at a convenient moment. This sort of "unprovoked" attack upon an inoffensive scapegoat is the commonest type of redirection.

It is also the type of redirection that has been most frequently confused with displacement.

Thus, to give some more examples from Tinbergen's list, the pecking at the ground by many passerines during fights, and other hostile encounters, is probably redirected attack pecking rather than displacement feeding.

More complex are such performances as "grass-pulling" in Herring Gulls. When two of these birds become engaged in a territorial boundary dispute, one or both may begin to peck and pull, violently, at the nearby vegetation. Tinbergen notes that the violence of this performance is probably an expression of redirected aggressiveness, but he also believes that the activity includes an additional nest-building component (which must be displacement in these non-nesting circumstances). He bases this belief upon the fact that vegetation is used as nest-material, and, more important, that the vegetation pulled up by "grass-pulling" is usually thrown away with a sideways jerk of the head, a sideways movement also shown during the construction of an actual nest. This evidence of displacement is not, however, completely convincing. There is no obvious reason why redirected aggressiveness should not be vented upon vegetation as well as any other object; and the distinctive sideways jerking might be nothing more than an immediate and simple reaction to the presence of some non-edible material in the bill. In other words, there are no real indications that any internal motivation has "sparked-over" in the course of this performance.

Similar explanations might easily account for many of the other supposed displacement activities in which pecking, biting, pulling, or pushing movements are conspicuous.

Discounting such certain or probable autochthonous reactions, at least provisionally, the remaining list of probable or possible displacement activities is very greatly shortened. The majority of the remaining patterns, moreover, are comfort movements such as preening or scratching; just the type of reaction whose causation, whether displaced or not, is most difficult to determine with any degree of assurance. The real nature of many of them, if not all, is still highly dubious.

The fact that real displacement activities are apparently rarer than sometimes assumed is not without significance in connection with the origin of ritualized displays.

Many displays, particularly the most elaborate hostile and sexual performances, contain elements that appear to have been derived and modified from such "extrinsic" or "extraneous" contexts as

sleeping, preening, or nest-building. There have been frequent suggestions that all of these "extraneous" elements must have originated, in the display situation, as allochthonous displacement activities. This theory may be quite correct, but we have very little evidence by which to judge it, and it is by no means the only possible explanation of the presence of these patterns in such peculiar circumstances.

Some of the supposedly "extraneous" elements in certain displays, of course, may be far more apparent than real. They may have been misinterpreted in the same way as some of the supposed displacement activities noted above. The pecking and throwing movements in the hostile and ritualized "choking" threat of the Black-headed Gull, for example, are rather misleading in much the same way as the similar movements in the "grass-pulling" of the Herring Gull (see Moynihan, 1955). They too should be classed as redirected attack, and they must always, therefore, have been strictly "intrinsic" as hostile reactions.

There are other components, however, in this and other displays, whose "extraneous" source is less easily questioned.

The ritualized "mock-preening" movements in the "courtship" of many male ducks (Lorenz, 1952), may be taken as representative of this group. They do seem to have been derived from real preening (although it is just barely possible that they might be modified forms of avoidance intention movements instead).

Assuming that they are indeed derivatives of preening, these movements may have been evolved from what was once displacement (conflict and thwarting are almost inevitable in "courtship" encounters); but such displacement preening, even if it did exist, was probably not the only source available. "Courtship" activities are also likely to provoke a considerable amount of purely autochthonous preening, during the performance itself or immediately afterwards, if only because vigorous activity of any sort is very apt to disarrange the plumage. Such ordinary preening may, therefore, have been the usual accompaniment of "courtship" in the males of the ancestral ducks.

It is extremely probable, moreover, that some conditioning would then result. In other words, the female ducks toward which such "courtship" was directed would then become conditioned to the associated movements, and autochthonous preening would thus acquire a "courtship" valence for them. This, in turn, would probably reinforce the connection between "courtship" and preening in the displaying males; as they would then become conditioned to the fact that preening movements had acquired a signal or symbolic function.

Granted the probability of this connection, it is easy to see that

such associated preening might well become incorporated, by natural selection, into the actual "courtship" itself. (This would be a case of "neurophysiological emancipation," as Tinbergen has used the term. These preening movements, as they became incorporated into "courtship," with increasing ritualization, would be less and less motivated by preening drives, and more and more motivated by "courtship" drives.)

This hypothesis is apparently adequate to explain the origin of "courtship" preening in male ducks; and also, perhaps, the appearance of many other display patterns, some of them derived from very different sources, in many other groups of birds.

Some hypothesis of this sort might even seem to be more plausible than the alternative theory that would derive "extraneous" display elements from displacement activities. It might be preferable, primarily, because it is somewhat simpler; i.e. it does not need to assume the existence of some original displacement "spark-over," a type of "spark-over" which may be very rare.

A final point, in this connection, may help to put the matter in perspective.

The exact process by which an "extraneous" pattern is incorporated into a display is certainly difficult to imagine in detail; as we know relatively little about the immediate causal, internal, factors involved in ritualization. There is no reason to believe, however, that the incorporation of an autochthonous "extraneous" pattern would be much more complicated than the incorporation of an allochthonous one. The ritualization of an autochthonous "extraneous" element, in fact, must be essentially the same as that of any other autochthonous pattern in its proper context. The consequences of this basic similarity are obvious. The physical differences between "extrinsic" and "intrinsic" elements are rapidly reduced as ritualization progresses; and this, of course, is the very reason why the two components are so difficult to separate and analyze in many cases.

*Summary.*—Display behavior patterns, other than vocalizations, seem to have been derived, in varying combinations, from the following sources.

I. Obviously autochthonous and "intrinsic" activities. These are all very similar in basic nature, but they can be rather arbitrarily divided into three major groups.

- (a). Intention movements of the drives producing the display.
- (b). Higher intensity movements of the drives producing the display.
- (c). Redirection activities belonging to the drives producing the display.

## II. Apparently "extraneous" activities.

It has been suggested that certain supposedly "extrinsic" or "out of context" elements, very conspicuous in many displays, must have been derived from allochthonous or displacement activities. There is considerable evidence, however, that displacement activities are by no means as common as sometimes assumed, and that the supposedly "extraneous" elements in displays, as a group, are actually heterogeneous and quite varied in origin. Some are not really "extrinsic" at all. They have been derived from purely autochthonous and "intrinsic" reactions, particularly redirection movements; and their physical resemblances to some "extraneous" patterns are purely fortuitous. Many of the really "extrinsic" components, moreover, may have been derived from "associated" activities rather than displacement activities in the conventional sense. That is, they may have been derived from autochthonous patterns of drives other than those producing the display with which they have since been incorporated, autochthonous patterns that often occurred in close temporal conjunction with the ancestral form of the display.

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### LITERATURE CITED

- BASTOCK, M., D. MORRIS, and M. MOYNIHAN. 1953. Some comments on conflict and thwarting in animals. *Behaviour*, **6**: 66–84.
- BENT, A. C. 1938. Life histories of North American birds of prey. *Smithson. Inst., Bull. U. S. Natl. Mus.*, **170**: viii + 482 pp.
- KORTLANDT, A. 1940. Wechselwirkung zwischen Instinkten. *Arch. neerl. Zool.*, **4**: 442–520.
- LORENZ, K. 1952. Comparative studies of the behaviour of the Anatinae. *Avicultural Magazine*. London.
- MOYNIHAN, M. 1953. Some displacement activities of the Black-headed Gull. *Behaviour*, **5**: 58–80.
- MOYNIHAN, M. 1955. Some aspects of reproductive behavior in the Black-headed Gull (*Larus ridibundus ridibundus* L.), and related species. *Behaviour*, Supplement No. 4, in press.
- SPURWAY, H., and J. B. S. HALDANE. 1953. The comparative ethology of vertebrate breathing. *Behaviour*, **6**: 1–34.
- THORPE, W. H. 1951. The definition of terms used in animal behaviour studies. *Bull. Anim. Behav.*, **9**: 34–40.
- TINBERGEN, N. 1952. "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. *Quart. Rev. Biol.*, **27**: 1–32.
- TINBERGEN, N., and J. VAN IERSEL. 1947. "Displacement reactions" in the Three-spined Stickleback. *Behaviour*, **1**: 56–63.

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