TYPES OF HOSTILE DISPLAY

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AMONG the commonest social behavior patterns in most birds are a great variety of hostile activities, i.e. behavior patterns produced by attack and/or escape motivation. (The terms "motivation" and "drive" are used interchangeably throughout this paper, in a very broad descriptive sense, as "the complex of internal and external states and stimuli usually or normally leading to a given behavior.")

Hostile activities include attack and escape movements of very different intensities, plus a large number of more complex and obviously ambivalent reactions. The most widespread, frequent, and conspicuous of these complex reactions are the "ritualized" patterns or displays; patterns that have become standardized and specialized as social signals or releasers.

Many hostile displays have been described at length in recent papers; (see, for instance, Bergman, 1953; Goodwin, 1952; Gullion, 1952, 1955b; Hinde, 1952, 1953a, 1953b, 1954; Morris, 1954; Moynihan, 1955a; Moynihan and Hall, 1954; Schaefer, 1953; Simmons, 1951, 1952, 1953; Tinbergen, 1952, 1953, 1954; Tinbergen and Moynihan, 1952; Williams, 1952).

It must be noted, however, that our understanding of these patterns is still far from complete. Some aspects of hostile display in the Passeriformes and Charadriiformes have been analyzed in detail, but other aspects, and other orders, have been studied less thoroughly.

A general discussion and review of our present knowledge might be useful, therefore, as a means of directing attention to some of the major problems that remain to be solved.

All attempts to arrange or classify the various hostile displays must be somewhat arbitrary, in one way or another; but a classification based on functional criteria would seem to be the most nearly "natural" one, and the most convenient for our purposes. These patterns can be divided into four or five main types, according to their usual effect upon the animals toward which they are directed. More precisely, as most hostile displays are commonest during intraspecific disputes, most of them can be classified according to their usual effect upon other individuals of the same species.

A word of caution might be inserted in this connection. Any hostile display may, at any given time, provoke (or appear to provoke) any number of different hostile and/or non-hostile reactions. This "fluidity," which is dependent upon both the internal and external situations of all the birds involved, may tend to confuse the observer;

and it must be stressed, therefore, that the "usual" response to a particular display can only be determined by observing repeated performances of the display at different stages of the annual cycle and in a variety of distinctively different environments.

The commonest types of intraspecific hostile display seem to have been evolved as means of obtaining certain advantages (which may differ considerably in different species at different times) without having to fight for them; thus obviating the risk of physical injury that actual combat would inevitably entail (see Tinbergen, 1952, Moynihan, 1955a, Moynihan and Hall, 1954). This ultimate goal can be achieved, however, by various methods, by reactions whose immediate effects are strikingly dissimilar.

These effects can be listed as follows.

Intimidation.—Intimidatory, or threat, displays are the best known of all the ritualized forms of hostility. They are also the most widespread and abundant; most species of birds having more than one of them.

Their primary immediate function is clear; they are "designed" to make an opponent retreat or flee. They tend to increase both the relative and actual strength of the opponent's escape drive.

(It is possible that some of them, at least, may occasionally stimulate the opponent's attack drive also, to some slight degree; but this subsidiary effect is so relatively weak that its outward expression is very often suppressed.)

The fact that threat displays are "designed" to make an opponent retreat or flee should not, of course, be taken to mean that they are always successful in accomplishing this. Their deterrent value may be shown in other ways. Thus, for instance, threat displays directed toward a particularly aggressive opponent, such as a territory-owner on its territory, will seldom induce an actual escape. They may, however, cause the owner to threaten back, or hesitate, before attacking with full force; and this, in itself, is an indication that even here, in the most unfavorable circumstance, they can produce a "frightening" effect of some sort.

The immediate causation of threat displays, i.e. their motivation, is fundamentally similar to that of all the other types of hostile display. Both the attack and escape drives of a threatening bird are activated simultaneously, and both are activated strongly enough to be expressed externally. (Overt elements of both drives may be visible in the display itself and/or in immediate temporal association with it.) Within this general framework, nevertheless, there can be appreciable

minor differences between the various threat displays of any one species and between those of different species. That is, both the attack and escape drives may differ in actual and/or relative strength in different threat displays (although the motivation of any given display remains relatively constant).

The escape drive may be slightly stronger than the attack drive in some threat displays, and the two drives may be equal in others; but the attack drive is definitely stronger than the escape drive in the majority of the most typical threat displays.

The predominance of attack motivation in most of these displays may help to explain the evolution of their physical form. Threat displays have been derived from many different sources, both hostile and non-hostile (see Moynihan, 1955b); and the most important of the hostile sources would seem to have been a whole series of unritualized and unspecialized "intention movements" or low-intensity reactions. Some of these "intention" patterns were probably locomotory, and others were probably indications of avoidance or retreat; but the great majority of them must have been attack movements such as pecking or pounding with the wings. It is these attack components, moreover, that have been most commonly exaggerated. Many of the morphological structures (releasers) that have been evolved to emphasize the visual conspicuousness of threat displays, to increase their effectiveness as social stimuli, are concentrated around those parts of the body (e.g. bill and carpi) that are most often used as offensive weapons in attacking (see figure 1).

Mimetic Induction.—Any threat display may provoke a threat display in return, very often the same display, in certain particular situations; but some types of threat display have this effect more frequently than others. Compare, for instance, the "Choking" and "Upright" patterns of the Black-headed Gull (*Larus ridibundus*). Both are undoubtedly threat; but the "Choking" induces return "Choking" by the opponent toward which it is directed, much more frequently than the "Upright" induces return "Uprights" (Moynihan, 1955a).

It is not too surprising, therefore, that some hostile displays have become particularly specialized along these lines; e.g. such patterns as the "Yip-reaction" of Jackdaws (*Corvus monedula*), (Lorenz, 1952); the "Curtsying" of Swallow-Tanagers (*Tersina viridis*), (Schaefer, 1953); and the "Piping" of Oystercatchers (*Haematopus ostralegus*), (Makkink, 1942). The infectiousness of these displays has been carried to a quite remarkable extreme; their performance by one

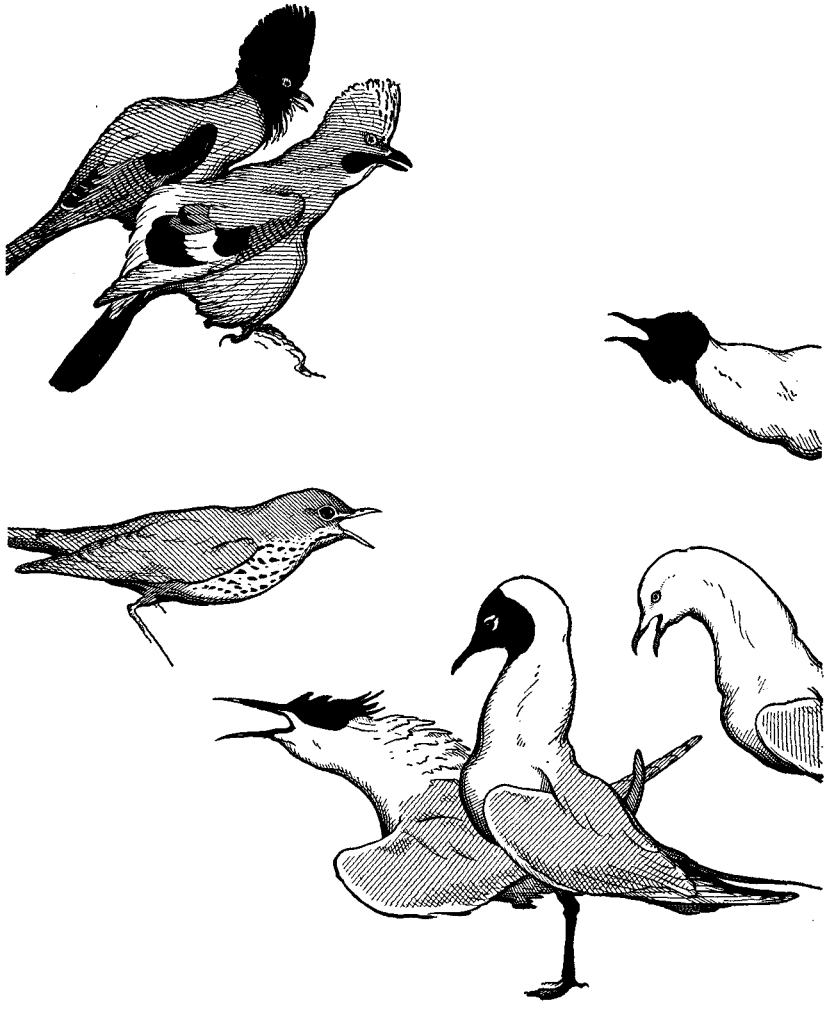

FIGURE 1. Some examples of relatively aggressive threat display postures, apparently caused by stronger attack than escape motivation, in two Old-World jays (after Goodwin, 1952), the Hermit Thrush (after Dilger, 1955), several gulls (after Moynihan, 1955a), and the Sandwich Tern (after van den Assem, 1954).

These postures include strong indications of advance and/or pecking; indications which are probably, in hostile situations, intention movements of attack.

bird almost invariably provokes identical performances by all the nearby birds of the same species (extreme "mimesis," in the sense used by Armstrong, 1951). Their infectiousness seems to be so much greater than that of the other hostile displays occurring during intraspecific quarrels that they probably deserve to be placed in a category of their own. They may perhaps be called "exemplary" displays; as, speaking in purely anthropomorphic and teleological terms, they provide an example to be followed.

Such displays have been found in very few species as yet; and, although others may be found when more species have been studied, their apparent rarity makes it difficult to draw general conclusions about their usual characteristics and significance. This difficulty is increased by the fact that the published descriptions of even the best-known cases are more or less seriously incomplete.

The only partial exception is provided by the Jackdaw's "Yip." Lorenz has shown that this display is a "communal reaction against a social delinquent." It seems to work as follows. If the owner of a nest-hole should find itself successfully attacked at the hole by a particularly aggressive and powerful intruder, it will immediately begin an excited series of "Yip" notes. All the other Jackdaws in the colony will then come over and begin to "Yip" also. This, in turn, will eventually induce the aggressive intruder to give up his attack and join in the general chorus. The physical combat is thus suppressed, apparently by the very infectiousness of the display; but the actual "mechanics" of this achievement, e.g. the changes in motivation of the responding birds, are by no means absolutely clear.

There is some slight evidence to suggest that the other exemplary displays of other species are also used in the communal suppression of overt fighting (or, at least, that they combine this function with more conventional intimidation or appeasement). The published accounts are so indefinite and vague, however, that any hypothesis must remain extremely tentative until these displays have been more thoroughly studied with this particular problem in mind.

The causation and derivation of exemplary patterns, by contrast, are much less obscure—but only because they seem to be much less peculiar. These displays seem to be produced by motivation like that of the least aggressive threat displays; and, as might therefore be expected, they seem to have been evolved from comparable sources.

Appeasement.—Appeasement displays, almost as common as threat, are particularly characteristic of disputes during the reproductive season.

They can be distinguished from both threat and exemplary displays by the fact that they are "designed" to prevent attack without provoking escape or widespread mimesis. They directly reduce the actual and relative strength of an opponent's attack drive; (and also, to a lesser extent, the actual strength of its escape drive).

They are produced, of course, by the usual type of hostile motivation; but the escape drive of an appeasing bird is almost always stronger, usually much stronger, than its attack drive. (A further causal difference between threat and appeasement, in many species, involves the other kinds of motivation which may also be activated simultaneously in the displaying individual. The production of threat displays is sometimes dependent upon the activation of a major instinct, such as the general reproductive instinct, but is comparatively seldom directly dependent upon the activation of "lower-order" drives, such as the sex drive. Many appeasement displays, however, do seem to be restricted or limited in just this way. They are confined, at least, to situations in which the presence of an additional motivation is apparently inevitable. Thus the immediate causation of many appeasement displays, apparently including three or more distinctly different drives, is far more complicated than that of the majority of threat displays.)

Most of the appeasement patterns have also been derived and ritualized from the usual hostile sources; but here again they show a few peculiarities of their own in matters of degree and emphasis. Thus, for instance, the most common and most conspicuous constituents of most appeasement displays are intention movements of escape (see figure 2). These often take the form of avoidance movements; and these, in turn, are often specialized to hide or withdraw the offensive weapons used for attack and, consequently, many of the sign stimuli revealed by threat (see Tinbergen and Moynihan, 1952). Appeasement displays, in fact, seldom reveal structures or colors evolved for appeasing purposes alone; although there are, of course, exceptions to this general rule (e.g. in the Night Heron, *Nycticorax nycticorax*, described by Lorenz, 1938).

The various contrasts between typical threat and typical appeasement, as they have been listed in the preceding paragraphs, might appear to be absolutely and necessarily clear-cut—and so they are in many cases. But it should be noted, nevertheless, that the two types of display are not always incompatible. Appeasement displays are sometimes superimposed upon threat (as in the Black-headed Gull and other Laridae, Moynihan, 1955a). More surprising still, perhaps, is the fact that threat and appeasement may even seem to

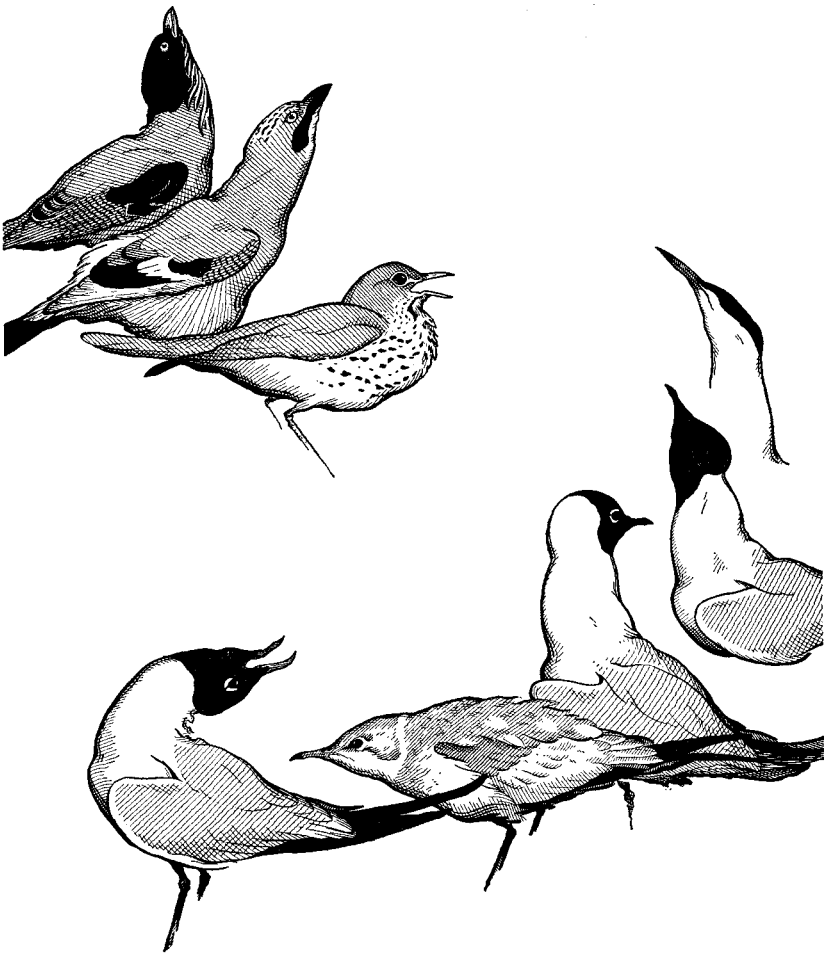

FIGURE 2. Some examples of relatively non-aggressive threat and appeasement display postures; behavior patterns which seem to occur when the escape drive is approximately equal to, or stronger than, the attack drive.

The postures of the jays, the Hermit Thrush, and the various larids are again drawn after Goodwin, Dilger, and Moynihan, respectively.

All of these patterns include strong indications of avoidance or withdrawal, intention movements of escape.

intergrade occasionally. Thus, for example, the "Anxiety Upright" and "Forward" displays of the Black-headed Gull, which must still be regarded as threat according to the criteria used here, are so weakly intimidatory that they seldom, by themselves, induce an escape reaction of more than low to moderate intensity. It is quite conceivable that weak threats of this kind might be transferred or incorporated into actual appeasement in the course of evolution; and such, indeed, appears to have been the history of some of the so-called "courtship" patterns.

Deception.—Some hostile displays, which may be called deceptive, are apparently "designed" to reduce an opponent's attack drive by a method very different from that of the conventional appeasement displays. They tend to reduce the relative (and probably the actual) strength of the opponent's attack drive by directly releasing and stimulating the performance of some particular non-hostile "friendly" or sexual activity.

The classic example of this process is provided by a reaction in cercopithecine monkeys. Should one of these animals find itself on the losing side of a dispute, or even find itself confronted by an obviously superior opponent, it will immediately assume a posture like that of a soliciting female, thus releasing copulatory behavior by the opponent (Zuckerman, 1932). This "pseudo-sexual" posture can be shown by juvenile monkeys of either sex, and by adult females at any stage of the oestrus cycle; and it seems to be extremely effective in averting or controlling the most violent forms of actual attack.

Deceptive displays of this general type are such less spectacular in birds, but they probably do exist in some species. Certain hostile displays of some passerines, for instance, are partly reminiscent of patterns used in social preening, e.g. the "Ruffle" display of the Spice Finch, *Lonchura punctulata* (Moynihan and Hall, 1954); and they may well exert a "soothing" influence by this resemblance alone.

These displays in birds, unfortunately, are not easily recognized as such, and they have been comparatively little studied, even less than the exemplary patterns. It is impossible, therefore, to analyze their evolution or causation in detail. One can only state that they seem to be motivated by stronger escape than attack drive and that they must have been derived, originally, from non-hostile or "extraneous" activities.

This concludes the list of functions subserved by the majority of hostile displays during intraspecific disputes; but there are several

other functions which may be subserved by the same or similar displays in somewhat different circumstances. These latter, rather miscellaneous, may be discussed more briefly. They can be divided into two categories.

Some hostile displays may be used as non-hostile intraspecific signals (and they rarely express antagonism toward the bird or birds for which they are "intended" then). Some of these displays may have a warning function, and others may play a role in sexual recognition or even (conceivably) in sexual stimulation.

Warning displays, including the ubiquitous alarm calls and postures, are the most peculiar of this group. They are usually quite distinct, morphologically; and they seem to have evolved and become ritualized for the specific "purpose" of alerting neighbors and companions to the presence of potential predators. Their motivation is similar to that of all the other displays cited above; but they represent another extreme, in the sense that the attack drive of a bird giving one of these displays is probably at an actual (and often relative) minimum. (This explains, of course, why escape intention movements are usually more important in alarm postures than in any other hostile displays, even appeasement postures.) It is perhaps remarkable, incidentally, in view of their causation, that these alarm displays are as rare during intraspecific disputes as they appear to be.

Other hostile displays, such as many passerine "songs" and their equivalents in other orders, have long been known to be important in pair-formation. The unmated females of many species seem to recognize sexually-motivated males by their performance of certain typically masculine and unmistakably hostile reactions, i.e. certain displays "advertising" the possession of territory. It is possible that these displays may also be attractive in themselves, and they may even have a positively stimulating effect upon the female sex drive; but this would seem to be unlikely on purely theoretical grounds, and such an effect, in any case, has never been proved to exist.

The most interesting aspect of these "advertising" displays, however, is the fact that they are usually displays which function as threat during fights and quarrels. They are usually, indeed, far more common as threat. This would seem to suggest that their evolution must have been controlled, primarily, by their intimidatory role, and that their role in pair-formation has been more or less definitely subsidiary.

The last group of displays includes a variety of patterns which may occur during interspecific disputes and which seem to function as interspecific signals.

Many birds may show threat toward an opponent of another species, but they have seldom evolved displays for this purpose alone. In other words, if a threat display is shown toward an opponent of another species, it is usually, apparently, one of the displays that is more frequently used to intimidate an opponent of the same species. These interspecific threats may seem to be remarkably effective; but, as they are usually interspersed with overt advance and attack movements, if is difficult to determine how much of their apparent effectiveness is due to the displays themselves.

The most elaborate forms of interspecific hostility are certain complicated predator-reactions; i.e. distraction and mobbing performances, both of which can combine unritualized attack and escape movements, apparently "extraneous" activities, and a whole series of displays (see Simmons, 1952). Most of these displays, however, with the exception of some alarm patterns (and, probably, some other less aggressive displays in distraction, which have not yet been properly analyzed), would also appear to be threat of the usual sort. They may occur in peculiar sequences and with unusual orientation in mobbing and distraction reactions; but their actual form would suggest that they too, like most of the simpler performances during interspecific disputes, were originally evolved to induce an intraspecific response.

Summary.—All intraspecific hostile displays (and probably all the interspecific hostile displays also), seem to have been evolved, originally, as social signals subserving the same general function. They enable a bird to obtain certain advantages (which may differ considerably in different species) without having to fight for them. More precisely, they enable a bird to obtain these advantages without being attacked.

Different types of hostile display can subserve this function by very different methods. The principal types of intraspecific hostile display can be most conveniently distinguished by their usual effect(s) upon the birds toward which they are directed. They can be listed as follows.

1. Threat displays. These are the commonest hostile displays. They are "designed" to intimidate an opponent, to make the opponent retreat or flee. They tend to increase both the relative and actual strength of the opponent's escape drive.

2. Exemplary displays. These seem to be much rarer than threat and have been very little studied. Their diagnostic character is their extreme infectiousness. Some of them seem to be "designed"

primarily to release a communal suppression of attack, to stimulate a communal display performance which will "dissipate" attack by an opponent.

3. Appeasement displays. These are almost as common as threat. They are "designed" to prevent attack by directly reducing the actual and relative strength of an opponent's attack drive, without provoking escape by the opponent or any general reaction by neighbors and companions.

4. Deceptive displays. These seem to be as rare as the exemplary displays, and they are also little known. They are "designed" to prevent attack by directly releasing the performance of some non-hostile activity by the opponent.

The causation of all these displays is very similar. They are produced by simultaneously activated attack and escape drives in the displaying bird (with or without the addition of other activated drives such as sex). There is reason to believe, however, that the typical combination, i.e. relative strength, of the two drives is usually different in displays of different types. Most threat, for instance, is produced by more attack motivation than escape, and most appeasement is produced by more escape motivation than attack.

The sources of many of these displays are also very similar. They have been derived from simple locomotory movements, attack movements, escape movements, "extraneous" activities, and calls, alone or in various combinations; but here again the relative importance of these elements is usually different in displays of different types.

Two further categories of hostile display are somewhat anomalous. Some hostile displays may subserve a hostile function during interspecific disputes; and others may have a non-hostile significance in certain particular intraspecific relationships at certain times. Such displays may be rather common; but it is probable that many of them, like the majority of hostile displays in general, were originally evolved to serve as stimuli during intraspecific disputes.

A final point should be emphasized in this connection. The various types of hostile display are neither absolutely incompatible nor always clearly separated. Many birds may alternate several displays very rapidly, or combine two distinctly different displays simultaneously (e.g. superimposing appeasement upon threat). Other birds may produce individual displays which combine two distinctly different functions in themselves (e.g. displays which are partly threatening and partly exemplary). The detailed implications and advantages of such complex interactions, as they occur in different species, can only be revealed by much more extensive and quantitative field studies.

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