

Messages of Vertebrate Communication

In communicating, most birds and mammals appear to use a very limited set of referents.

W. John Smith

Animals possess in their behavioral repertoires acts that have become specialized in the course of evolution to convey information and are called "displays;" these acts include postures, movements, vocalizations and other sounds, the release of volatile chemicals, and so on (1). Each species has from about 15 to 40 or 45 displays, and most displays of one species differ in form from those of another. Although certain general features of the form of displays recur with some regularity, for the most part it is difficult to establish homologies at the genus or higher taxonomic level; thus the list of different displays of animals is very long. Yet it is beginning to appear that the "messages" of displays [the "messages" are the information carried (2)] are not nearly so diverse or numerous as the displays themselves. All birds and mammals, and perhaps other vertebrates, may encode as messages selections from the same small set of referent classes. I propose here a list that could include most or all of the messages conveyed by nonlinguistic vertebrates (that is, vertebrates other than man) with social patterns of more than minimal complexity. I suggest why the total set is small, and what circumstances may foster the evolution of displays carrying exceptional messages.

Displays do not resemble the words of our languages, and the messages of displays are not closely similar to the referents of most words. Most display messages make the behavior of the communicator to some degree more predictable by the recipient of the message. The information conveyed probably permits the recipient to select ap-

propriate behavior. But natural selection can have acted only if the response to the message conveyed meets the needs not only of the recipient but of the communicator as well.

Not surprisingly, it is not always easy for us to deduce what the messages of a given display are. Consider a vocal display of a small North American bird, the eastern phoebe (3). This brief call sounds like "twh-t" and is uttered in several different sorts of situations: by unmated males while foraging alone and patrolling their newly defined territories, early in the spring; by mated males just after singing in the predawn twilight, in the period in which their rather aggressive mates approach and sometimes permit copulation; by a male warily associating with his mate, if one of his foraging flights should take him close to her; by either member of a pair, when watching a potential predator in the vicinity of the nest; and by a male following a defeated intruder from his territory. In this variety of circumstances there is one important consistency about the way in which the call is used: It almost always comes just as the bird alights, or when it appears hesitant about continuing its flight. But the call is not associated with all flights. For instance, a great many flights are simply ordinary foraging flights, and on these the bird is silent. Because of the broad range of situations in which the call is made, we cannot conclude that any particular motivation, excitatory or inhibitory, is always present. Without seeing the bird we can know only (i) that it is hesitant about flying and (ii) that it is an eastern phoebe, since the form of the display is species-specific.

Many other birds have displays with patterns of use quite similar to that of the "twh-t" display. This leads us to sus-

pect that information about the probability of locomotion is important to these birds. When one considers the circumstances under which the displays are used and the kinds of contextual information (2, 4) that is available to recipients, one readily sees why the information is valuable. For instance, only unmated, territorial phoebes do much flying and stopping along an extensive perimeter in early spring. They are hard to see, but newly arrived migrant female phoebes could easily locate them by their calls. A phoebe uttering the "twh-t" call in the nest area is upset by a potential danger to the nest, and if the mate is aware of this and comes, the two of them may be able to harry and drive off the predator. In each context, the information that the communicator may or may not cease flying indicates a certain type of situation.

The search for a general set of messages entails comparison of the display repertoires of animals with similar and different social behaviors, since the display repertoire, and the use made of it, in any species presumably evolves to facilitate social behavior, and social behavior in different species involves different forms of pair-bonding, of flocking, of seasonal changes, and so forth. Further, since it is not obvious that all species must solve their problems of communication in the same ways, a range of comparisons over different phylogenetic distances is required. Finally, the different sound environments, habitats, and other ecological factors associated with different species influence some aspects of the evolution of displays and must be taken into account in studying messages. In a large number of species of the same family as the phoebe (Tyrannidae), the messages of displays have now been studied (5), although not all the analyses have been completed. The large size and unusual diversity of this family makes it especially suited for such comparisons. Outside this family, analysis of displays for message content has so far been completed for only one species, the winter-flocking Carolina chickadee (6), but work on bird species in three other families is in progress. In mammals, studies of the displays of captive prairie dogs and young captive gorillas are being made (7).

This comparative base is still weak, and the provisional list of messages given here is more a progress report than a confident statement. Changes in

The author is associate professor of biology at the University of Pennsylvania, Philadelphia. An earlier version of this article was presented 28 December 1967 at the New York meeting of the AAAS.

the list will be required, but some clear trends have emerged. Some difficulties remain—that of ensuring the comparability of messages found in the course of the comparative studies, and that of matching these messages with messages derived from communication studies reported in the literature. Moreover, the complete range of uses of a display must usually be known before the messages the display carries can be determined, and learning this range is difficult in the field and perhaps impossible for animals in captivity. Further, it often appears necessary to isolate small details of behavior, like the correlation of a phoebe's "twh-t" with the act of alighting. Since most studies reported in the literature were designed for purposes other than that of developing a comparative list of messages, the data reported are necessarily incomplete and must always be reinterpreted. For present purposes I have limited my use of the literature to some particularly detailed examples.

The Message Set

When we speak of the messages of a display we mean the information available to an individual as a result of having received just the display; all other sources of information are considered contextual. The messages, it is believed, specify or predict classes of activities that the communicator may perform at about the time of displaying, or specify a probable change in his activities. Because most messages indicate some selection within the behavioral repertoire of the communicator, an investigator recognizes each message by the particular class of behavior consistently correlated with the displays that encode it. The remaining messages are effectively modifiers, and every display encodes two modifiers plus one or more of the other messages.

1) *Identification*. The identification message is a modifying message, specifying the categories or classes to which the communicator belongs and the behavioral repertoires of members of these classes. In some extreme cases, like that of the convergent vocalizations often called predator alarm calls, a class may be definable only as, say, small birds. At the other extreme is the class represented by one individual. The most common classes are probably species, sex, maturity, and one individual.

Any act within a particular reper-

toire will be performed in a fashion typical of, or at least possible for, a member of the class having that repertoire. Furthermore, once a communicator is identified, the classes of individuals with which he is prepared to interact socially is known, so the identification message facilitates what Marler (8) has called the specification (that is, selection) of recipients.

We recognize identification messages by comparing the form of the displays of communicators belonging to different communicator classes. It is assumed that the behavior typical of each communicator class will be in some senses unique. Actually, comparing in detail the behaviors typical of these communicator classes would be very tedious, although comparable with the methods used to determine other messages.

No display encodes only identification, but the identification message is present in all displays. Because of its universality, usually I do not mention it here in giving examples of displays to illustrate the encoding of other messages.

2) *Probability*. The probability of occurrence of each behavioral act specified by a display is indicated in the display. These indications yield the relative probabilities of occurrence of the acts predicted by a single display, and also the relative probabilities of occurrence of acts predicted by different displays that carry similar messages. For instance, when a greenbacked sparrow, *Arremonops conirostris*, uses the "chuck notes" display, attack is less probable than escape; when the sparrow uses the "medium hoarse notes" display, attack is as probable as escape (9); and when it uses the "hoarse scream" display, attack and escape are, again, equally probable, and more probable than they are when the sparrow utters the "medium hoarse notes." In this example, three different displays combine the same attack and escape messages with different probability information. In other species the form of a display may be varied to indicate changing probabilities. For instance, as the "repeated vocalization" of the eastern kingbird gets harsher, attack becomes more probable (5), whereas a rise in pitch in the cawing of a rook, *Corvus frugilegus*, correlates with increasing probability of escape behavior (10).

Finally, some displays are not graded and indicate only a range of probabilities; a recipient then needs contextual

sources as an aid in predicting relative probabilities. Contextual sources include the manner of displaying: for example, an alteration in the rate of repetition of the display (11).

3) *General set*. Many species have one or two displays which are used in association with a number of different activities that range from maintenance activities (foraging, preening, resting, and so on) to most social activities, and which appear, therefore, to refer unselectively to the whole set of behavior patterns in the species' repertoire. For example, the "tsit" display of tanagers (of the genus *Chlorospingus*) is used at all seasons, by birds of both sexes; the communicator may be "performing any type of locomotory or prelocomotory movements, or sitting or standing in almost any type of unritualized posture" (12). The very fact that such displays are used so widely and so abundantly makes the gathering of sufficient quantitative data on their occurrence or absence in association with different acts and in different situations very time-consuming, and none of these displays has as yet been fully studied. Although present evidence about the message implies a lack of information permitting prediction of which act the communicator will select within its general set of acts, further research will probably show the message to be somewhat less broad than it seems. One possibility, for instance, is that the message specifies that a change in the type of the communicator's activity is likely. In addition, the message may always be combined with modifiers indicating probability; for example, the "tsit" mentioned above is rarely used by solitary tanagers and indicates that association behavior is probable, relative to other possibilities.

The general-set message is sometimes encoded in displays together with another, more selective message. Examples are given under the headings "Locomotion" and "Escape."

4) *Locomotion*. Some displays are used only during locomotion, or at the beginning or end of locomotion. The function of the locomotion is largely irrelevant; it may be foraging, patrolling, following a mate or parent or flock member, avoiding, attacking, chasing, fleeing, and so on. In well-understood cases there is usually indication that displays are also associated with behavior conflicting with the initial locomotory behavior. Such displays usually come primarily at the end of locomotion.

tion (when the bird alights and sings, eats, or does something else which requires perching) or during slowing or turning, as described above for the "twh-t" of the eastern phoebe. In cases of slowing or turning, the conflicting behavior may itself be locomotory, with orientation opposed to that of the initial locomotion. (Examples are a bird's approach to copulate as opposed to its flight to escape; its following of a mate as opposed to its return to the nest.) Three vocalizations described by Smith (6) for the Carolina chickadee can be ranked in order of descending probability of correlation with flight and in order of increasing probability of correlation with other behavior; "high tee" is usually uttered in flight or, less often, during rapid pivoting on a perch; "chick" is uttered on alighting or during rare, extraordinarily erratic flight; and "dee" is usually uttered from a perch, often immediately after alighting. (The three vocalizations often occur in succession as a bird is alighting, and constitute the sound commonly called "chickadee.")

Typical of these "locomotory hesitance" displays is the fact that the function of the associated locomotion and of the behavior in conflict with the initial locomotion differs in different usages. Thus, in these displays a locomotory message is compounded with the general-set message. (If the chickadee's "high-tee" can be shown to have an escape message, it will have to be reclassified.)

Many displays reported in the literature may be locomotory hesitance displays or may encode only locomotory messages. Moynihan (12) described wing-flicking and tail-flicking displays of tanagers (of the genus *Chlorospingus*) which are restricted to pre-flight situations in which the probability of the bird's taking flight is usually increasing (13). Blurton Jones (14) says that "the Canada Goose seems to have . . . special calls given whenever locomotion (to whatever purpose) is blocked." In other cases, while both locomotory and other behavioral possibilities are typically associated with most presentations of a display, sometimes there may not be conflicting possibilities. For example, the "tit flight-call" of buntings (15) and the "flight call" of the chaffinch (16) are both used in flight, even though they are more commonly used on taking flight. Night monkeys use "gulps" and "sneeze-grunts" displays throughout periods when they are very active (17). Perhaps

the situations in which such calls are made during locomotion have not yet been examined in sufficient detail to rule out the possibility that these are locomotory hesitance displays, or perhaps locomotory behavior may be specified in the absence of opposing behavioral possibilities. In either case, the message does not indicate a very narrow selection of possible communicator behavior.

5) *Attack*. Of the various acts more closely specified than locomotion, the most common are probably agonistic or hostile acts, a class comprising attack, escape, and ambivalent behavior when both attack and escape are possible. The attack message is encoded when the communicator is attacking or is making "intention movements" toward an object or other animal which are sometimes followed by attack. (Ethologists refer to movements that appear to be incomplete forms of other, identifiable movements of any sort—for example, flight, striking, nest-building, and so forth—as "intention movements." The term is misleading; it is intended to be simply descriptive and not to imply that a motivational analysis has been made.) Both attack and escape messages are commonly encoded in the same display.

6) *Escape*. A display used when a communicator is escaping, is gradually withdrawing, or is making oriented movements away from an aversive stimulus carries an escape message. Often the probability of other acts nearly balances the probability of escape in the case of a particular display, and this near-balance leads to observed behavior that satisfies the criteria for locomotory hesitance except for the fact that escape per se is always specified as one of the alternatives. For example, the "jump-yip" display of black-tailed prairie dogs occurs when attack, nonaggressive social behavior, or maintenance activity is likely to be interrupted or prevented by escape behavior. The display is usually used just as the prairie dog stops running or just as he appears to be about to start, or about to emerge from a burrow (7). It thus carries the general-set and escape messages, with relative probabilities of occurrence nearly equal for the two.

7) *Nonagonistic subset*. A nonagonistic subset is a large subset within the general set of behavior. It is not uncommon for a display to carry both the nonagonistic subset message and an escape message. The "tseet" call of the Carolina chickadee (6) is given in a

variety of circumstances—when the communicator may flee or withdraw, may associate with a flock mate, forage, continue eating, and so on, but will not attack. I once viewed messages of this sort as a distinct category—*anxiety messages* (5). I now believe anxiety messages to be simply a compound of weak escape messages and this message specifying a wide range of other, nonagonistic acts.

8) *Association*. Some displays occur when one individual associates with another by approaching and remaining near (but not attempting to make contact) while at the same time avoiding approaches made by the other (but not escaping from it). Or the communicator may passively permit another individual to approach. The association message is carried by the "chatter vocalization" of most tyrannid species studied, but apparently usually in combination with another message indicating that the association is directed only toward mates. The "lispering tee" display of the Carolina chickadee is used by birds associating with mates, families, or members of foraging flocks (6).

The complex "jingle vocalization" of the spice finch (18) appears to carry an association message. The call is used by a male separated from his companion or companions, or clumped with companions but separated from his mate. Sometimes a lone "jingling" bird is approached by another spice finch. He continues to "jingle" only so long as he remains perched, and he tries to avoid letting the other bird initiate contact behavior. Finally, a male will "jingle" before mounting his mate for copulation, but he always remains beside her while using this display and mounts after completing a "jingle." In all these remarkably varied usages the communicator lacks, avoids, or delays some form of contact with an individual of the same species.

Some birds belonging to the order Galliformes have an array of intergrading vocal displays best known for their occurrence in a social activity called "tidbitting" (19). In the chukar partridge three vocal displays are recognized, the most variable of which (the "food call," which is not restricted to events involving food) overlaps the other two in form. It appears to encode association and general set messages, being used by a male associating with another male in an agonistic encounter, or used in various encounters between a male and a female, or by a bird showing novel food to other birds

of particular classes. The remaining two vocal displays of the chukar partridge are discussed below.

9) *Bond-limited subset*. The bond-limited subset of the behavioral repertoire comprises acts occurring between mates, between parents and offspring, and among members of larger organized groups, which are permitted because of the persistent behavioral convention that I call a "bond." The behavior included in this convention is behavior that fosters cohesion between individuals. Different species have different social relationships, but in general the bond-limited subset includes association, grooming of other individuals, huddling, caring for others (that is, feeding them, guarding them), copulation, and the like. As a message category, this subset is poorly understood and may be an artifact of the current inadequacy of our understanding of some displays. For instance, the message sometimes refers to the probability of occurrence of some act in the subset and at other times it seems to be only a modifier of a narrower message—such as association.

There are displays, like the courtship calls of the chaffinch (16), which appear to be largely mate-oriented and more or less restricted to the period of what is usually called "courtship" behavior (20). This period is characterized primarily by mate association, and perhaps some such displays carry only association messages. Most are clearly not associated solely with copulation or with precopulatory behavior, although they are often called "sexual." Many genera of tyrannid flycatchers have a "chatter vocalization" and a visible "nest-site-showing" display in which there is often ritualized nest-building behavior (3, 5). Communicators associate with other birds when using this display, or remain at a site and permit association if the partner appears. A closely similar vocalization is found in galliforms as one of the three displays of the "tidbitting" group of displays; this vocalization is associated with a nest-building display, under circumstances similar to those observed for tyrannids. In fact, such calls (usually staccato series) and nest displays are unusually widespread in birds and occur in several families.

In addition, there are displays that appear to encode a similar sort of message, are used within a larger, bonded group, and are not restricted to a "courtship" period. Grooming of other

individuals is seen in many social birds and mammals (21) and is usually considered to be at least partially a display. Such allogrooming is apparently limited to individuals who recognize each other; it reduces agonistic acts within the groups, and it may indicate a probability that the communicators will select further behavior from a bond-limited subset of behavioral acts. It apparently does not help create or reinforce status distinctions, but minimizes the potentially adverse effects of such distinctions.

10) *Play*. It is apparent that, among bonded individuals, various nonaggressive contact activities are often initiated and sustained with little or no displaying (22). However, displays associated only with play are known, especially in primates. Most resemble in form a parody of elements of non-play fighting. Among the best understood is the "relaxed open-mouth face" display (23). Other primarily facial displays, often called play signals (for example, laughter), usually occur in various non-play situations as well.

11) *Copulation*. Displays used only before or during copulation occur in a number of species, although apparently not in tyrannid flycatchers or chickadees. The chaffinch, for instance, has a special variant of song—"congested song"—associated with copulation (16), and a male chukar partridge running to mount a female uses a "copulation-intention call" display (19). This call is the third of the "tidbitting" group of vocalizations mentioned above; the three appear to encode, respectively, association, the bond-limited message, and the copulation message. Perhaps the copulation message is characteristically encoded in displays that are relatively minor variants of other displays, the responses to which would not be entirely inappropriate should a recipient fail to distinguish correctly.

12) *Frustration*. Some displays are used only when some particular behavior would occur if the opportunity were available, or when the opportunity for a particular behavior that has been occurring has gone (24). The substituted behavior differs from case to case, although it often shows orientation components related to the pattern of the behavior that is not possible. The substitute may be a display, or it may be accompanied by a display, and one message of such a display is taken to be "frustration." Because frustration cannot be recognized except in rela-

tion to the frustrated behavioral possibility, the message must be combined with at least one other message.

Displays encoding frustrated escape are used when the communicator is trapped or cornered. Screams occasionally heard from a prey animal held by a predator, or by birds caught in mist nets (nets woven of very fine threads) are probably good examples. And animals often "freeze" in stereotyped poses when they are cornered by dominant individuals. The distinctive "cowering" posture of gorillas appears to be a display of this sort. According to Schaller (25), this posture is assumed by individuals "attempting to escape the slap of displaying males" or behaving submissively, and by a small infant terminating vigorous play with a larger infant. A young gorilla in the Philadelphia Zoo "cowered" after escaping from her cage into a hallway; she then responded with infantile clinging when picked up. The younger of the zoo's two males was once attacked by the older while mounting the latter's female cage-mate. He quickly dismounted and "cowered" (7). Similar cowering displays occur in many other species; for example, a gull too young to fly and under vigorous pecking attack from an older gull may alternate escape behavior and the "bill-down crouch" posture (26).

There are also displays that encode the message combination "frustrated attack." Kingbirds have a "tumble flight" display (5) used primarily by territorial males, usually in the absence of an appropriate opponent (that is, an opponent visible and within the territory). The "swoop and soar" display of the black-headed gull is probably closely similar (27). Two displays of male parrots of the genus *Agapornis* appear to encode "frustrated copulation" messages (28). Several species of New World songbirds of the genera *Arremonops* (9), *Ramphocelus* (29), and *Chlorospingus* (12) have "plaintive notes" displays which appear to encode "frustrated association" messages. Probably other messages are combined with the "frustration" message in the displays of some species.

Why There Are Few Messages

These 12 message categories are all I have identified as yet, and it seems likely that not many more will be found. If this is the case, then a very

few messages have a great deal of work to do in facilitating social interactions.

Of course, the fact that messages are combined in many ways in different displays, and that one of the messages in each display is a probability modifier, is important. Different species use different combinations of messages and specify different probabilities in coping with their species-specific problems. Yet 12 messages, two of them (identification and probability) modifiers of the other ten, constitute a very small set.

Interestingly, within any one species the number of displays is also quite small—usually between 15 and 45, when all modes of displaying, in all of the species so far studied, are counted. In some species there is much intergrading of displays, but even when allowance is made for personal preferences in splitting up such continua, one can rarely recognize more than about 50 displays and functionally similar activities of different evolutionary status. Although there is not a one-to-one correspondence between the number of messages and the number of displays, the latter is only slightly larger.

It is not clear why each species has so few displays. One plausible explanation is that displays must be sufficiently distinct from one another to be recognizable by the recipient. Since the number of ways of producing displays is limited, there must be limits on the range of forms the displays can take. But there is little reason to think that selection acting to keep displays distinct would set as low a limit as we find. Moynihan (30) has argued that limitations on the acceptable range of elaboration, and on the frequency of occurrence of the rarer displays, will also act to limit the number of displays.

Whatever the evolutionary explanation of the small number of displays per species, there are clearly more functions served by displaying than there are displays. This augmentation of function appears to result from the use of most displays under more than one set of circumstances. That is, vertebrate communication appears to require extensive use of contextual information by the recipient of a display. Most of the 12 message categories listed above are broad, and probably the recipient must depend heavily on context if he is to make appropriate responses. Contextual information

greatly extends the set of events concerning which there can be communication by means of displays (31).

It is not clear whether the small number of displays per species is the cause of the small number of messages or its result, or whether both have some other cause. However, in most arguments about the small size of specific display repertoires the number of available messages is not seen as limiting. Probably it is the converse that is true: because each species can have few displays, natural selection has favored the messages which can be used most broadly (that is, in the greatest number of contexts) and which can thus generate the maximum number of different responses. Of the messages that could evolve, those that can be used very broadly are probably rare, so it is not surprising that we have as yet empirically demonstrated only 12, and it would not be surprising if we were to find only a few more.

Circumstances Fostering Exceptional Messages

Again, the basic assumptions of this article are (i) that each message must do a great deal of work and serve in the maximum number of contexts because the number of available displays in the repertoire of any species is severely limited, and (ii) that much communication is more effective (more free of errors) when signaling is stylized. Examination of these assumptions leads to the prediction of other possibilities in certain cases.

1) Context-dependent messages may not always provide sufficiently unambiguous information, and evolution of the display repertoire may favor the inclusion of more precise messages ("exceptional messages") to elicit a particular response in the shortest possible time. It might, for instance, sometimes be very difficult for an animal to initiate play-fighting if the recipient of the message could not determine whether or not the first animal's approach was attack. For the same reason it might be difficult for an animal to initiate mounting for copulation, the other case for which a specific message is clearly known. There are other possibilities. Many highly social animals may be gregarious in part because the group provides them with an efficient predator-detection device, and a relatively finely divided set of messages

about escape probabilities would have a high selective value in the evolution of the display repertoire. In any case in which a message is precise, however, the precision is achieved at the cost of tying up one of the few displays available to the species.

2) Certain circumstances limit, sometimes severely, the availability of contextual information. For instance, much contextual information is obtained visually, and a recipient belonging to a nocturnal species has a relatively context-poor environment; such a recipient may need relatively precise messages.

3) There may be ways of circumventing the size limitations of the display repertoire—ways other than communication through human speech. Two displays may be used in such a way as to provide contexts for each other and thus modify each other's messages, but such modification seems to be primarily modification of the probability message (32). It appears that new classes of messages are not generated by this technique. In two cases cited above, however (the galliform "tidbitting" group of vocalizations and the song and "congested song" of the chaffinch), new messages were encoded in minor variants of a display that encoded a broad, context-dependent message. In both cases the new message was copulation, a particular nonattack contact message with a very restricted range of usage; in both cases the new message was encoded by a variant of a display which encoded an "association" or "bond-limited" message. Adding a new message to the repertoire through minor variation of a display is perhaps the communicator's only economical way of encoding a message that is so narrowly defined as to be nearly independent of context. The risk that the recipient will fail to distinguish between the original display and its variant is relatively high, but when the responses to the message carried by the original display and that carried by the variant are sufficiently compatible as to make such failure of little significance, the display repertoire may evolve to include the variant.

4) Finally, there are species in which the number of types of social interaction is so limited that the display repertoire includes fewer displays than are potentially available, and each display may then be very specific. One would expect this to be the case in

many nocturnal, nonterritorial frogs. Even the bullfrog, however, uses at least some of its approximately six vocalizations in more than one context (33).

It is difficult to make an a priori evaluation of the extent to which these potential sources of exceptional messages are operative. Empirically, however, it appears that very precise messages are few in number and even totally lacking from the displays of many birds and mammals, and that even nocturnal species use many displays in more than one context. Assessment of the use of minor display variants is a fairly difficult problem, as is the detailed study of relatively asocial animals. Nonetheless, it does seem that the basic list of message classes given above, or some list that is similar to it in many respects, is likely to be very generally representative. If it is, then there are broad implications both for the evolution of patterns of communication (including at least the origins of language) and for the evolution of social systems.

References and Notes

1. M. H. Moynihan, *Proc. Int. Ornithol. Congr. 12th* (1960), pp. 523-541.
2. W. J. Smith, *Amer. Naturalist* 99, 405 (1965).
3. ———, *Behaviour*, in press.
4. ———, *Amer. Naturalist* 97, 117 (1963); ———, in *Animal Communication*, T. A. Sebeok, Ed. (Univ. of Indiana Press, Bloomington, 1968).
5. ———, "Communication and Relationships in the Genus *Tyrannus*," *Nuttall Ornithol. Club, Cambridge, Mass., Pub.* 6 (1966), pp. 1-250.
6. S. T. Smith, thesis, Harvard University (1968).
7. The studies of captive mammals are being made at the Philadelphia Zoo by me and the following members of my group: S. L. Smith, L. Oppenheimer, and J. G. deVila (prairie dog studies); A. Maizel (gorilla studies). I am making additional studies of infant mammals with C. Ristau and studies of abnormal displaying with M. Bernstein. The types of overt behavior observed in these latter studies present special problems which are not dealt with here.
8. P. Marler, *Science* 157, 769 (1967).
9. M. H. Moynihan, *Auk* 80, 116 (1963).
10. C. J. F. Coombs, *Ibis* 102, 394 (1960).
11. For a discussion of grading, see M. Konishi, *Z. Tierpsychol.* 20, 349 (1963).
12. M. H. Moynihan, *Auk* 79, 310 (1962).
13. Movements, such as these flickings of wing and tail, which resemble postures or movements representative of the acts of taking flight or landing are common in displays [see A. Daanje, *Behaviour* 3, 48 (1951)]. The form alone, however, does not necessarily indicate that a locomotory message is encoded by the display.
14. N. G. Blurton Jones, *Wildfowl Trust Ann. Rep. 11th* (1960), pp. 46-52.
15. R. J. Andrew, *Ibis* 99, 27 (1957).
16. P. Marler, *ibid.* 98, 231 (1956); ———, *Behaviour* (Suppl.) 5, 1 (1956).
17. M. H. Moynihan, *Smithsonian Inst. Misc. Collections* 146, No. 5, 1 (1964).
18. ——— and M. F. Hall, *Behaviour* 7, 33 (1954).
19. A. W. Stokes, *Condor* 63, 111 (1961); ———, *Animal Behaviour* 11, 121 (1963); ———, *Auk* 84, 1 (1967); H. W. Williams, A. W. Stokes, J. C. Wallen, *ibid.* 85, 464 (1968).
20. D. Morris, in *L'instinct dans le comportement des animaux et de l'homme*, M. Auriol, Ed. (Masson, Paris, 1956).
21. J. Sparks, in *Primate Ethology*, D. Morris, Ed. (Morrison and Gibb, London, 1967), pp. 148-175.
22. There may or may not be a message specifying the general subset of nonattack contact behavior patterns. And although there are some narrowly predictive messages each specifying the probability of only one type of contact, these appear to be few and rarely encoded. In addition to play and copulation messages, some authors have proposed food-finding or food-giving messages. Acts, like allogrooming, which are only partly displays remain hard to interpret. Some other iconic gestures (that is, gestures resembling acts that have functions other than communication) may or may not be displays. For further discussion of these gestures, see W. J. Smith, *Semiotica*, in press.
23. J. A. R. A. M. van Hoof, in *Primate Ethology*, D. Morris, Ed. (Morrison and Gibb, London, 1967), pp. 7-68.
24. These are two of the three criteria for motivational thwarting proposed by D. Morris [*Behaviour* 9, 75 (1956)].
25. G. B. Schaller, *The Mountain Gorilla* (Univ. of Chicago Press, Chicago, 1963), pp. 1-431.
26. M. H. Moynihan, *Behaviour* 14, 214 (1959).
27. This display has been studied by M. H. Moynihan [*Behaviour* (Suppl.) 4, 1 (1955)] and G. H. Manley [*Ardea* 48, 37 (1960)]. The greeting ceremony which usually precedes this aerial display appears to Moynihan and to me to contain many real attack components; Manley feels that intra-pair hostility "may be more apparent than real."
28. W. C. Dilger, *Z. Tierpsychol.* 17, 649 (1960).
29. M. H. Moynihan, *Auk* 79, 655 (1962).
30. ———, in preparation.
31. Apart from its use in specialized communication, contextual information has been shown to be of profound importance in modifying the response of monkeys to all sorts of stimuli [see E. W. Menzel, in *Naturalistic Viewpoints in Psychological Research*, E. P. Willems and H. L. Rausch, Eds. (Holt, Rinehart and Winston, New York, 1969)].
32. See, for example, the modification of the "regularly repeated vocalization" display of the eastern phoebe by changes in the relative numbers of the display's two components (W. J. Smith, *Behaviour*, in press) or the hostile displays of the green-backed sparrow [M. H. Moynihan, *Auk* 80, 116 (1963)].
33. R. R. Capranica, *MIT (Mass. Inst. Technol.) Press Res. Monogr.* 33, 1 (1965).
34. This study is based on research done under the following grants: National Science Foundation grants G19261, GB2904, and GB6108; Air Force Office of Scientific Research grant F-44620-67-0057; and National Institutes of Health grant FR-07083-01. I thank S. T. Smith, C. Snowdon, and D. L. Anderson for criticizing the manuscript.

Science and Social Attitudes

Growing doubts require that science be put more recognizably at the service of man.

Robert S. Morison

Like all people with some scientific training, I suffer from feelings of unease when attempting to deal with the actions, and especially the attitudes, of people. For one thing, I do not have at my command the sampling and interview techniques wielded with so much aplomb by my colleagues in the social sciences. Fortunately for my own piece of mind, my scientific training was accompanied by enough exposure to the art of medi-

cine so that I retain considerable respect for clinical intuition and judgment. This discussion relies much more on these elusive instruments than it does on quantitative scientific analysis.

As a matter of fact, it puts no great strain on one's clinical intuition to observe that large numbers of people in various parts of the world—including, perhaps most significantly, the advanced parts—are less happy about science and

technology than they once were. The evidence is of various kinds. Perhaps the most quantitative is provided in the United States by the relative decline in students entering the sciences and the scientifically based professions. In some instances, such as engineering, the numbers have fallen absolutely in the face of a steady increase in the total number of potential students in each age class. Even more quantitative, and certainly more compelling to the individual scientist, is the evidence provided by the slowdown in appropriations for science. Third, one may cite the intuitions and reflections of thoughtful social clinicians like René Dubos (1), who has so courageously summarized the shortcomings of scientific approaches to human problems. True enough, he finally draws the con-

The author is director of the division of biological sciences, Cornell University, Ithaca, New York. This article is adapted from an address presented at a conference on "Science and the Future," held in Boulder, Colorado, from 13 to 19 April under the joint sponsorship of the British Association for the Advancement of Science and the AAAS.