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Source: *Science*, New Series, Vol. 157, No. 3790 (Aug. 18, 1967), pp. 769-774
Published by: American Association for the Advancement of Science
Stable URL: http://www.jstor.org/stable/1721361
Accessed: 07/04/2010 01:33

Animal Communication Signals

We are beginning to understand how the structure of
animal signals relates to the function they serve.

Peter Marler

Central to the notion of communication is the reception of information through a stimulus that an organism perceives from the external environment. As the sole basis for a definition of communication, however, the occurrence of such information transfer is unsuitable, for the whole subject of exteroception is potentially included. It is not easy to narrow the definition to exclude stimulus reception from the physical environment while still encompassing the kinds of behavioral exchanges that the biologist intuitively accepts as communicative. Is the mouse rustling in the grass communicating with the owl that hunts for it? Clearly not, for mice have undoubtedly been selected for avoidance of emission of stimuli that a predator might detect. To restrict the definition to intraspecific stimulus exchanges is no solution, for communicative relationships sometimes exist between species which have evolved in symbiosis, such as pollinating insects and flowering plants. There may not be much point or profit in pursuing an exclusive definition, but the essence seems to lie in the evolution of synergistic interplay between participants, both of which are committed to maximizing the efficiency of interchange. Such relationships can arise across species boundaries, but more characteristically they involve members of the same species.

There is great difference between setting out to understand a new language and embarking on an analysis of nonhuman communication. With animals, there is no choice but to approach the analysis as a nonparticipant. In this circumstance, clues to the occurrence of communication between two animals

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must be found in changes in the behavior of one upon its perception of a signal from the other. This is the essence of the pragmatic approach to the analysis of the human language, and methods of C. W. Morris (1), for example, can be adapted to considerations of animal communication in comparable terms (2). On the other hand, to force systems of animal communication into functional categories designed for human language detracts from the subtlety of the realtionships between structure and function in animal signals. What alternative approaches are there?

With the response elicited by a signal as the point of departure, several questions can be asked. The first concerns an issue vital to almost all animal communication, but an issue which rarely arises in discussions of human language: Is the response to the signal spatially oriented to the signal source? A basic function of many animal signals is to help individuals locate or avoid each other. Even such elementary functions as these can have profound implications for signal structure.

Second, we can ask: What pattern of behavior does the signal elicit in the recipient? Answers to this question, which are in fact estimates of the probability that the behavior will change in certain directions, will specify the type of response pattern evoked, whether sexual, aggressive, parental, and so on.

Further understanding of the communicative process is possible if we have an independent answer to another question: In what other kinds of stimulus situations do the same responses recur? From this information, we can draw inferences about the kind of situation that the signal represents to the recipient. Only in this way can we determine whether symbolic representa-

tion plays any part in animal communication.

As a fourth question, we may ask: Are there correlations between variation in properties of the signal and variation in the patterns of response elicited? We hope to determine whether the relationship between signal and response is of an all-or-nothing nature or whether the signal and response are related in a more complex way.

Finally there is a special interest in knowing whether some particular part or property of a signal is responsible for evoking a given response. Knowledge of the minimal unit necessary for effective communication can lead to further search for possible recombination of such elements to elicit other responses in the recipient. Such recombination could provide evidence for the occurrence in animals of that attribute most distinctive of man, an ability to make grammatical rearrangements of signals to generate new messages, with new meanings.

Orientation to the Signaler

To what extent does the function of enabling respondents to localize a signaling animal require a particular type of signal structure? With sounds, some general predictions are possible. Certain sounds are readily located, while others have a ventriloquial property. Birds and mammals rely mainly on binaural detection of differences of intensity, phase, and time of arrival for the localization of a source of sound. Whenever circumstances permit, these animals probably use all three methods, and localization will be most efficient when a sound provides cues for all of them. Localization by means of differences in intensity is most efficient with high-frequency sounds, particularly when wavelengths are shorter than the width of the head and when the sound-shadowing effect of the head is maximum. Conversely, localization by means of phase is most efficient with low frequencies, when wavelengths are longer than the distance between the ears. For localization by means of differences in time there must be transient frequencies and abrupt discontinuities, the timing of which can be compared at the two ears. For the ease of localization by an avian or mammalian respondent to be maximum, a signal should include cues for all three methods. That

is, the sounds should be broken and repetitive, with a wide range of frequencies—properties shared by most animal sounds.

What of the converse possibility, that the localization of a signal might be a disadvantage in some situations? Such is the case with certain alarm calls used by small birds in the presence of a hunting hawk. Here, sound production may place the signaler in great danger by enabling the predator to locate the signaler. If a sound could be produced that is hard to locate, the danger to the signaler would be minimized, and at least something would be added to the chances of the other birds' escaping. One can, in fact, design such a sound. It is a pure tone, fading in and fading out, with no transients or discontinuities. It is pitched at an intermediate frequency, between the optima for localization by differences in phase and intensity. A number of small bird species have evolved sounds of this type, which are given in response to a hawk overhead. The sounds do indeed have a ventriloquial property for the human observer (3). Thus, if the function of a sound signal includes the facilitation or hindrance of localization, this inclusion will be reflected in the kind of signal structure that natural selection is likely to favor.

The properties of chemical signals or "pheromones" also affect the ease with which their source can be localized. At a distance, the direction of movement of the medium, a breeze or a water current, is the only cue. It takes time for such signals as the sex attractants of female moths to be transmitted to the distances over which they must function. The substance used must, therefore, be durable. At close range, the concentration gradient created as a signal diffuses away from the source can be used for orientation. Here, a substance with a rather durable effect could be a disadvantage if there is any possibility of the signal accumulating around the source. The alarm signals of ants function at close range and serve to orient respondents to the source of the signal. Unlike pheromones used as sex attractants, the alarm substance of the fire ant, for example, is highly volatile and ceases to elicit a response after about 35 seconds. But while it is active it creates a steep concentration gradient and thus facilitates the location of danger by other ants. For chemical communica-

tion of location over distances to be achieved without reliance on movement of the surrounding medium, a trail can be laid, a method extensively exploited by ants and bees (4). Selection for efficient performance of the function of localization brings forth structural modifications of both sound and chemical signals.

With visual signals, perception of the source is direct and there is less need for the signal itself to have special characteristics that permit localization. Except for species with the most primitive light receptors, an animal can hardly detect a visual signal without at the same time getting a fair idea of its source. Of course, the eye must be pointing correctly in the first place. One of the great advantages of simultaneous visual and auditory signaling is that the acoustical cues permit approximate localization, while with subsequent scanning movements in that direction the respondent can accurately localize the source visually.

Response Elicited by a Signal

The importance of communication signals in the orientation of the behavior of members of a community one to another is relevant when we proceed to analyze the elicited responses. The ultimate consequences of a respondent's receiving a given signal at a distance may be a specific, qualitative change in behavior, but the first response that the human observer can detect is often merely a change in the respondent's spatial relationship to the signaler. Thus, two signals that eventually elicit very different responses (such as attack or copulation) may first elicit responses that are indistinguishable (that is, approach to the signaler). Sometimes the change of orientation is accompanied by other motor activities that allow the observer to predict the final consequence: an aggressive approach may be distinguishable from a sexual approach. Often additional cues are lacking, and the human observer may have difficulty in predicting what the consequences of a change in spatial orientation of receiver to signaler may be. One reason for this lack of predictability is that the behavior of the receiver is sometimes further determined by stimuli received after the reorientation is accomplished. The consequences of an aggressive approach, for example,

may vary according to further signals, perhaps elicited by the change of relative position (5).

Movement oriented by reference to the signaler's position might take a respondent closer or farther away. Both alternatives can occur in exchanges of threat signals for example. Another effect might be that the respondent would maintain a stable distance that could be adjusted if the signaler changed position. Some of the sounds used by groups of foraging primates probably have this effect (6). The signaler can orient the response of the receiver in yet another way that we can illustrate by the behavior of baboons. A sentinel male observing certain predators gives a distinctive two-phase bark (7). The first response of other baboons is usually to look at the signaler, who continues to watch the predator continuously or intermittently. They observe the direction of his gaze, look the same way, and may then move in the direction indicated by the signaler's head. Thus the respondent's behavior is oriented by secondary orientation cues provided by the signaler, these being analogous to human pointing. The dances of honey bees orient the behavior of respondents in a still more abstract way. As yet another possibility, the response elicited by a signal may bear no consistent spatial relationship to the signaler. The response to alarm signals is often rapid movement to the nearest cover.

It is customary to speak of signals as being sexual, aggressive, or alarm signals and so on, but, as I have noted, distinguishing the responses that such categories of signals will elicit is often difficult. Both aggressive and so-called alarm signals may elicit withdrawal of a respondent in certain circumstances. In different situations, both signals may elicit approach. A classification of response types based on behavior subsequent to spatial rearrangement of signaler and receiver may give a better approximation of what actually happens in the field.

Withdrawal alone usually suffices for the response to a signal to be classified as a form of escape behavior. Our confidence in categorizing it in this way is increased if we see signs of extreme arousal and excessive autonomic activity. The movement may be followed by tense immobility in a place of concealment. It remains as something of a paradox that the active and inactive phases of withdrawal are usually re-

garded as belonging in the same behavior category. Be this as it may, the number of behavioral patterns that succeed withdrawal from a signaler is relatively small.

Approach to a signaler may be followed by many possible types of behavior in the respondent. There may be genital contacts of various kinds; suckling, nursing or other behavior arising in relations of parent and young; food sharing, exchange, or stealing; sharing or competition for resting or breeding sites; attack on the signaler or on another animal close by the signaler, such as a predator; or a variety of other social activities such as standing close, sleeping together, grooming, and so on. We can exclude activities, such as foraging behavior, which may continue irrespective of changes in the spacing of the signaler and respondent. Inevitably one wonders to what extent the alternative selected by the respondent is specified by the signal that also elicited the approach. Although we have little information to go on, it seems likely that in many cases the specification is partly or largely a function of further signals received during or after the approach. Sometimes, as already noted, the human observer can see signs that the response pattern is at least partly specified when the approach begins, as when a male manifests signs of sexual arousal on receiving a signal from a sexually receptive female at a distance. Often such signs are lacking until proximity is achieved.

If the first response to many signals is approach, one might question what advantage a species gains from having different signal types for long-distance communication of information concerning different types of behavior. Could not one signal type suffice to elicit approach? The answer is that diverse signals may be required to specify the appropriate respondents. When a signal of the type we are discussing is emitted, only certain classes of individuals within the population respond. According to the structure of the society, signals from a sexually receptive female will elicit approach and sexual responses from adult and subadult conspecific males, from adult males alone, from adult males with high dominance status, or from one individual adult male of the species. The communicatory roles of different individuals in the society are not completely interchangeable (8). Actions of suckling or nurs-

ing will be elicited in a different class of respondents than will sexual activities, thus such activities require a different signal. While sexual and parental responses are normally restricted to members of the same species, activities such as staying together, resting, even sharing food or nest sites may be elicited in other species as well.

Thus there may have been selection for much of the signal diversity in animal communication systems as a consequence of the advantage obtained from signals specifying a certain class of respondents. It follows that the investigator seeking to comprehend such a system must determine the presence or absence of a response to a signal in all possible classes of recipients before he can understand what is going on. The appropriate respondent may be specified according to species, sex, age class, dominance status, individuality, and so on. A signal might also specify the respondents' environmental context or physiological state. A certain alarm signal may elicit a response from individuals out in the open but not from those in cover. A food signal evokes a response from a hungry animal, but not from a satiated one.

There are likely to be contrasting trends in the evolution of signals that select different classes of respondents. A high degree of species specificity will be likely in signals eliciting responses where restriction to members of the same species is favored. The converse will be true when the facilitation of interspecific communication conveys some advantage. Specification of sex, the individual, or age class may be favored in other cases, and this will be reflected in the type of signal that a species employs.

We have concentrated on signals that elicit approach from a distance. The specification by the signaler among the alternative response patterns of the respondent becomes more narrow at close range, when many of the difficulties of communication are eased. There is less chance of error in identifying the signal. Over short distances the opportunity to receive compound signals with several sensory modalities cooperating is greatly increased. Problems of species or individual specificity become minimal at close range. As will be argued later, this may in turn permit greater exploitation of signals that are highly graded in structure rather than stereotyped.

Other Situations for Similar Responses

How do we decide whether animals use communication signals in a semantic fashion, whether signals serve as symbols for things (8, 9)? Suppose that a signal elicits a pattern of behavior in a respondent without the addition of other signals. We review all the other stimulus situations in which that pattern of behavior occurs and infer that the signal in some way represents those stimulus situations to the respondent. Hockett (8) shows how a call that elicits feeding may be discussed in these terms.

Several difficulties can arise in this type of analysis. As already pointed out, the first detectable behavioral response to many signals is a change of position by the respondent. Its movements take it into new stimulus situations, and it is hard to separate the influence of these situations from that of the initial signal in the determination of the ultimate behavior of the respondent. Does a food call elicit specific preludes to feeding, such as salivation, before stimuli from the food are encountered? Or does a food call simply elicit approach in a certain class of animals, namely those that are hungry, with feeding dependent on subsequent stimuli from the food? In the latter case it is less easy to decide whether the food call really represents food to the respondent, for other stimuli will also elicit approach even in a hungry animal.

Field study of the vocalizations of the vervet monkey reveals at least six sounds that seem to be provoked by the presence of predators (10). The call given correlates with the identity of the predator, so that a snake elicits a different call than does an eagle or a leopard. The behavior of the predator is also significant. Flying and perched eagles elicit different calls, for example. There is some evidence that the signals represent different environmental situations to respondents. The initial responses that they elicit are in some cases different. The "snake chutter" of the vervet elicits approach and examination of the snake from a distance. When they hear a "chirp" call, given in response to a leopard, the monkeys run to trees and climb to the topmost branches. In response to a "rraup" call, given for an eagle, they run from open areas into thickets and descend from treetops. Direct perception of these three types of predator may elicit the

same three patterns of response. Although the relationships are not specific enough for us to think of the three signals as names for the three types of predator mentioned, in principle, these signals begin to approach the phenomenon of object naming.

Unlike the calls used, for example, in parental and sexual situations, the predator calls of the vervets elicit similar responses in all members of the group, except perhaps in infants, which are likely to run toward their mothers in response to all the calls. Variation of another kind has been described which is related to the environmental circumstances of the respondent. A "rraup" call may elicit running or crouching depending on whether the respondent is out in the open or in cover at the time the signal is received. Thus, the environmental context in which the signal is received can contribute to variation in response even without there being perception of any other communication signals (11). In such cases, the role of the context must be taken into account in a consideration of whether a semantic system is involved.

Although vervet alarm calls can be thought of as representing different environmental stimulus situations, sexual or aggressive signals often seem to lack any such denotatum in the external environment. Would it be fruitful to consider them as representing a stimulus situation that is internal to the signaler—a physiological state, in other words? In doing so, there would be a danger of circularity, for all sounds, like all behavior, represent some change of physiological condition. It may also be questioned whether a signal, such as a sexual one, can be properly thought of as representing a complex of physiological and behavioral states of which it is itself a part (9). On the other hand, there is much in common between the showing of incipient feeding behavior in response to a food call, which has an obvious external denotatum, and the showing of incipient copulatory activity in response to a sexual signal. Just as the food call cannot be eaten (8), so copulation cannot take place with the sexual signal. A sexual signal given at a distance may not need to be repeated for copulation to ensue once proximity between the participants is established, so it is not a necessary element in the situation ultimately evoking copulation. If we consider food and sexual signals from the viewpoint of the respondent that they specify, again there

are many similarities. The appropriate respondents are in both cases defined at least partly by their physiological states—whether hungry or sexually motivated.

The concept of semanticity, which requires the identification of the external referents in a signal-response relationship, provides no way of handling alarm and sexual signals in similar terms (9). Yet their biological functions are not so very different. It remains to be seen whether the concept of semanticity as traditionally used is valuable as a framework for understanding how animal communication systems operate, however important it may be in the comparison between animals and man.

Variations in Signal and Response

Many of the communication signals of animals seem to be delivered in an all-or-nothing way. Inevitably there is some variation in succesive renderings of a signal, but the variations often seem to lack communicatory significance. Thus a large part of the signal repertoire of many animals is made up of discrete, nonoverlapping categories. For some animals, these generalizations do not hold. For example, the signals of some birds and primates are highly variable, and there is extensive intergradation between signal types (12, 13). The complexities of the communication process in species using graded signals are such that it will be difficult to prove that the variations of signal structure are correlated with variations in the response elicited, though we know that such correlations exist in the dances of honey bees (14). Yet the extensive use of graded signals seems relatively unusual among animals, and it is tempting to speculate that it serves a special function, adding a more subtle dimension to the effects that signals can have on the behavior of respondents. The circumstances in which the signals are used seem at least consistent with this notion. For example, the sounds used by various primates in close-range communication have this highly graded quality. Some of the sounds used for longer range communication or, in the night monkey, for signaling in the dark (13), are more stereotyped, presumably because of the greater danger of mistaken identification. At close range in daylight the danger is reduced, and signals perceived through other sensory modalities

cooperate to increase the accuracy of the communicative process. Thus a diurnal species living in close-knit social groups should be free to exploit the potential advantages of highly graded signals. Many higher primates satisfy these conditions. It remains to be proven whether this potential is in fact manifest in the response patterns that these graded signals elicit.

Signal Parts and Response Elements

The response that communication signals elicit is often complex. In human language some complexity is a function of the several elements that we put together to make words and sentences. The same elements can be put together in different ways to elicit different responses, endowing language with immensely rich communicative potential (15).

In trying to decide whether animal communication systems possess this potential for fragmentation and recombination, the first problem one encounters is that many animal signals are discrete, as I have noted. Fragmentation of such signals does not occur in the course of their normal usage. Thus nature provides no opportunity for detection of a recombination of the parts to elicit new responses. Exploration of this possibility must wait for experimental presentation of complete and artificially fragmented signals. With bird songs it seems that different elements do differ in their communicatory significance, although the possibility of recombining the elements to elicit new response patterns has yet to be explored (16).

An experimental approach to communicatory function is greatly complicated by the participation of many signals in compound signal systems. In a different context, however, there is a further question we can ask of such systems. With evidence on the possibility of recombining fragments of signals lacking, what of the possibility that the elements of a compound signal are rearranged to elicit new responses? Altmann (9) has reviewed suggestive evidence that this occurs in primates. A gesture may elicit different responses when associated with different sounds, and so on. Whether or not one considers such recombination of animal signals as bridging some kind of a gap with human language, the phenomenon is well worthy of more detailed study and experimentation.

Various Sensory Modalities

A great deal of human communication involves the cooperation of several senses. In the course of a conversation, visual signals may contribute as much as auditory signals, or even more, depending on the circumstances (17). At close range, tactile and even olfactory signals may play a role, particularly in sexual and parental behavior. Similarly, in animal communication there is extensive collaboration between the senses.

The usefulness of certain modalities may be restricted by an animal's habits. A strictly nocturnal species has less use for visual communication than a diurnal animal has. A solitary species may have less use for tactile signals than does an animal in constant proximity with many companions. The different sensory modalities have certain intrinsic advantages and disadvantages that are reflected in the particular functions that they serve. At one level this is obvious. Taste and touch find little application in communication over distances. If we compare the usefulness of hearing, sight, and smell for communication over distances, we find differences there as well.

The great sensitivity of odor receptors and the durability of chemical signals gives olfaction a special advantage in communication over distances. The one condition to be satisfied is that emission coincides with movements in the surrounding medium. This serves both to broadcast the signal and to aid in location of the source. Auditory receptors can also be very sensitive. Another characteristic shared by sound and chemical signals, but generally lacking in visual signals, is that energy can be directed into their production. Their intensity can thus be raised above the level of other sounds and odors in the environment. Conspicuousness of visual signals can be maximized by contrast and movement, but, except when the organism itself generates light, the intensity of visual signals is limited by ambient lighting. Visual signals have limited value at night or in the darkness of a closed nest, such as a beehive, as well as the further disadvantage that their transmission is liable to be blocked by vegetation and other obstructions. Chemical and sonic signals bypass obstacles more readily. Thus, several considerations suggest that vision is a less satisfactory medium for long-distance communication than are

olfaction and audition. There may be exceptions in special circumstances. Sea birds, for example, live in an unobstructed and well-lit environment that provides a homogeneous background for the display of visual signals.

Visual signals have the supreme advantage of being easy to localize; localization is less accurate with sound signals and slow and uncertain with olfactory signals except under special conditions. The directionality of light and its detectability by visual receptors permits the use of spatial patterns to a degree that is inconceivable for chemical and sound signals. Compound signals with many simultaneous, separable elements can be exploited fully to generate an immensely complex and extensive repertoire of signals. Independent variation of the elements is possible. The potential richness of coding is further increased when the variables of color and brightness and the possibility of exploiting rapid temporal patterning are added. Some elements of a visual signal can be relatively durable, such as an object in the environment or aspects of external morphology, while others, such as a brief movement or display of a concealed structure, are transient.

When the ecology of the species permits its use, vision is in many respects the ideal medium for close-range communication. Thus diurnal animals, living in a fairly open environment with a relatively close-knit society and a complex social organization, are ideally qualified to exploit the subtleties of a signal complexity possible in visual communication. These qualifications are well met in some of the higher primates, and it is no accident that some of the greatest complexities of communication in such animals as baboons and macaques are being found in visual systems (18, 7).

When the usefulness of vision is limited by the environment or by inadequacies of the visual receptors, there tends to be more reliance on olfaction, for both close-range communication and for communication at a distance. The potential durability of the signals can be a great advantage here. The durability of chemical signals varies according to the substance used, and the distinctive temporal characteristics of olfactory signals can be used to build a communication system of great complexity and sophistication (19). When the members of a population occupy a reasonably stable position in space, long-lasting

chemical signals are useful. This occurs in many nocturnal mammals including primates. The variety of compounds that can be produced provides a ready basis not only for specific identification, exploiting the specificity of receptor function that is possible, but also for group or individual identification as well. The diversity of signals available readily permits the use of different signals for different functions.

When rapid exchanges of information between animals call for modification of signal characteristics at short notice, the relative durability of chemical signals has drawbacks. Temporal coding reaches its greatest complexity in sound signals, such as the bird and insect songs that are used for distance communication. The transient nature of sound facilitates rapid exchanges of changing signals. This can be especially valuable for members of highly mobile species that require brief, accurate exchanges of information when they meet.

There is another, more subtle advantage to sound as a means of communication. Some of the occasions for communication between animals are significant enough to warrant the cessation of other activities while signals are being generated. But, in some situations, it can be an advantage for ongoing behavior to continue during signal emission. This is impossible if the process of signal production involves a major part of the animal's motor equipment, as many types of visual signaling do. Ongoing behavior is interfered with if the eyes of the respondent must be used to watch the partner during visual communication. On both counts sound signals have an advantage. The use of respiratory air movements to generate sounds allows signal production to proceed simultaneously with other types of behavior, as occurs, for example, in the flight calls of flocking birds or the soft grunts heard in foraging groups of many social mammals. These sounds can be generated and heard without other activities being disrupted.

Conclusions

Thus, each modality has its special advantages and disadvantages. Species that have the necessary sensory equipment tend to make use of all of the senses that can be used over distances for communication in different situations.

We can detect several types of relationships between the structure of animal communication signals and the function that they serve. The almost ubiquitous requirement for aid in or hindering of the localization of signals has led to the evolution of many distinctive properties of both auditory and olfactory signals. The ease of localization of visual stimuli is one of several factors that make vision peculiarly suitable as a means of social communication when circumstances permit.

The diversity of signal structure in animals must exist partly to maintain species specificity, partly to permit a signaler to elicit different responses from another animal, and partly to select among the various classes of respondents that are available. With the evolution of a complex society, in which different animals have different roles to play, the specification by different signalers of appropriate respondents may require a considerable increase in the number of signal types used by a species, irrespective of any increase in the number of response patterns that may occur.

There is still no plausible explanation for the emergence of the cultural transmission of patterns of sound production in man. The change must somehow have been related to the advantage of an increased repertoire and flexibility of sound patterns, not necessarily related to sex or age class. The use of tools obviously played a vital role (20, 15). Increase in the subdivision of labor in early human society, such that members of the same sex and age class might assume many different roles, and the need for a signaler to select respondents among the array of possibilities, would create a need for dramatic increase in signal diversity. Perhaps this contributed to a switch from , genetic to environmental control of variation in patterns of sound production in a population. Once established, albeit for the satisfaction of a relatively simple linguistic requirement, the increased flexibility of the patterns of sound production would pave the way for the more remarkable changes in the processes of communication that ultimately made human language a unique phenomenon in the animal kingdom (21).

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22. I thank Stuart Altmann, Anita Pearson, and Thomas Struhsaker for their criticisms of this paper. It was begun at a Wenner Gren Foundation for Anthropological Research Symposium on animal communication organized by Thomas Sebeok and held in July, 1965.

Agricultural Production in the Developing Countries

G. F. Sprague

At least half the world's population endures some degree of malnutrition. The gap between food production and world population is constantly widening. It has been estimated that by 1985 this situation could become catastrophic.

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Two approaches appear obligatory: (i) a substantial decrease in the rate of population growth, and (ii) full utilization of our biological technology to increase food production on all economically arable lands. The utilization of microorganisms, algae, or petrochemicals to produce protein has been suggested by many. These and other possibilities should be actively explored and, where feasible, utilized. However, the total impact of such possible developments cannot greatly lessen the need for an expanded agriculture limited only by the ecological potential.

This article is concerned primarily with the possibilities for increasing agricultural production in the developing countries through improvement in varieties, in fertilization, and in management practices. As background, a brief review of selected examples of progress achieved in the developed countries with the three most important food crops—rice, wheat, and corn—during the past 35 years seems desirable.

Rice Production in Japan

Japan has the highest acre yields of paddy rice among the major rice-producing countries. There is evidence that rice was cultivated in Japan as early as 300 B.C. Through the centuries there