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On the Analysis of Social Organization among Vertebrates, with Special Reference to Birds*

N. Tinbergen

The study of social organization of animals is still in a transitory stage between purely descriptive and more causal-analytical investigation. Yet at present, we possess very few descriptions of social organization that might be called more or less complete, and the available analyses are still more fragmentary. A study of recent textbooks such as those by Alverdes (1925), Deegener (1918), and Murchison (1935) will show this. Even Allee's books (1931, 1938), while containing many analytical data, especially about the effects of crowding, offer an incomplete picture of social organization, as is natural in the present stage of work in this field.

It is often assumed that social relations in the higher animals are so variable, even within the species, that a general picture of social organization in a given species is impossible. Admitting the influence of individual differences on the form of social organization, I should like to point out the fact that there is always a framework of relationships that is characteristic for the species, even among the highest mammals. This has been demonstrated best by Carpenter's monograph (1934) on the Howling Monkey.

The most important work of a causal analytical character has been done on birds. Valuable contributions have been published by Heinroth (1910) on Anatidae, by Howard (1907-1915) on the old world warblers, by Verwey (1930) on the European Blue Heron, by Noble and his associates on fishes, lizards and birds, by Huxley on the Crested Grebe (1914) and on the Red throated Diver (1923), and by Lorenz (1931) on the European Jackdaw and other Corvidae. Based in part on the data of these authors, and on a wealth of new material, Lorenz (1935) offered a very suggestive analysis of social relations in birds. His work has been particularly fertile, and it will serve as the basis of the following account.

The conclusions to be presented in this paper will be substantiated by a few selected examples. These will be taken in part from the available literature, in part from unpublished work on the European Blackbird (*Turdus m. merula* L.), the Herring Gull (*Larus a. argentatus* Pontopp.), and the Three-spined Stickleback (*Gasterosteus aculeatus* L.), done in the Zoological Laboratory at Leiden.

I wish to emphasize the fact that this paper aims to point out certain causes that play a part in social integration. It neither presents a descriptive review of different types of animal communities nor does it deal with the functions of aggregative behavior.

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Defining sociology as the study of the relations between individuals of the same species, it is obvious that the sociology of any species offers a wealth of problems, for species without any interindividual relations probably do not exist among Vertebrates. In those species in which no flocking occurs, there exist, nevertheless, interindividual relations between, e.g., the members of a pair, and in addition often we find relations between parents and offspring, and among the young. In flocking species, especially in those species which reproduce gregariously, a complex system of relations between the members of the flock or herd exists.

The interindividual relations which form the primary aim of sociological research are always processes of one individual or group of individuals (for the sake of convenience called the *Actor*, or *A*) influencing another individual or group (the *Reactor*, or *R*). This influence rarely is a direct one; often it is a highly complicated chain of processes: some activity of *A* is received by *R*, then, through *R*'s sense organs, nervous system and effector system a special response of *R* results. As a consequence, the causal analysis of social organization has to be based on the study of individual behavior.

The complex of processes building up an interindividual relation may be divided into three phases: the activities of *A*, the means of communication proper, and the activities of *R*. They will be treated in reverse order, because this is the natural way followed in actual investigation.

THE ACTIVITIES OF R

In order to find the causes of *R*'s behavior we will have to divide it into as many elements as possible. Different elements may have different causes, and by treating them all alike rather than separately an attempt at causal analysis would be extremely difficult.

The simplest known reaction to an external stimulus, the reflex movement, rarely, if ever, constitutes the complete reaction of *R*. The activities, released by *A*, are always highly complicated. A simple example will serve to show this complexity. A shoal of socially swimming fishes makes a sudden turn as a reaction to the change in direction of one of them and swims with increased speed in the direction taken by the individual which happened to make the first change in its movements. This communal flight can be observed in any aggregating species of fish. The *increase* in speed may be a relatively simple response to a reflex; the *turning* in a special direction certainly is a spatially directed movement (orientation movement, taxis)¹. The difference between reflex (and similar reactions) and a spatially determined movement (taxis) depends on the part played by external stimuli. In the first category external stimuli are merely *releasive*, in the second they are *directive*. A few examples may illustrate this difference.

¹ The word "taxis," in the sense in which it is used in the German literature, is preferred here to the term "tropism" because of its wider meaning (Cf. Kuehn, 1919).

When a group of *Daphnia* is swimming in well aerated water, the animals will spread irregularly in the available space. When CO₂ is added, it works as a releasing stimulus: the animals hurry to the surface. The movement is released by a chemical stimulus, but it is directed by light. If lighted from underneath, the animals will swim down. Thus what seems to be one movement can be analyzed as consisting of two components, working in succession.

A similar successive functioning of releasive and directive mechanisms is found in the foodseeking reactions of the carnivorous larvae of the freshwater beetle *Dysticus marginalis* L. The perception of chemical stimuli provided by a frog larva or some other prey urges the animal to dive to the bottom where it searches for the prey. The downward movements are entirely directed by light, and light coming from below causes the animal to "dive" to the surface. The diving cannot be released by visual stimuli, it has to be released by chemical stimulation first (unpublished observations of G. Kamerbeek and P. Nieuwdorp).

Several ground-breeding birds, such as Terns, Gulls, and Geese, have a special reaction to the situation "egg-outside-the-nest." Such a bird stretches its neck toward the egg, brings the bill behind it, and rolls it back to the nest, balancing the egg on the ventral surface of the mandibles. In this relatively simple response, a complicated mechanism of cooperating behavioral elements could be analyzed (Lorenz & Tinbergen 1938). The first phase, consisting of bringing the bill behind the egg, is an involved movement, provisionally called appetitive behavior (Craig 1918). The actual rolling movement can be divided into two components, viz., a consummatory action (Craig-Lorenz) or instinctive action (in the narrow meaning in which Lorenz uses the word, cf. Lorenz 1937) and a spatially directed component (taxis). Both elements are at work simultaneously, resulting in an apparently simple movement. The movement of the head toward the breast in the sagittal plane is the instinctive movement. Its principal properties are: 1. that it, when once released, runs its full course without requiring renewed stimulation, and 2. that its pattern cannot be changed by changing the external situation, e.g., by substituting a larger or a much heavier egg. The sideward balancing movements are spatially directed, and their pattern is continuously influenced by stimuli from the rolling egg. When a cylinder is substituted for the egg, the usual sideward movements are eliminated and no "taxis"-component can be observed. The complex nature of the egg rolling movement can be demonstrated by removing the egg after the reaction has been released. The first component continues: the head will be moved toward the breast, but the balancing movements are now absent.

A fourth instance demonstrates another method of analysis and points to a similar mode of integration of these two components. Young Passerine birds such as thrushes, while in the nest, show "gaping" movements as a response to the food-carrying adult. During the first few days after hatching both releasive and directive stimuli are mechanical: a light tap on the nest releases reaction; stato-stimuli direct it. At about the ninth day, the reaction can be released by an optical stimulus (moving object). At first, it is still directed by the static organ, and 2 or 3 days may elapse before visual stimuli

influence its direction. Then the young no longer gape vertically, but turn their heads and necks toward the bill of the adult.

Consequently an analysis of the recognition marks that release the movements and of those that direct them toward the head of the adults, shows that the two stimulating situations are entirely different. Any object, provided it is larger than 3 mm. in diameter, moving, and above the horizontal plane of the young bird's eye, releases the gaping movement. Objects smaller than 3 mm., immobile, or those below this plane may be seen by the birds, but will not release the reaction. The head of the adult, however, *directing* the gaping movements, is recognized by the following characters: it changes the torso's outline, it is situated higher than any other part of the body, it comes closer to the young, it has a diameter of about one third of the torso and it is marked off from the torso by an indentation. The experiments that led to this conclusion are summarized in Fig. 1.

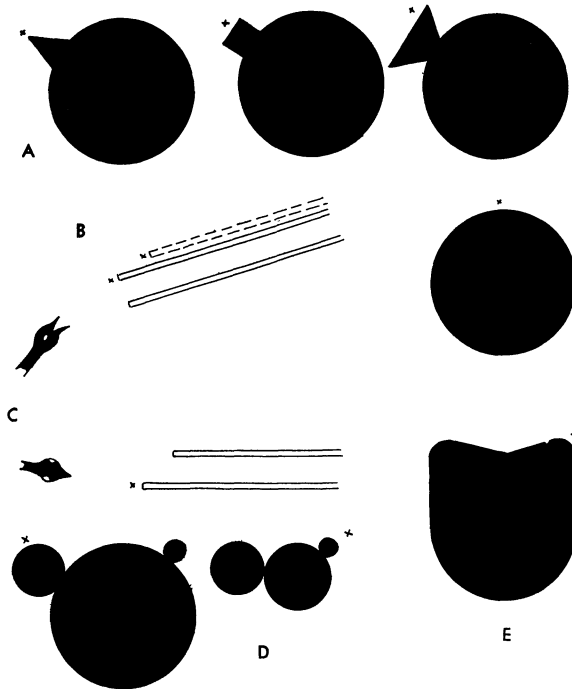


Fig. 1. A summary of experiments serving to analyze the recognition marks that *direct* the gaping movements of young thrushes to the head of the adult bird. Crosses mark the parts of the models toward which gaping is directed.

- A. Changes in the torso's outline.
- B. Gaping toward the highest parts of the model.
- C. Gaping toward the part closest to the young.
- D. Preference for one of two "heads" depends on relative size as compared with the torso rather than on absolute size.
- E. The head with an indentation is preferred.

These two facts, viz., that optical stimuli may be effective as releasers of the response while still lacking any directive power, and that the optimal releasive situation differs from the optimal directive situation, indicate that in the gaping response, again, two mechanisms are at work simultaneously: a releasing and a directing mechanism (unpublished work, Tinbergen & Kuenen).

These analyses are recorded here in such detail for the purpose of emphasizing the complicated nature of an apparently "simple response." They show, that *A*'s behavior may influence *R*'s reactions in two fundamentally different ways.

R's readiness to respond depends on several circumstances. The endocrine condition, for instance, determines whether sexual or parental activities can be evoked at all. Apart from this, the nervous condition of *R* may vary, as the following examples may show.

In many cases *R*'s readiness is not influenced by individual experience, and the innate connection between a special sense-impression and a special response remains the same throughout the period of the individual's life during which the reaction is shown. Although we have much evidence of this in lower animals its common occurrence in birds can be doubted.²

Many innate S-R sequences may be changed by conditioning. As an instance of a fixed, innate S-R sequence the social and sexual responses of the Guppy (*Lebistes reticulatus* Peters) as studied by Noble (1938) may be mentioned. Noble reared Guppies in isolation and together with individuals of other species: at maturity, all of these individuals showed sexual and social responses to their own species only.

In many cases the responses are conditioned during individual life. An easy means of recognizing reactions that have been conditioned is afforded by individual differences in behavior which result from the different experiences of individuals. In social relationships, however, the conditioning occurs frequently under circumstances very much alike for all individuals. The young of those Passerine birds, for instance, that have a specialized song have to learn that song from the adults. Since all young of one species learn their song in much the same way, it is much alike. One of the most prominent characteristics of learned responses, viz. the individual differences, fails here. In many cases, therefore, the conditioning process can be discovered only by very careful observation and experiment.

Since the theories of learning are still in a chaotic state, and the knowledge of sociological facts is so fragmentary, it is impossible to present a well-classified review of the different types of learning that could be used in establishing interindividual relations. Consequently I must confine my discussion to a few individual cases, which indicate the different possibilities.

² It should be noted that this applies to *sequences* between specific sense-impressions and reactions (Stimulus-Response [S-R] sequences) and not to the *pattern* of the reaction itself.

Perhaps the simplest instance of a learned reaction can be observed in places where birds of several species are breeding in close proximity to each other, as for instance in mixed colonies of Terns and Gulls. The Gulls learn to flee at the alarm-call of the Terns. In much the same way, birds of one species can learn to "understand" the threatening behavior of individuals of the other species. Black-headed Gulls, for instance, learn to avoid threatening Sandwich Terns in colonies in which both species mix.

A more complicated case is demonstrated by those birds which learn to confine their parental activities to their own young by refusing to feed or brood other young. In some species of Terns (Watson & Lashley 1915 for Sooty Terns, Dirksen 1932 for Sandwich Terns) and in the Herring Gull (Tinbergen 1936) the parent birds will feed all young of the same species they meet (provided they are of the same age as their own young) during the first few days after hatching of the eggs whereas they will direct their parental activities solely toward their own young after 3-5 days (varying according to the species). The adult Herring Gulls actually kill every strange young that happens to come onto their territory.

The establishment of rigid peck-orders (Schjelderup-Ebbe 1922 and others) involves similar learning processes. The members of a flock in which a peck-order occurs know each other individually revealing not only an amazing power of discrimination, but at the same time the working of rather intricate conditioning processes by which an animal forms separately special habits in relation to every individual.

A similar complicated relationship exists within a Herring Gullery. Every Herring Gull reacts to the alarm call of other individuals, but the pattern and the intensity of the reaction depends on which neighbors are calling. The call of neighbor *P* always causes sudden flight, whereas a similar call uttered by neighbor *Q* may result in only a slight increase in attentiveness. The animal "knows" by experience that *P* warns only when danger is near, and that *Q* often warns because of a distant disturbance.

Many birds, about to breed for the first time, return to the place where they were born. By extensive banding of birds this phenomenon has been revealed in many species. It is especially striking in the Herring Gull, a species that matures four years after birth. During these years every individual wanders widely, but at the beginning of its first reproductive season it returns to the colony in which it was born. Subsequently it returns, as a rule, year after year, not only to the same colony, but also to the same territory within that colony.

The following observations made on the Three-spined Stickleback suggest two different learning processes. The male of this strictly "territorial" species selects a locality in spring, a small part of the area in which it lives during the rest of the year, and confines its reproductive activities to it. Several activities, such as digging in the sand (the preparation of nest building) and sexual fighting are at first displayed in a rather large area. In the course of a period varying from five minutes to two hours, as the case may be, these activities are gradually restricted to a particular part of the area. The digging activities for instance include at first an area of about 20 x 40 inches, then of 15 x 30 inches, then 10 x 20 and so on, until it is ultimately confined to a spot of approximately 2 x 3 inches. In this way the depression for the nest is made.

A striking contrast to this gradual learning process is revealed by the following observation on the same species. The male, after finishing the nest, is ready to react to visiting females by piloting them to the nest. During experiments with decoys, designed to determine which "recognition-marks" of the female caused the male to guide her to the nest, a sudden change was observed in several males. After having reacted with complete piloting behavior to several decoys, lacking different recognition marks of the living female, such a male would suddenly "refuse" to respond to any decoy and would guide only optimal, living females. Without attempting further analysis, I wish to stress merely the difference between this learning process and that involved in the foregoing case.

Heinroth (1910) and Lorenz (1935) described a learning process that *might* differ fundamentally from other kinds of learning. A young Grey Lag Goose learns during the first *minute* of its life to direct its infant-parent-activities to the living being which it sees during this first critical encounter. If a chick hatches in the incubator and is handled by man, it will always consider man as its social companion. The only possible way to force such a chick to join adult geese, it to put it into a box or sack immediately after opening the incubator, and carry it to a Goose family with newborn chicks. Lorenz (1935) called this phenomenon "Prägung" ("imprinting") and emphasized its irreversibility; he claims that an imprinted S-P sequence cannot be "forgotten" and hence is comparable to the process of induction known in the physiology of development. Opinions regarding the nature of this process of imprinting differ of course greatly owing to the fragmentary character of the available factual material.

In many cases a change in the behavior of an individual may be due to causes other than learning processes. An innate activity does not always function at birth, but may sooner or later come into play. Flight reactions of young birds, for instance, may suddenly appear in the fledglings, and may be directed toward situations previously not flight-inducing. Sexual activities may also be entirely innate and may become apparent only after the animal has reached maturity. Many other instances could be cited. In man, many changes in behavior appearing during individual development might have an innate basis at least. The new reactions may appear gradually and pass through a slow maturation process. This maturation may concern the motor side of the reaction or it may concern the receptive side. Often it may concern both elements of the reaction. Frequently it is difficult to recognize a maturation process as such without experiment. An instructive instance can be found in the work of Noble & Vogt (1935) on sex recognition in the Redwinged Blackbird. They found that year old males apparently did not discriminate between sex in mounted specimens of the same species, and that they copulated with stuffed males as well as with stuffed females. Two year old males, however, copulated only with females. Apparently, the motor side of the reaction was fully matured, and the authors assume that the difference in discrimination between year old and two year old birds was due to conditioning of the older birds. Conclusive evidence for this opinion, however, is not presented and the possibility of a maturation process still remains.

Apart from these learning processes, summation of sense impressions may play an important part in complicating the simple stimulus response of an innate reaction. We know from many cases of courtship activities in birds, that a stimulating activity of one individual may seem to be without any effect on the partner, although after repeated performance it may elicit the partner's response. Some lasting effect of the first stimulations must be assumed.

This summation process may even have an important influence beyond the nervous system. Craig (1908) was the first to prove that sensory stimulation, derived from the courtship behavior of the sex partner, may induce both sex organs and endocrine glands in pigeons to develop. The courtship activities in these birds serve primarily to synchronize the sexual cycles of the partners, so important in regard to the specialized method of rearing the

young. The same synchronization process probably occurs in the Ruffed Grouse (Allen 1934). Recently Darling (1938) developed a hypothesis that in colony breeding species of birds a similar stimulation and synchronization of the cycles of all individuals of the colony is effected by the courtship behavior. The evidence for this assumption, however, is very meager.

Another interesting feature is the fact that the learning ability for certain situations may be dependent on the endocrine condition. I observed a striking example in young male Eskimo sledge dogs. These dogs live in packs in much the same way as do wolves in winter. Every pack has a pack territory which is defended by all members of the pack. Young males, sons of one of the pack's females, do not defend the territory as long as they are sexually immature. Nor are they aware during that period of the boundaries of strange territories, and trespass over and over again without learning that the punishment (attack by other dogs) depends on the locality. In two animals which were carefully watched during this period, defense of their own territory was assumed together with mature sexual behavior (copulation), and in the same week in which these two new reactions appeared, the dogs suddenly learned to avoid strange territories! (Unpublished observations).

Some observations seem to show that in individuals developed under natural conditions, learning processes play a rôle only in a part of the behavioral elements; some reactions are conditioned whereas others are not. Apparently in some reactions the S-R sequence functions from the very beginning while in other reactions conditioning is necessary. One could say, that for some reactions an "innate ability to be conditioned" is inherited, for others not. Lorenz first called attention to this fact in some non-social action chains (Lorenz 1935).

The following facts illustrate another interesting point: the conditioning of different reactions in objectively the same or very similar situations often concerns different elements of such a situation.

As an example the brooding reactions of the Herring Gull may be compared with the reactions of feeding the young. The reactions of settling down on the eggs are evoked by a stimulus-situation including a few marks of the eggs, the nest basin, and a highly complicated combination of marks characterizing the place of the nest. Experiments show that the brooding response is entirely independent of the marks that characterize the bird's own clutch as different from other clutches. Even animals that lay "blue" eggs (in which the superficial brown pigment is lacking), that are so strikingly different from the normal brown eggs of the species that they are considered very valuable by "oölogists," do not prefer their own eggs to brown ones, though they might be expected to be conditioned to the conspicuous color of their eggs. The learning process is confined to those marks of the entire situation that characterize the *place* of the nest.

From the 5th day after hatching on, the reactions of feeding the young are confined to the bird's own young. The adults, conditioned to the individual characteristics of their own young, feed them irrespective of their location in the nest. The difference as compared with the brooding reaction is

obvious. Equally obvious is the fact that both kinds of response fit in both cases in the special structure of the environment: the eggs do not move away from the nest, whereas the chicks do. This is, of course, no solution of a problem, but merely the recognition of its presence.

THE MEANS OF COMMUNICATION PROPER

A comparative study of the means of communication ("language") in different species reveals an enormous diversity. All these different processes of communication can be classified in two groups. A flight reaction of one member of a flock of Jackdaws or Sandpipers or of a shoal of Sticklebacks will evoke flight reactions in the other members of the flock. When one member of the flock starts eating, the others join. Here the Actor induces the same movement in the Reactor.

Threatening behavior of a territorial male Stickleback induces flight reaction in a stranger Stickleback. The distress call of a young Duckling induces maternal activities in the mother. Aggressive behavior of the male Bitterling, which defends a mussel (*Anodonta*) causes the mature female to swim downward to the mussel, where she will deposit her eggs. In all of these cases the response of *R* is different from *A*'s action.

The question arises: which processes elicit *R*'s activities? By which means do *A*'s activities influence *R*? The answer to this question differs in two respects from that expected at first glance. Some instances may illustrate this.

A male Stickleback ejaculates sperm shortly after a female has laid eggs in the nest he built. Some simple experiments show that the ejaculation is released by the smell of fresh, unfertilized eggs. Optical stimuli have no influence, although the eggs are plainly visible. Incapability of the optical apparatus cannot account for this because the eye is capable of good color, form and movement reception, which appears when an analysis of other reactions is made. This leads to the conclusion that the releasing behavior of *A* may act merely through part of *R*'s sense organs, although potential stimuli for the other sense organs may be "broadcast" by *A*.

There is, however, a second restriction. The eyes of a fourteen day old Blackbird enable it to discriminate form fairly well. When directing its begging movements to the head of the adult, it reacts to recognition marks of less than 2 mm diameter.

The stimulus situation required for the *releasing* of the begging movements does not include any form character, as will be remembered. Every figure, provided it is larger than 3 mm in diameter and moving above the eye level evokes a full response, definitely independent of its shape.

Lorenz, in one of his studies on the sociology of the Jackdaw, emphasized a still more striking example of this phenomenon. A Jackdaw reacts to the sight of a predator which is carrying a Jackdaw by giving the alarm call. This again evokes an attack by all members of the breeding colony. The alarm call is released by a very vaguely determined stimulus situation, for a man

wearing a black bathing suit and even a Jackdaw carrying a black feather to its nest evoked the reaction. Simultaneously some other reactions e.g., sex behavior, are confined to an individual Jackdaw. The birds can distinguish at a glance between two individuals and by this capacity they show that their optical receptors do not cause them to react in the same way to a Jackdaw and a bathing suit.

Numerous instances of the same phenomenon could be given. They all lead to the conclusion that central processes are at work in deciding which factors of the receptual field have or have not releasing or directing effects on a certain reaction. One of the main points in Von Uexküll's "Umweltlehre" has been the demonstration of the fact that every reaction of an animal has its own "releasing mechanism" (Auslösendes Schema). The mechanism, or the coupling of special stimulus and special reaction, is innately fixed in many cases, even in the highest mammals, man included. Undoubtedly a human female has an inborn mechanism pertaining to feeding and other reactions toward the baby. The following characteristics of the latter probably belong to this mechanism: crying, performance of maladjusted movements, and the possession of thick cheeks. The courtship of a mature human male in presence of a female certainly responds to an innate mechanism of the female by a display of strength, smartness or by another form of superiority over other males. Of course in both cases the innate mechanism is modified and highly supplemented by important learning processes.

It does not seem to be generally recognized that different reactions, evoked by and directed toward the same object in different situations may have different mechanisms. For instance, an animal may have different reactions to a sex partner: copulation, joining it in feeding, calling it, assisting it in nest building, or relieving it in incubation. Each reaction may have a different releasing mechanism. Sometimes, when a partner is defective in some way in its reaction pattern, an animal may take two partners, one principally for coition, and the other for assistance in nest building. Consequently it is misleading to speak of the "mechanism" (Schema) of the "sex partner" or of "the social companion," since one can speak only of the mechanism of a certain reaction. Likewise, it is futile to try to corroborate or to negate a conclusion regarding the releasing mechanism of reaction (a) in species (S) by studying the mechanisms of the same (and much less of another) reaction in species (X). There are as many mechanisms as there are behavioral units.

The concept of "mechanism" involving few recognition marks raises one fundamental question: are these marks the only effective factors in an absolute sense or can an influence of the other parts of the sensory field, however slight, be demonstrated? In the latter case, the difference between effective and non-effective parts of the sensory field would be merely one of degree.

Although until recently experimental methods have been too gross to justify a definite conclusion, there are some available facts that elucidate the question.

The male *Gasterosteus aculeatus*, when ready to receive a female in its nest, shows the same first reaction to every approaching Stickleback, irrespective of its being a red male (—a male in full breeding dress), a pale male, an immature female or a mature female. Many other animals are welcomed in the same way. The response of the other individual determines either the male's attack or its guiding behavior. The same state of affairs is found in animals of various groups: spiders (Holzapfel), the Squid *Sepia officinalis* L. (L. Tinbergen 1939), the Fighting Fish *Betta splendens* Regan (Lissman 1932), pigeons (Craig 1909, Whitman 1919, Heinroth 1928) and other birds (Tinbergen 1935, 1939). We must conclude that the mechanism of this first reaction possesses only a few recognition marks.

However if a male and a female are presented to the male at the same time, he will show slightly different responses to them, which proves that the releasing mechanism must include some differentiating marks of either female or male. This has been observed in *Gasterosteus*. These differentiating marks are unimportant, for the reaction occurs in optimal or almost optimal intensity whether they are present in the external situation or not. It is not known, however, whether these additional marks belong to the inborn mechanism or are caused by individual conditioning.

Despite the emphasis on the "innate releasing mechanism" I am fully aware of the more complicated means of communication. As a matter of fact, the more highly organized mammals, especially man, probably have few, if any, unmodifiable mechanisms, and the mechanism of every reaction has been changed into an amazingly complicated nervous connection. Yet as emphasized before, the underlying mechanism can often be recognized.

On the basis of the previous discussion it should be stressed that there is no controversy between the assumptions of a conditioned response and an innate releasing mechanism. A response cannot be conditioned unless it is present before the conditioning. Conditioning means changing something that is already present, but it does not bring about a new reaction.

THE BEHAVIOR OF A

The activities of *A* which give rise to *R*'s response, may result in the stimulation of different sense modalities. In the preceding paragraphs, several instances of this were given. Often an activity which has communicative value may stimulate *R* by means of more than one modality. Even if restricted to one modality, the stimulus is almost always a rather complicated one. A female Stickleback in egg laying mood prefers following red males which move in a special way. This special movement, together with a color pattern, form the optimal situation for the release of the female's reaction.

Often the behavior as well as the displayed structure which serve as a means of communication differ from the behavior or structure employed in any of the other activities of the animal; in short by specialization they are adapted to their communicative function.

The adult thrushes which evoke the gaping movements of their nestlings, accomplish this without any specialization. Since they are moving, larger than 3mm., and are in the upper hemisphere of the young's optical field, their communications do not evolve from activities other than actual feeding nor are they brought about by the use of special structures.

Other species of altricial birds display special activities which serve to evoke the gaping reactions of the nestlings. Kuhlmann (1909) says about the Redwing Blackbird that the young react to "the special clucks of the parent birds, used especially for this purpose. . . ." (p. 64).

Defecation of the nestlings ordinarily occurs shortly after feeding, and the adult bird waits for the feces to carry them off. In the Wren-Tit, Erickson (1938) observed that "If none is forthcoming, the adult often pecks the nestling in the region of the anus as if to stimulate defecation." (p. 292).

Although further analysis in both cases would be necessary to ensure that these activities are especially adapted to communication, the examples suggest a way in which specialized movements may arise.

Such movements are often augmented by conspicuous structures. When a Herring Gull feeds its day old young, it points its bill to the bottom, and, after regurgitation, takes a tiny piece of food between the mandibles and presents it to the young. The newly hatched chick has an innate tendency to peck at all red patches and as a result it gets food by pecking at the red patch on the parent's bill (Goethe 1937). This is the only known function of the red spot. It would be worth while to study the reactions of the chicks of those species that have no red spot, or of species with other color patterns on the bill (Ring Billed Gull).

A more specialized case is offered by the wing patterns of Anatidae. Every species has its own pattern so that a colored picture of duck's wings works "like a flag-directory" (Lorenz). In fact, they have about the same function as a flag viz., to designate the species. Heinroth has given a most convincing illustration of this principle: he observed in the Berlin Zoo, that Anatidae with black and white wing marks evoked social reactions only in those species possessing the same wingmarks regardless of taxonomic relationship.

Lorenz (1935) called all movements and structures producing a response in the social companion "Auslöser" ("releasers"). The more general term *signal* is perhaps preferable since the activities and structures may have releasive or directive influences, or both simultaneously. The smell of unfertilized eggs of the Stickleback, for instance, releases the fertilizing movements of the male, although it certainly does not direct them; orientation is optical and tactile, but not chemical. For the Lapwing, the danger call may have primarily releasive function, whereas the white tail mark may have primarily directive function. It is quite possible, therefore, that the concept of "signal" should be subdivided into "releaser" and "director," although most of the signals may have both functions.

Lorenz' concept of signal offers the best explanation of the function of conspicuous structures and modifies the views derived from Darwin's thesis of sexual selection. The basic assumption of the theory of sexual selection implies that the conspicuous structures serve to influence sexual or fighting responses in other individuals. A few examples will suffice to show that signals may serve for the release of many responses other than sexual or fighting ones. The red spot on the Herring Gull's bill and the wing marks of the Anatidae were mentioned above. Two other kinds of signals can be found in the nestlings of many Passerine birds. When "gaping," the inner surface of the mouth is shown; it is very conspicuously colored, often displaying various patterns in different species. Often this pattern is highly specialized, as for instance in the European Bullfinch. For excellent pictures of these "Sperrachen" the reader is referred to Heinroth's "Die Vögel Mitteleuropas." The other signal structure found in Passerine nestlings is an erectile ring of conspicuously colored feathers around the anal aperture. This signal is displayed shortly before defecation and releases as well as directs the feces taking movements of the adult.

A very striking demonstration of Lorenz' thesis that special signals of *A* are connected with special reactions of *R* is described by him of the Mallard. The adult's relieving reactions to a chick in distress are released by the chick's distress call. This call is quite similar in different species. If a chick of another species is caught by the experimenter, its distress calls will cause a mother Mallard to attack the predator and force him to drop the chick. As soon as the chick is saved, the Mallard will attack and kill it. According to Lorenz, the guiding and brooding activities of the adult female are dependent, not on the distress call, but on the color pattern of the young's head and back, which is much more specific than are the calls.

Lorenz pointed out that signals have two general properties: they are 1) relatively simple, and 2) specific ("unwahrscheinlich"), that is to say, they are different from other structures that may occur in *R*'s environment. The simplicity seems somehow to be connected with the fact that every inborn mechanism is a relatively simple complex, composed merely of a few marks. This empirical statement, of course, has no explanatory value and only points out a problem.

The specificity of a signal is like that of a key. It is obvious enough in the morphological signals. It should be emphasized that the same holds true for the signal *movements*. The movements of a female Stickleback ready to lay eggs serve as a signal for the courting male. Her behavior consists of swimming toward the male, holding her body in a semivertical position, pointing the head upward as shown in Fig. 2. This is indeed an unique movement among fishes. Experiments have shown that dead females, dead males (provided they were not red) and even dead fishes of other species, when held in this posture, were capable of releasing the male's guiding behavior.

Sounds that have communicative value are often very specific too. The

specificity of the song birds and of the migration calls of birds are convincing proof of this.

Since few cases of the functions of a signal structure or movement have been studied seriously the reported observations indicate the desirability of further study of different kinds of signals. The results of the available studies justify the assumption, as a working hypothesis, that conspicuous and highly specialized structures, whose participation in non-social processes cannot be found have a social, communicative function.

A comparative study of signals in closely related species should reveal suggestions of their phylogenetic origin. Although such a comparative study of special groups has yet to be carried out despite a start in some groups, one general rule is readily tenable: Signal movements may occur without morphological structures, but not vice versa. Heinroth emphasized the fact long ago that whenever a conspicuous structure is found in a bird, the bird possesses one or more innate reaction patterns which utilize these structures. On the other hand if two species perform similar movements, they are "augmented" by a special structure in one of them, whereas this is not so in the other. Lorenz gives several examples from Ducks (1935) and Grebes (1938). The obvious conclusion is: "the ceremony is older than its organ." Actually more arguments seem to suggest the conclusion that special inborn behavior elements are probably more constant in evolution than many morphological structures. For instance, no single morphological character has been found in all members of the family of the Columbidae (pigeons) yet they all have a behavioral trait not known in any other bird viz., they "pump" while drinking. Of course, this constancy during evolution effects merely one category of behavioral elements and not the more adaptive elements.

In much the same way as the evolution of morphological structures is studied by comparative morphology, the evolutionary origin of the movements with signal function can be revealed by comparative behavioral study.

Since the conclusions and arguments presented in the following are not based on previously published material, they must be afforded a more detailed treatment.

A bird, starting to fly, presses its feathers against the body and thus appears as thin as possible. At the same time its neck is more or less stretched as the bird stands in an alert posture. In the Herring Gull and in other species, this behavior has communicative value causing the companions to react to it promptly. The "intention" to start walking or flying is expressed in an even more pronounced form in other birds e.g., in the Anatidae, in which special movements of the head, often recognizable as incipient or preparatory flight movements, precede the take-off. Heinroth (1910) calls these kinds of motions "Intentionshandlungen"; I propose calling them "*preparatory movements*." They presumably play a part in many inter-individual relations. Often the preparatory aggressive movements have a threatening function, especially so in *Gasterosteus aculeatus* L. By special planting of the vegetation it is possible to have two males of this species occupy a territory and build a nest in one relatively small tank. Repeated

fight result in a sharply defined border of the two territories. After some time "border incidents" are reduced to alternating incipient attacks by both males, each of which in turn swims toward the other, causing the latter's retreat before any fighting begins. A series of back and forth movements follows. Exactly the same phenomenon was observed during boundary disputes between two male Snow Buntings (Tinbergen 1939). Pickwell (1931) describes a similar occurrence in the Prairie Horned Lark.

In many Anatidae, the preparatory flight movements were specialized during evolution and consequently they may scarcely be recognized as such.

Another category of incomplete movements are the "symbolic activities" as described by Portielje (1928, 1938). They are prevalent during the mating period: birds furnish many examples. Frequently birds show incomplete nest building movements before actual nest building begins. A female Yellow Bunting may take a piece of grass or moss in its bill, carry it for a few seconds and then drop it (Howard 1929). A common Tern may make some nest hollowing movements shaping a very incomplete "scrape" and then abandoning it (Tinbergen 1931). Howard (1929) called attention to the incomplete coitions which occur in many species of birds, especially at the beginning of the breeding season. It is characteristic of all these movements, that if the external stimulating situation should be optimal the incompleteness of the actions must then be attributed to a lack of internal stimulation.

Since the knowledge of both preparatory and symbolic movements is still very fragmentary, further analyses of these certainly are needed.

The symbolic activities appear to have evolved as "language" from many sources. Many signal actions are exactly alike or very similar to symbolic actions. A striking case is found in the courtship of the Common Tern. This species, like other Terns, uses a fish in courtship. The courtship develops in three phases, each lasting several days. The first phase is performed in flight, a fish-bearing partner being joined by a fishless partner with both participating in a ceremonial flight. During a later phase of the courtship the members of such a pair (still temporary) alight on the ground and assume a special walk with the fish bearing bird still keeping its prey. During a third phase the fish is fed to the partner and often copulation results. This sequence of events leads to the interpretation of the first phases as "symbolic feeding." This symbolic feeding is always a part of the premating behavior of the species.

Symbolic feeding shows two characteristics that differentiate it from the real feeding which occurs during the incubation period, when the non-incubating partner feeds the incubating bird, and from the subsequent feeding of the young. First, the movements are markedly different from the real feeding movements. The fish bearer bends its head and makes a sound typical for this situation whereas the other bird does not make the begging movements but assumes another attitude, equally different from the begging movements.

Second, the courtship is often performed in exactly the same way, *but without the fish*. This elimination of the adequate object and the "formalization" of the movements are probably principles of very wide application. A comparative review of the courtship activities of widely different representatives

of the Terns, with especial reference to these "fish-flights" would be of great interest. As in comparative morphology, this work should be based on arranging series of behavior elements as found in related species, but at present the descriptions of these functional units which are to represent the members of such series are almost entirely lacking.

A third category of formalized signal movements has a different origin. During boundary flights, during the presence of a predator near the nest or young, and during courtship birds often display activities which closely resemble movements belonging to another functional cycle. In the Snow Bunting, for instance, threatening males often show movements highly simulating feeding movements, but which on careful observation appear to be incomplete; food is never taken and the bill does not even reach the ground (Tinbergen 1939). This behavior is shown especially during boundary disputes, when neither of the two birds actually attacks, but both indulge in threatening. I propose calling these incomplete feeding movements "*substitute feeding*," because they replace fighting activities induced by the situation.

Substitute feeding has been observed in several species of birds. I saw it performed by domestic cocks, which made pecking movements during short pauses in a prolonged fight. Lorenz (1935) observed the same. Pickwell (1931) also observed it in the Prairie Horned Lark during boundary fights, and I saw it under the same circumstances in Skylarks, Blue Tits and Coal Tits (Tinbergen 1938). Makkink (1936) describes substitute feeding in the European Avocet; food "mowing" is shown by this species when human beings come too near the nest; it is likewise shown during hostile encounters of Avocets *inter se*. The following observation, made by J. J. Ter Pelkewijk, refers to substitute feeding in the Garganey. A female with chicks foraging along the borders of a small canal, left this border as soon as the observer came too near, and as long as he stayed, the bird swam restlessly to and fro in the open water in the centre, stretching its neck and every now and then making the typical feeding movements ("slobbering") of this species. As soon as the observer withdrew, she resumed her ordinary attitude and continued foraging at the border. Since the water in the centre was quite clear, open and not covered with food plants as at the border, the observed movements probably should be interpreted as substitute feeding.

In species like the Avocet and the Garganey, which have very specialized feeding movements, the interpretation of substitute activities as feeding is easy; in species with less specialized movements the pecking movements might be, e.g., incomplete nesting movements.

Carpenter (1934) reports behavior which possibly is related to substitute activities in the Howling Monkey: "A most interesting type of behavior has been observed in two situations: (1) The observer is quiet and partially concealed; a howler behaves as if seeking to get a better perspective by approaching nearer to the observer; it may casually pluck leaves and eat them as it approaches, (2) an animal may approach another and begin feeding, continuing to eat casually until within striking distance of the animal approached; then it may spring on the second individual and begin playing. I have observed similar sham feeding as the clan males approached a solitary male" (p. 37). Carpenter's interpretation of this case differs considerably from the interpretation of substitute activities in lower Vertebrates which will be presented in the following.

Another common substitute activity in birds is preening. Huxley (1914) describes preening activities as part of the courtship in the Great Crested Grebe, and calls them "habit preening." A very clear cut example was observed by me in the European Starling. A male Starling, observed singing in front of a hole in March, showed aggressive behavior to all other Starlings which came too close to the hole. Whenever another Starling alighted within a few meters' distance he walked in a lowly bent, flat attitude towards him. When the stranger flew away, he reoccupied his singing post

and resumed singing; but in case the other stayed, the owner did not actually attack, but remained in front of him and instantly began to preen his feathers, with "exaggerated" vigor. As soon as the other went on, he instantly stopped preening and returned to his singing post. This was observed repeatedly. According to Lorenz (1935) the Crane *Megalornis g. grus* (L.) shows preening under the wing in hostile situations. In courtship, substitute preening is used in a more or less formalized way by several Anatidae e.g., the Shell-Drake (Makkink 1931) and the Grey Lag Goose (Heinroth 1910, Lorenz 1935).

Other substitute activities observed in birds are: sleeping, and probably singing. Instances of these types, however, seem to be less common than feeding and preening.

The different situations in which substitute activities occur allow a psychological interpretation. In all cases in which substitute activities are observed, external and internal causes seem to be sufficient to evoke the normal reaction in maximum intensity, but the normal reaction seems to be blocked in some way. Blocking of the normal reaction appears to be the result of different conditions.

First, the animal may be under the influence of two antagonistic drives, the simultaneous expression of which is a physical impossibility. In the boundary disputes, as well as in the situation "human being too close to the young," flight and attack are evoked at the same time. The result is that expression in both functional cycles is inhibited and that a substitute action occurs.

In the case of substitute activities appearing during courtship, the normal sexual responses seem to be blocked in another way. Substitute feeding as part of the courtship of the male Snow Bunting occurs only when the female refuses copulation initiated by the male. Since coöperation of the female is necessary for coition, the normal reaction of the male is blocked by the lack of the external releasing situation and the reaction chain breaks off. At this moment the substitute activity appears. It seems to me that this is the main cause of the appearance of substitute activities in courtship. The situation of the antagonistic drives, however, may also play a part. In the European Blue Heron the male's sexual drive is obviously counteracted by the flight drive and a newly mated individual repeatedly defends itself against too close an approach of the partner (Verwey 1930). A similar antagonism between flight reaction and sexual attraction might play a role in other birds too.

Still another situation may cause substitute activities. Exhaustion of the normal reaction after a number of performances may result in substitute behavior. A Whitethroat shows "injury feigning" when disturbed at the nest. It will repeat the reaction twice, thrice, and then sit down somewhere and preen. Preening in this case might be interpreted as substitute preening.

Huxley (1914) in describing substitute preening in the Great Crested Grebe calls it "habit preening." The fact, however, that the substitute actions appear to be fixed and characteristic of the whole species, suggests that they consist of inborn patterns. This seems to apply equally well to several of the substitute activities of the highest mammals. Man certainly has the innate tendency of substitute preening (scratching himself behind

the ear) in certain situations. Dr. G. Finch draws my attention to the fact that Chimpanzees when they are not allowed to take expected food, show typical substitute actions, which are approximately the same for every individual. Scratching is almost always involved.

Certainly in Man and presumably in lower animals too, habit may influence the kind of substitute action. Winding one's watch and lighting a cigarette may be mentioned in this connection.

MacDougall's thesis "... the animal in which any instinctive impulse is excited does not suspend action, even though the object be remote; the impulse probably always expresses itself in action" (1931, p. 207) requires completion, for the animal does not display random movements, but shows very special behavior, viz., special innate or learned patterns. A closer study will be necessary to understand why special substitute activities are linked to special situations. A few suggestions may be given.

Herring Gulls show "substitute nestbuilding" when threatening birds which intrude into their territory (Tinbergen 1936, Goethe 1937). The same substitute nest building is displayed on the feeding ground when defending prey against a competitor. Though fights for food occur throughout the year, substitute nest building is limited to the reproductive season. This shows that the direction of the outlet varies with the endocrine condition of the animal.

During an investigation of the egg rolling movements of the Grey-lag Gooses Lorenz and I found that, if the internal, specific cause of the rolling movements was exhausted by repeated performance of the reaction, the external (sensory) stimulus offered by the situation "egg out of the nest" caused the animal to move straws to the nest instead of the egg. This suggests that the substitute action tends to "use" a pattern closely related to the normal reaction.

In the same way as described for the symbolic actions, these substitute activities have been subject to "formalization" and to loss of the adequate object during phylogeny. In the premating period the male Blue Heron often makes the "snap-movement," which was interpreted by Verwey as the fish-capturing movement without a fish. The same applies to all the feeding actions mentioned previously: the prey is invariably lacking. The preening movements made by the Shelldrake prior to coition is formalized to a great degree.

The process of formalizing, when accompanied by the loss of the object, often renders it extremely difficult to recognize the origin of a substitute activity. A territorial male Stickleback threatens its opponent by assuming a nearly vertical position, head down, and at the same time making biting movements. At present it is not known whether this is derived from the nest digging movements or from feeding movements. The digging is the first phase of nest building. It is hoped that a comparison with closely related species together with a careful observation of the variability of the threatening movement will bring the solution. It may be of significance that *Gasterosteus*

pungitus, a species which builds a hanging nest above the ground and which does not dig, has similar, though still more formalized made of threatening. This would point to its interpretation as a feeding movement.

Obviously not all substitute activities have necessarily communicative function. The point in question is that "signal" movements often have originated as substitute activities.

It is evident that this review of substitute actions is highly fragmentary and tentative. Further study of them as well as of the other signal movements is needed.

Causal analysis in sociology as well as in other sciences requires experimentation. A beginning has already been made and we owe much to the use of "Attrappen" (models, artificial animals, decoys) for the analysis of mechanisms. However, sociological experiments seem to call for special caution. Several published experiments show certain shortcomings which are apt to lead to (and have led to) premature conclusions, and therefore will cause needless confusion.

In the first place, no experiments should be started before simple observation of behavior in natural surroundings has discovered the outlines of the behavior patterns. This is important in two respects. First, the undisturbed course of activities always gives provisional clues to causes; owing to changing conditions "natural experiments" result, a fact emphasized by Selous long ago (1901), and stressed again by Verwey (1930) and by Lorenz (1935). Second, by watching undisturbed behavior without premature restriction to one functional cycle or even one reaction, one is forced to keep in mind that different reactions have different releasing mechanisms. The neglect of this fact has often caused needless scientific quarrels. As an example the discussions between Hess and Von Frisch (Von Frisch 1914) on the color discrimination of the honeybee may be mentioned here. Hess claimed color blindness, basing his view on good experiments, while Von Frisch, with equally convincing experiments, could prove color discrimination. The diversity of views was due to the fact that Hess analyzed the flight reactions, which are directed to the part of the visual field that offers light of the highest (subjective) intensity, while Von Frisch analyzed the feeding reactions which are directed to flowers of special colors.

The same confusion can still be found in studies of animal sociology. Allen found (1934) that a male Ruffed Grouse in sexual condition showed the same first reaction to approaching males as to approaching females of the same species. The author concludes that the male Ruffed Grouse (and "birds" in general) does not discriminate between the sexes. Yet the next reaction in the chain is different towards females than towards males. This second reaction, therefore, shows that the bird can discriminate. In the same way one could conclude that a Jackdaw cannot discriminate between a bathing suit and a Jackdaw because it shows the social alarm call to both. In this species other reactions also show that the animals discriminate much more sharply than could be expected by examination of the alarm call.

Another source of confusion affects directly the nature of an experiment

in general. The sensorial perception which releases *R*'s reaction is always an interrelated whole of several factors, a "Gestalt". If the experimenter presents the optimal situation, less one factor, the reaction will often occur "just as well" as after optimal stimulation. A slight difference of intensity may escape attention owing to the fluctuations due to other causes. This result, however, does not permit a conclusion regarding the value of the isolated factor. The same factor can be shown to exert influence when added to a situation which by itself would not evoke the reaction. The following facts may serve as an illustration. The Three-spined Stickleback is sexually dimorphic. In order to test the question whether the red belly of the male had any influence on the female's egg laying activities, Leiner (1930) observed courtship and egg laying in monochromatic light of different colors. Finding the behavior following a "normal" course, he concluded that the colors of the male were without influence. Ter Pelkwijk & Tinbergen, however, could show that the red color was effective by evoking the female's reactions by means of red painted dead females, which were ineffective before painting. The species is capable of discriminating red, as shown by experiments concerning the feeding reactions.



Fig. 2. Courtship-display of *Gasterosteus aculeatus* L. Female (right) in "signal"-attitude, indicating readiness to follow the male (from Ter Pelkwijk & Tinbergen 1937).

The difference in methods is a minor one, though of considerable importance. The dead female lacked sufficient marks to evoke the reaction. When the factor *red* was added, the releasing value of the situation was increased. Living animals apparently offer signal movements which remain effective after the color factor has been eliminated.

The complex of influential factors in the Gestalt can be effected by the intensity of the animal's motivation. Abnormally high motivation has a profound influence on the structure of the perceptual field. Factors that are influential in a normally motivated animal may become entirely worthless

when the animal's motivation rises. In reflex-like, released movements, this results in a "lowering of the threshold" of the reaction. In oriented directed movements, the disappearance of parts of the perceptual field is shown by the fact that the animal ceases to direct its activities towards certain details (Tinbergen & Kruyt 1937). During experiments it is necessary, therefore, to keep motivation as "normal" as possible, or at least at a same degree throughout. The fact that an isolated male canary courted a woolen doll representing a chick does not allow the conclusion that a normally motivated male would not require some more recognition marks in its sex partner (Koehler 1926).

Another point of importance is the fact that one signal may have more than one function. It has been proven by experiment that the red color of the male *Gasterosteus* has a signalling function to other males, evoking attack in a territorial male, and evoking flight in a male outside of its territory. Other experiments already cited prove that the red color also has an influence on the female. The red belly, therefore, is at the same time a "gladiatorial vestment" and an "attracting device".

Consequently, from experiments showing the influence on the male only, it cannot be concluded that a certain structure has no influence on the female. To mention a concrete example: the fact that the "moustache" of the male Flicker releases attack of a territorial male, allows by no means the conclusion that this is its only or even its primary function. Yet Noble went beyond this conclusion by stating: "It follows that sexual selection in the Darwinian sense, that of female choice, has played no role in enhancing the color of the Flicker." (1936, p. 281).

I am aware of the fact that this review of social organization is very schematic. I would like to stress once more that in most cases communication processes are much more complicated than mere fixed innate reactions. Recognition of the existence of signals does not imply the assumption that every signal works by means of an immediate, innate reaction of *R*. Many "internal" processes in *R* may influence the mode of response: endocrine processes and the nervous processes of summation, learning and all so-called "higher mental processes."

A special kind of these internal nervous processes may be mentioned because it concerns an important problem of evolution: the problem of sexual selection. Apart from having a momentary or a summative stimulating influence, signal structures may enable *R* to *make a choice* between different individuals which show differences of degree in the development of structural or behavioral signals. That in species with a pronounced sexual dimorphism the animals of one sex (ordinarily females) make a choice between several individuals of the other sex, is probable in the case of some birds. Actually this has been proven by Noble (1938) in the case of the Jewel Fish. He was able to evoke an expansion of the male's erythrocytes by injection with yohimbine without changing its behavior. The females preferred the excessively colored males.

SUMMARY

Social integration depends on relations between Actor and Reactor.

Such a relation comprises always an action of *A* influencing *R*'s sense-organs; subsequently through nervous system and effectors *R*'s response is effected.

Activities of R. To find the external causes, *R*'s behavior has to be divided into its components. Special mention is made of two groups of behavioral elements, differing according to the way in which sensory stimuli influence them: reflexes and similar reactions which are merely *released*, and oriented movements (tropisms, taxis) which are *directed* by external stimuli.

Arguments are presented for the conclusion that even "simple reactions" of *R* may be composed of two simultaneously working mechanisms, an "instinctive action" (Lorenz) and a "taxis".

Endocrine and neural processes (summation, conditioning, "higher mental processes") may influence the innate mechanism (Schema).

Learning processes may be confined to special reactions and to special parts of the perceptual field.

Means of communication proper. *A*'s behavior may evoke either the same behavior in *R* or a different reaction.

In two respects the external stimuli influencing *R*'s reaction may be only part of the external situation received by *R*'s sense organs: a) only one or two of the sense organs may have influence, b) only some factors of the receptual field may be effective. Thus we are led to the conclusion that there must exist special S-R sequences (mechanisms, Schemata) between certain factors of the sensorial field and certain reactions.

These innate mechanisms are also the basis of the highly modified, conditioned and other "higher" responses of *R*.

The behavior of A. *A*'s activities provide signals for *R*. Movements that act as signals are sometimes "emphasized" by morphological structures.

Signal movements, like morphological signals, are often very specific ("unwahrscheinlich").

Signal movements have evolved from "preparatory movements," "symbolic actions" or "substitute actions".

Substitute activities appear when the reaction evoked by external and internal stimuli is blocked, either by an antagonistic reaction, or by lack of stimulation for the next reaction of the chain, or by exhaustion of the normal reaction.

Substitute activities, like symbolic actions, as signals have undergone profound changes during evolution: they became formalized and the adequate object was eliminated.

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DISCUSSION

MacGinitie: Can learning be a part of the experience of birds if that learning has to do with something not having been repeatedly a part of the evolutionary experience? In the evolutionary experience of a certain bird species there are many situations which reoccur many times. Can a bird learn in any case without a background in this evolutionary experience?

Tinbergen: There is no evidence for this influence of "evolutionary experience". The only experiments I know of are those of MacDougall with rats which showed that learning ability for a certain situation was improved in the offspring of trained generations even after application of a contra selection. However, this work has been criticized rather severely by geneticists.

MacGinitie: I have seen birds and mammals in circumstances in which they could not learn much of benefit to them. For instance, I have seen a woodpecker drill a hole for acorns in the side of a house where it was thin, pack into it perhaps a bushel or two of acorns and starve during the winter because he couldn't get at the acorns. In cuts made during road building gophers with a tendency to close an opening expend a

great deal of useless energy by working themselves poor trying to close that hole opening on a vertical surface of a road cut. These experiences do not occur every day.

Tinbergen: Apparently, the woodpecker offers an example of an immediate reaction to a few elements of the external stimulating situation, and that it did not occur to him at all that the wall of the house was *not* solid. Before interpreting such observations it should always be considered that an animal often, or perhaps always, does not see the environment as we see it. It seems quite possible to me that the storing reactions follow "automatically" the drilling of the hole, and that the difference between solid and non-solid wall did not exist at all for the bird. Consequently, the storing activity would not be a failure but a satisfaction, and there would be no incentive for a change of behavior by learning.

Emerson: Early naturalists were inclined to assume function in everything they saw. Some of the criticism applied to the naturalist and also to modern ecology is due to such superficial guessing. At the same time modern experimentation of this type is showing that many of these organisms do have functional relationship to the environment. The mechanism of natural selection could explain these functions reasonably well. Nevertheless, naturalists dealing with a great many species of the same genus are impressed by the number of seemingly non-functional characteristics. It is unnecessary to assume direct function for every specific characteristic according to modern genetics. If a character develops through selection, the genes involved may influence other structures in the body.

Tinbergen: Obviously, a function can not be found for every structure. A few hairs or spines on the thorax of an insect may be mere by-products and, in a sense, be without function, but in all cases of highly specialized structures it is necessary to assume a long, directed development, including many evolutionary steps, and in such cases it seems improbable that the structure should have no function.

Emerson: At the same time the existence of a highly specialized functional structure would be difficult to explain through any other process than by natural selection working on genetic variation through a long period of time.

Noble: Fighting in fish is correlated primarily with the territorial habit. It is well known that the female salmon seeks a breeding territory and that the males contend with one another for the opportunity of fertilizing the eggs. The literature contains various references to salmon having fought vicious battles, using their enlarged snouts as battering rams. In striking contrast to salmon, non-territorial fish, such as tuna, may migrate enormous distances without having any marked sexual dimorphism. The dimorphism of the salmon is definitely correlated with the territorial habit and not merely with long migration.

Emerson: The European cuckoo supposedly lays its eggs in various other birds' nests and the color markings of its eggs are the same as those of the host. What is the explanation of this?

Tinbergen: It is well known that an individual cuckoo lays in the nests of the same species during its whole life, and that its eggs resemble those of the particular host very closely, and further that a cuckoo lays in the nests of the species that reared it. The fact that the cuckoo lays eggs of the same color as those of the host may be due, in part, to the selective influence of the host. Rensch showed that several host species removed eggs from their nests that differed too much from their own eggs. They threw out the egg differing from the majority of eggs, without recognizing their own eggs. When Rensch changed all eggs but one for an equal number of stained eggs, the birds threw out their own egg and incubated the stained ones.

Mayr: It is highly probable that the cuckoo will lay in the nest of the species by which she was raised but there is no proof for it. In Finland, several species of birds lay solid blue eggs. The cuckoos parasitizing on these species also lay blue eggs. In Germany, very few cuckoos lay blue eggs. On the other hand in the cow-bird, also a nest parasite, no such adaptation of the eggs has been observed. If a cuckoo does not find enough nests of her favorite host species, she will lay an egg into the nest of another species, which, however, may throw out that egg.