Introduction to
Ethology

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This volume is a translation of the first edition of *Einführung in die Verhaltensforschung,* published by Paul Parey Verlag, Berlin and Hamburg, in 1976. It contains additional material that was included in the second German edition of the work, which was published in 1979 concurrently with the preparation of this translation.

Preface

Ethology, the study of the biology of behavior, has grown tremendously during the last few decades. The large number of accumulated facts is difficult to survey, understanding and an appreciation of the ethological approach to the study of behavior have grown, and the number of attempts at holistic explanations for certain behavioral phenomena has increased. Because of this development it has become more difficult to gain an overview of the field, to keep up with new developments, and to update the subject matter by the inclusion of new facts in the proper place. The nonspecialist is unable to evaluate the more general statements in the popular literature, especially when such works are aimed at a broader audience.

Hence, this book has a dual purpose: (1) to lend some order to the dizzying array of information and thus simplify inquiry into ethology; and (2) to present relevant facts and knowledge that will help the reader confronted with numerous studies and articles in the ethological literature.

It is always difficult to select material for such a survey and to arrange it in some logical manner. Hence, this volume offers but one of many possible ways to present this material. This book is based on a course of lectures of the same title that I have offered during the past 12 years at the universities of Braunschweig, Berlin, and Bielefeld in West Germany. These lectures were continually modified in response to questions that indicated what knowledge in which particular places would enhance the understanding of certain relationships. Thus, this book can be regarded in its organization as a sort of stepping-stone on the path to a solution. This, I hope, will be the clearest and simplest way to present the relationships among facts, hypotheses, and theories.

For reasons of space, limitations existed on the selection of material. This is why the physiological basis of behavior, which is generally offered in texts and surveys in physiology, is treated less comprehensively than the area of "classical" and comparative ethology. However, even here focal points had to be chosen; thus, the treatment of topics in the currently popular style of teaching by illustration and example is somewhat uneven. As a result, some areas, such as aggression, where general regularities of behavior and methods of study can be clearly demonstrated, have been presented in more detail than have some others. The extensive area of learning has been presented in comparatively condensed form, since numerous texts on the subject are readily available.

Since this is an introduction that is primarily designed to provide the means for a more intensive involvement with the field, the author has not participated in the sometimes controversial discussions about basic concepts in the various "schools" of ethology. These are pointed out in those instances where certain kinds of explanations and theories are still being debated.

With respect to humans it must certainly be accepted that some characteristics of human behavior developed as the result of the evolutionary process, and are hence comparable to corresponding aspects of the behavior of animals. Hence, ethology is in a position to point out a certain regularity that in some way is also applicable to humans. Such applications must, however, be made with great care since insufficiently supported comparisons could, as has been shown repeatedly in the past, only harm ethology in its attempts to make more general statements about behavior, and thus to aid in a better understanding of human behavior as well.

Ethology is a biological science. Each behavioral characteristic of an animal can be understood and interpreted properly only when its biological significance, i.e., what its importance is for the particular species in its natural environment, is known. This has not always been the case in the history of the study of animal behavior to the extent that is necessary. The continued reference to such ecological relationships, and to adaptations that have developed during the course of evolution, is an additional aim of this book.

Since an introduction of this kind is also directed to readers interested in ethology who may not have any special biological background, it was necessary to explain certain basic concepts that are important for an understanding of the biological significance of a particular behavior. These are found in the text and in footnotes. This also applies to special terms that are not properly a part of ethology.

The scientific names of the animal species cited are given only when a proper common name is not available.

I am indebted to the illustrator, Mr. Klaus Weigel, of the Faculty of Biology of the University of Bielefeld, for the preparation of the drawings, which he carried out with great care and understanding. Thanks are also due my colleagues and assistants in Bielefeld for their stimulating ideas and discussions during the writing of this book.

Klaus Immelmann

Bielefeld, March 1976

This English edition contains additional material that was included in the second German edition, which appeared while the English translation was in progress. Two new chapters, one on domestication and one dealing with ethology and human behavior, were added. These chapters deal with research

that may lead to a better understanding of human behavior as well. However, the facts that have been collected so far permit only limited conclusions to date. For this reason, these chapters are of a more speculative nature than the previous chapters. Indeed, the last chapter was added only in response to requests for its inclusion, although there has been no change in the views expressed on this subject in the introduction to the first edition.

Klaus Immelmann

Bielefeld, July 1980

Contents

Aims, Methods, and Areas of Ethology

1.1. Definitions of Concepts

The goal of ethology is the investigation of behavior with the methods used in the natural sciences. However, to define the concept of *behavior* is not as simple as it may seem, and the use of this term in the literature is not consistent. Here is a problem from which ethology has suffered in particular: the difficulty of clear definitions. This is due to the variety of the phenomena studied, which in turn has led to some premature interpretations.

As a rule, the word BEHAVIOR is used in a very broad sense in ethology. It refers to movement patterns, vocalizations, and body postures of an animal, as well as to all externally recognizable changes that serve in reciprocal communication and that can release behavior patterns in another animal, including changes in coloration or the release of odors. Hence, behavior is not restricted to movements, and an animal that appears to be quite inactive may "behave" in this use of the word. For example, a male antelope standing motionless on a termite hill indicates his ownership of a specific area as its territory, and a female butterfly releasing an odor (pheromone) with which to attract a male "behaves" according to this broad definition.

The term ETHOLOGY (from the Greek *ethos*—habit, convention), as is used today for the biological study of behavior, is quite old, but it was originally not used as it is today. The term first appeared in the middle of the 18th century in publications of the French Academy of Sciences, where it was applied then, as later in the 19th century, to the description of life-styles in general, i.e., what is at present considered under the heading of the ecology or general biology of an animal species. The application of the term to the study of behavior in a more limited sense was introduced in 1950 by N. Tinbergen.

In the early years of ethology the synonym *animal psychology* (German: Tierpsychologie) was widely used. Today, with the increasing physiological emphasis in ethology, the term is no longer as appropriate and has come into disuse as a result. However, the term ANIMAL PSYCHOLOGY is still applied in this more limited sense by ethologists when it refers to individual, subjective (to the degree that this can be investigated by objective criteria), and disease-related phenomena in the behavior of animals. Important psychological knowledge has been gained from animals in the zoo and circus. In the United

States and Great Britain the subject matter of ethology is usually referred to by the term ANIMAL BEHAVIOR in a more general sense. The term COMPARATIVE PSYCHOLOGY refers to the comparison of species with respect to categories of behavior traditionally of interest to American psychologists, such as learning, motivation, and others that were usually investigated with the animal as a model for human behavior.

1.2. Descriptive Ethology

Ethological analysis consists of two important steps: observation and the interpretation of an animal's behavior. Interpretation or explanation in turn has its functional, causal, and phylogenetic aspects, which deal with the adaptiveness of behavior, and the underlying mechanisms and probable course of development of the behavior during its evolution. The "goal" of ethological research has been reached when it is possible to predict the future behavior of an animal or a sequence of behavior patterns and to justify the explanations.

The starting point and basis of the scientific study of behavior is a precise and detailed compilation of behavior patterns that are typical for a species that is as complete as possible. In the early years of ethology this "ethogram" consisted primarily of the analysis of protocols or notes taken during observations. Today, various aids are available that not only simplify the taking of notes but make possible a more accurate analysis and a more permanent storage of information. It is now possible to use event recorders, and especially tape recorders, which allow dictation of the observations without the need to take one's eyes off the animal. Activity can be registered automatically with photo cells, where an animal interrupts a light beam or activates a magnetic contact that triggers counters or event recorders. Videotapes, film, and audiotapes permit the analysis of movement and sound patterns in great detail. These can then be compared and quantitatively analyzed. This is facilitated by the use of slow or fast motion and single-frame analysis, and in acoustic research by the use of sound spectograms. Finally, computers make possible the rapid analysis and plotting of results.

The part of ethology that deals with the compilation of ethograms is sometimes referred to as the morphology of behavior because behavior patterns are just as unique to a species as are their morphological characteristics (see Section 3.9.1), and ethologists often use the methods of morphologists when dealing with phylogenetic questions.

From the very beginning ethologists tried not to look at the behavior of a species in isolation, but they compared it to other species as well. Good examples are the studies of Charles Otis Whitman on doves and Oskar Heinroth on ducks and geese. Such compilations of behavior repertoires of an entire genus or family, called a "group ethogram," can give us indications about the relationships within systematic groups and be a valuable contribution to the systematic classification of a species. It can further clarify the phylogenetic development of single behavior patterns (see Section 10.3). The

emphasis on comparative, phylogenetic questions in ethology is reflected in the term COMPARATIVE ETHOLOGY (German: *vergleichende Verhaltensforschung*).

Another important task of descriptive ethology is to bring some order into the numerous observations, i.e., to name behavior patterns, to categorize them, and if warranted, to break them down into more basic, recognizable units. We already referred to the difficulty in finding truly objective terms that are free from the excess meaning that is present in the popular use of words. In naming behavior patterns it is best to describe their form. *Spreading of gill covers*, *head-nodding*, and *raising of wing* are neutral terms free of excess meaning. It is more difficult to name a behavior according to its function, at least when this occurs before the function or meaning of the behavior is precisely known. An example is the term *courtship flight* for the flight found in several species during which birds sing. The term is misleading inasmuch as most of these songs are not components of early courtship but rather they attract a female or indicate the possession of a territory. Still, the term is widely used. However, one is not justified to name a behavior pattern according to function when the behavior occurs in more than one context and hence may have several functions.

A classification of behavior can be made according to several criteria. Most important are FUNCTION and LEVEL OF INTEGRATION. In the first, a distinction is made between several "functional systems," which refer to a group of behavior patterns with the same or a similar purpose or effect. Examples are locomotion, eating, courtship, care of young, or aggression. Within each functional system further subdivisions can be made. Thus, care of young includes behavior patterns of nest building, feeding, or defense of young, while eating includes behavior patterns involved in obtaining, preparing, or in some cases the storing of food.

Another principle of classification is based on the level of integration of behavior patterns. The behavior is arranged hierarchically (see Chapter 4) from the simplest behavior elements (e.g., movement of a single muscle or group of muscles) to units of an intermediate level of complexity (e.g., the movement of individual parts of the body) up to the complicated behavior sequences that consist of many components. The less complex a behavior component, the more frequently it generally appears not only as an element of a single functional system but also in several behavior categories.

In ethological investigations it is important that the appropriate level of integration be selected for a particular problem. If one studies the dependence of song on the male sex hormone in a species, then it is sufficient to look at the entire song as a unit. However, if one is interested in the information content of a song for certain conspecifics, e.g., rivals or sexual partners, then each discriminable song component must be examined singly or in various combinations with the others.

Descriptive ethology is not limited to a mere inventory of behavior patterns of a species. Ethologists can also provide important conclusions about the organization of behavior. This requires that behavior be not only qualita-

tively described but quantitatively assessed as well so as to determine which behavior components occur together, which exclude one another, or which occur in what particular temporal sequence. A temporal order can be the expression of common or opposing internal causes with respect to the behavior patterns in question (see Chapter 4).

1.3. Experimental Ethology

A sequence and temporal organization of behavior patterns can be determined simply by description. Broader statements about causation can usually be made only after some artificial manipulation of the behavior has occurred. In the beginning such experiments were quite simple. This is illustrated by one of the classical examples in ethology. The female of the sand wasp *Ammophila campestris*, digger wasp, deposits its eggs into nests that she has dug in the ground and into which she carries food she has caught and immobilized or killed—usually some caterpillar. After laying an egg, she closes the nest but returns when the egg has hatched to provide the larva with food as needed. Finally, she brings three to seven caterpillars, sufficient nourishment until the larva metamorphoses, and closes the nest. Observation alone is sufficient to learn about the sequence of this broad care behavior, which consists of an orderly sequence of many components. Furthermore, one can recognize that the female's behavior is appropriate to the situation, i.e., that the size and number of the prey is adjusted to the size and hence the food requirements of the larva. It is not known how the sand wasp, which simultaneously cares for several nests that contain larvae of various ages, remembers their size and hence the amount of prey needed at each nest. This cannot be determined by mere observation.

However, even a simple experiment can help here. The female can be deceived by the addition or removal of larvae. As a result of such manipulations, the wasp will adapt her behavior to the new situation. She will bring either more or less prey than she would have otherwise. Hence, it is not the memory of her own previous brood care behavior at the same nest that determines how much food is brought, but the information available from the content at each nest. However, this adaptability of the wasp shows a peculiar temporal limitation: an artificial change in amount of prey in the nest is compensated for only when this is done prior to the early morning "inspection
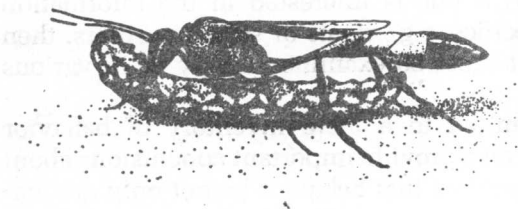

Fig. 1.   A sand wasp carries a caterpillar she has caught to the nest (after Baerends 1941, from Tinbergen 1951).

visit" of the wasp. Once the female has inventoried the food situation at a nest, the information obtained then determines how much food is brought for the remainder of the day. After that, the wasp will not respond to changes in the amount of prey in the nest.

The conclusions drawn from these simple manipulations give an indication of the opportunities in experimental ethology, which employs increasingly sophisticated methods. Models play an important role as well. The word MODEL is used in ethology in a different sense from that in everyday language, where one may think of as realistic an imitation of an object as is possible. Ethologists often use quite unnatural models. Any representations at all are considered models, as long as they are effective in releasing a response in an animal so that the stimulus properties that elicit a given behavior may be analyzed. Hence, models of only part of an animal's body are used, such as a beak or head. Various properties of the object to be imitated are changed (enlarged, made smaller, presented in a different form or color). Even completely unnatural objects (e.g., wooden spheres or cubes of various colors) may be used as models, as well as tape recordings or vocalizations and artificial odors. Elements of the natural example or cues can be changed, which makes it possible to test the effective components of the stimuli. Thus, it is possible in acoustic research to detect by changing tape-recorded sounds (e.g., transpositions of components in total sequences, changes in rhythms, elimination of certain frequencies) which characteristics of biologically significant sounds are important, for example, in the song of a rival.

One of the earliest experimental investigations, in which models were used to a greater extent, dealt with the pecking reaction of young herring gulls. Hungry gull chicks peck at a red spot on the yellow bill of the adult bird and thus trigger the regurgitation of food. Which cues on the gull's head were effective in releasing the pecking response in the chick was determined with the aid of cardboard models on which various combinations of colors of the spot as well as the bill 'and head were painted. The results of the experiments show that the necessary cues are located on the bill, while the

Fig. 2. A herring gull chick pecks at the bill of the adult bird (after Tinbergen 1951).
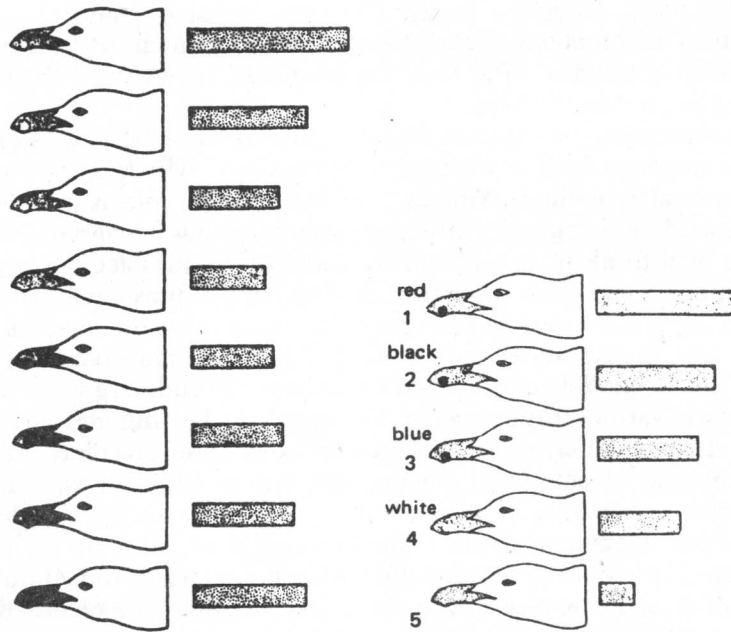
Fig. 3 (left).   Cardboard models used to test the effectiveness of the spot on the lower part of the bill in releasing pecking. The length of the bars indicates the relative frequency with which inexperienced herring gull chicks peck at the model. They show that the frequency of pecking increases with **greater** contrast of the spot against the background (after Tinbergen 1951).

Fig. 4 (right).   The color of the spot is also important: a bill with a red spot releases more pecking than one with other colors, even though they may show greater contrast to the background (after Tinbergen 1951).

shape of the head, its size, and its color have no effect. On the bill, the red spot plays an important role. It is effective by its color as well as by the degree of contrast from the background of the bill. Thus, if models with medium-gray bills and spots ranging from white to black through various shades of gray are presented, the chick's pecking is released more frequently the "whiter" or "blacker" the spot is, i.e., the more it contrasts with its background. On the other hand, a model of the natural yellow bill color and a red spot is more effective than a black spot, although the latter offers more contrast.

Similar analyses of relevant stimulus situations using models have since been carried out on a number of animal species. Usually, the models are presented either successively or simultaneously with two or more stimuli. Simultaneous presentation offers the advantage of immediate comparability for the animal, while during successive tests habituation and fatigue can lead to a situation in which the animal's state at the beginning of the test is not comparable to subsequent presentations of the stimuli. Hence, the reactions would not accurately reflect the "value" of the model.

Fig. 5. A male zebra finch courts a female model, which consists of a stuffed skin attached to a perch with a wire. This test allows one to find out if the visual, nonmoving characteristics of the female are sufficient to release sexual behavior in the male and which courtship patterns of the male can be elicited without the auditory (voice) and dynamic-visual (movement) cues normally provided by the female. In successive presentations this test can be used to examine sexual preferences. This can then be compared with tests of simultaneous presentations (see Figure 46, Section 7.4.7.1).
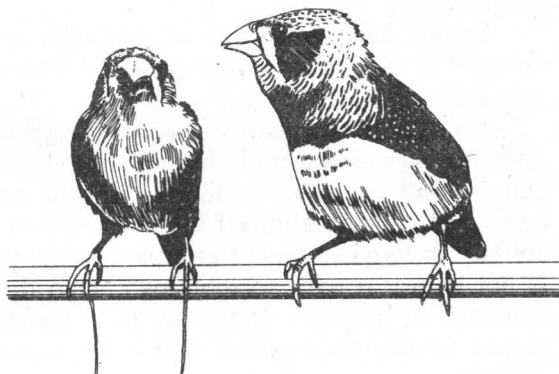
Various subareas of ethology have their own specific methods of testing and will be discussed in the appropriate places.

1.4. Areas of Ethological Research

It is possible to define several areas of ethology beyond the classification as descriptive and experimental ethology. These areas focus on specific questions that are treated either descriptively or experimentally. There is much overlap with other areas of biology such as ecology, physiology, and genetics. While their methods may be used and similar questions asked, these refer not to body structures but to the behavior of the animals. Sometimes it is not possible to distinguish whether a study is more ethological, ecological, or physiological. Hence, it is not always possible to delimit an area of ethology precisely.

The area of ECOETHOLOGY is a comparatively new branch of ethology in which the relationships between the behavior of a species and other living and nonliving components of environment are investigated. Ecoethology can proceed in one of two ways: it can emphasize or focus either on a group of species or on a particular habitat or biotope. In focusing on the biotope, one would be interested in the parallel behavioral adaptations that are found in certain habitats, for example, deserts or tropical rain forests. This is of interest even in species that are not closely related, and whose behavior may be considered typical for the particular biotope. In the second case, we look at a group of closely related species with an interest in how the various species differ from one another and whether or not and how such differences can be considered adaptations to various habitats, i.e., what is the "biological" significance of a behavior. Especially interesting results can be expected when within a related group of species there is one that lives in an entirely different