

Facsimile of
On aims and methods of Ethology

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On aims and methods of Ethology

By N. TINBERGEN¹⁾

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Ethology, the term now widely in use in the English speaking world for the branch of science called in Germany „Vergleichende Verhaltensforschung“ or “Tierpsychologie” is perhaps defined most easily in historical terms, *viz.* as the type of behaviour study which was given a strong impetus, and was made “respectable”, by KONRAD LORENZ. LORENZ himself was greatly influenced by CHARLES OTIS WHITMAN and OSKAR HEINROTH — in fact, when LORENZ was asked at an international interdisciplinary conference in 1955 how he would define Ethology, he said: “The branch of research started by OSKAR HEINROTH” (1955, p. 77). Although it is only fair to point out that certain aspects of modern Ethology were already adumbrated in the work of men such as HUXLEY (1914, 1923) and VERWEY (1930), these historical statements are both correct as far as they go. However, they do not tell us much about the nature of Ethology. In this paper I wish to attempt an evaluation of the present scope of our science and, in addition, to try and formulate what exactly it is that makes us consider LORENZ “the father of modern Ethology”. Such an attempt seems to me worthwhile for several reasons: there is no consistent “public image” of Ethology among outsiders; and worse: ethologists themselves differ widely in their opinions of what their science is about. I have heard Ethology characterised as the study of releasers, as the science of imprinting, as the science of innate behaviour; some say it is the activities of animal lovers; still others see it as the study of animals in their natural surroundings. It just is a fact that we are still very far from being a unified science, from having a clear conception of the aims of study, of the methods employed and of the relevance of the methods to the aims. Yet for the future development of Ethology it seems to me important to continue our attempts to clarify our thinking, particularly about the nature of the questions we are trying to answer. When in these pages I venture once more to bring this subject up for discussion, I do this in full awareness of the fact that our thinking is still in a state of flux and that many of my close colleagues may disagree with what I am going to say. However, I believe that, if we do not continue to give thought to the problem of our overall aims, our field will be in danger of either splitting up into seemingly unrelated sub-sciences, or of becoming an isolated “-ism”. I also believe that I can honour KONRAD LORENZ in no better way than by continuing this kind of “soul-searching”. I have not hesitated to give personal views even at the risk of being considered rash or provocative.

¹⁾ Dedicated to Professor KONRAD LORENZ at the occasion of his 60th birthday.

Ethology a branch of Biology

In the course of thirty years devoted to ethological studies I have become increasingly convinced that the fairest characterisation of Ethology is "*the biological study of behaviour*". By this I mean that the science is characterised by an observable phenomenon (behaviour, or movement), and by a type of approach, a method of study (the biological method). The first means that the starting point of our work has been and remains inductive, for which description of observable phenomena is required. The biological method is characterised by the general scientific method, and in addition by the kind of questions we ask, which are the same throughout Biology and some of which are peculiar to it. HUXLEY likes to speak of "the three major problems of Biology": that of *causation*, that of *survival* value, and that of *evolution* — to which I should like to add a fourth, that of *ontogeny*. There is, of course, overlap between the fields covered by these questions, yet I believe with HUXLEY that it is useful both to distinguish between them and to insist that a comprehensive, coherent science of Ethology has to give equal attention to each of them and to their integration. My thesis will be that the great contribution KONRAD LORENZ has made to Ethology, and thus to Biology and Psychology, is that he made us realise this close affinity between Ethology and the rest of Biology; that he has made us apply "biological thinking" to a phenomenon to which it had hitherto not been as consistently applied as was desirable. This is, of course, not to belittle LORENZ's concrete, factual contributions, which we all know are massive, but I submit that the significance of all his contributions is best characterised by saying that he made us look at behaviour through the eyes of biologists. I also submit that this is an achievement of tremendous importance and that, if anything deserves the much-abused name of "a major breakthrough", LORENZ's achievement does.

I shall devote the next pages to some remarks on each of these four problems as they apply to behaviour. If these remarks appear to some readers unsophisticated, I should like to remind them of the fact that Ethology is a science in its infancy, where even a little plain common sense can help.

Observation and Description

One thing the early ethologists had in common was the wish to return to an inductive start, to observation and description of the enormous variety of animal behaviour repertoires and to the simple, though admittedly vague and general question: "Why do these animals behave as they do?" Ethologists were so intent on this return to observation and description because, being either field naturalists or zoo-men, they were personally acquainted with an overwhelming variety of puzzling behaviour patterns which were simply not mentioned in behaviour textbooks, let alone analysed or interpreted. They felt quite correctly that they were discovering an entire unexplored world. In a sense this "return to nature" was a reaction against a tendency prevalent at that time in Psychology to concentrate on a few phenomena observed in a handful of species which were kept in impoverished environments, to formulate theories claimed to be general, and to proceed deductively by testing these theories experimentally. It has been said that, in its haste to step into the twentieth century and to become a respectable science, Psychology skipped the preliminary descriptive stage that other natural sciences had gone through, and so was soon losing touch with the natural phenomena.

Ethology was also a reaction against current science in another sense: zoologists with an interest in the living animal, overfed with details of a type of Comparative Anatomy which became increasingly interested in mere homology and lost interest in function, went out to see for themselves what animals did with all the organs portrayed in anatomy handbooks and on blackboards, and seen, discoloured, pickled and "mummified" in standard dissections.

Much of the early ethological work contained a good deal of description and, in these first days of reconnaissance, of taking stock, we tended to think of "ethograms" as hundred-page papers which could contain about all we wanted to know about a species. Even this modest aim, a very sketchy description, was reached for very few species only. We must hope that the descriptive phase is not going to come to a premature ending. Already there are signs that we are moving into an analytical phase, in which the ratio between experimental analysis and description is rapidly increasing. This is a natural outcome of LORENZ's own work, and it is, of course, imperative that work on causation should be intensified and refined. However, we would deceive ourselves if we assumed that there is no longer a need for descriptive work. Misgivings about this wholesale swing towards analysis have been expressed, for instance by NIELSEN (1958), who wrote: "In 'modern' Ethology nobody pays the slightest attention to anything but the 'why'. It is a very peculiar situation: we have a science dealing with the causal explanation of observations but the collection of the basic observations is no longer considered a part of the science" (NIELSEN 1958, p. 564). While at first glance this is a surprising remark, which very few Ethologists and non-Ethologists will agree with, we cannot brush it aside entirely.

The issue is admittedly not a simple one. Description is never, can never be, random; it is in fact highly selective, and selection is made with reference to the problems, hypotheses and methods the investigator has in mind. In the early days of Ethology these limitations of our descriptions were not always obvious — mainly, I believe, because most of us were not sufficiently conscious of our limited aims, and certainly were not sufficiently aware of the criteria we used for selection.

The variety of behaviours found in the animal kingdom is so vast, and their description is so much more laborious than the description of structure, that selectiveness of description will become increasingly urgent. This will only be possible by a more explicit formulation of the problems we wish to study, and by growing certainty about the nature of the data we need. Yet even with the most economic procedures the amount of description to be done will long remain very large, so large in fact that we shall soon have to resort to a policy of filing descriptive material in libraries or archives (including film libraries) rather than publishing it in the usual journals. Already there are journals which demand a reduction of descriptive material to the absolute minimum required for an understanding of the experiments reported on (or even to less than this minimum); the descriptions (and often the argument behind the work) one has to pick up in personal conversations at conferences.

However, if we overdo this in itself justifiable tendency of making description subject to our analytical aims, we may well fall into the trap some branches of Psychology have fallen into, and fail to describe any behaviour that seems "trivial" to us; we might forget that naive, unsophisticated, or intuitively guided observation may open our eyes to new problems. Contempt for simple observation is a lethal trait in any science, and certainly in a science as young as ours.

It seems to me that one of the lessons we can draw from LORENZ's work is that our science will always need naturalists and observers as well as experimenters; we must, by a balanced development of our science, make sure that we attract the greatest possible variety of talent, and certainly not discourage the man with a gift for observation. Instead we should attract such men, for they are rare; we must encourage them to develop their gifts of observation and help them ask relevant questions with respect to what they have seen.

Causation

At an early stage in his work (e.g. 1935, 1937) LORENZ made three statements which I should like to emphasise because I think that modern Ethology derived much of its inspiration from them: (1) animals can be said to "possess" behaviour characteristics just as they "possess" certain structural and physiological characteristics; while LORENZ emphasised this particularly for the relatively stereotyped motor patterns which he called „Instinkthandlungen“ we know now that it applies to many other aspects of behaviour; (2) what we call behaviour is, even in its relatively simple forms, something vastly more complex than the types of movements which were then the usual objects of physiological study (and this applied equally to the sensory, the motor and the central nervous processes involved); and (3) the initiation, coordination and cessation of behaviour patterns are controlled by the external world to a lesser extent than reflex-physiologists were at that time prepared to admit.

I should like to elaborate these points to some extent.

(1) The first statement was based on an unrivalled store of first-hand experience as well as on much that had already been published, notably in the works of HEINROTH (1911) and of WHITMAN (1919). It led LORENZ to consider behaviour patterns (and by implication the mechanisms underlying them) as *organs*, as attributes with special functions to which they were intricately adapted. This again facilitated causal analysis without interference by either subjectivism or teleology. By subjectivism I mean here the procedure of replying to the question "What causes this behaviour?" by referring to a subjective experience, i.e. a process which per definition can be observed by no one except the subject. It seems to me worth pointing out that Ethology has not yet completely succeeded in freeing itself from subjectivism in this sense. It is true that one rarely meets with it in its crudest form ("the animal attacks because it feels angry"), but in its subtler forms it is still very much with us. Concepts such as "play" and "learning" have not yet been purged completely from their subjectivist, anthropomorphic undertones. Both terms have not yet been satisfactorily defined objectively, and this might well prove impossible; both may well lump phenomena on the one hand, and exclude other phenomena on the other hand (and thus confuse the issue by a false classification) simply because the concepts are directly derived from human experience. In both fields the growing tendency to ignore the term and to return to the phenomena (which are singled out for study because they are suspected of having a different causation than other phenomena), is, I think, an inevitable result of the consistent application of biological thinking to behaviour.

Teleology also can be said to have ceased to be a source of confusion in its cruder forms, in which function was given as a proximate cause, but it may well be a major stumbling block to causal analysis in its less obvious forms. Throughout Biology we tend to classify, and hence to give names, on the basis of criteria of common function. The more complex the behaviour

systems we deal with, the more dangerous this can be. For instance, although the more sophisticated ethologist is fully aware of the fact that the term "Innate Releasing Mechanism" refers to a type of function, of achievement, found in many different animals; and that different animal types may well have convergently achieved "mood controlled selective responsiveness" by entirely different mechanisms, the term has given rise to misunderstanding on this point, as LEHRMAN's criticism (1953) showed. And who knows what different mechanisms we are lumping under terms such as learning, displacement activity, drive-reduction?

Another type of difficulty which may have to do with our thinking in terms of function is caused by our habit to coin terms for major functional units such as nest building, fighting or sexual behaviour and treat them as units of mechanism. For instance, while the fact that all fighting acts fluctuate together in the natural situation, as do all components of escape, *does* justify us to use "fighting tendency" and "escape tendency" when we are involved in the first step of analysis of movements caused by the *simultaneous arousal of the two*, as soon as we begin to analyse the causation of each of them separately, it is pre-judging the issue if we take for granted that each is in itself a causally closely-linked complex of components. We may then find that some components have closer links with processes outside this functional system than with other parts of the same functional system (see BEER [1962] on incubation and HINDE [1958, 1959] with respect to nest building). Our habit of giving names to systems characterised by an achievement has made thinking along consistent analytical lines much more difficult than it would have been if we could have applied a more neutral terminology. But rather than to advocate such a dry, non-committal terminology, I would like to accept any frankly functional term, as long as this is done consciously. No physiologist applying the term "eye" to a vertebrate lens eye as well as to a compound Arthropod eye is in danger of assuming that the mechanisms of the two are the same; he just knows that the word "eye" characterises achievement, and no more.

The treatment of behaviour patterns as organs has not merely removed obstacles to analysis, it has also positively facilitated causal analysis, for it led to the realisation that each animal is endowed with a strictly limited, albeit hugely complex, behaviour machinery which (if stripped of variations due to differences in environment during ontogeny, and of immediate effects of a fluctuating environment) is surprisingly constant throughout a species or population. This awareness of the repeatability of behaviour has stimulated causal analysis of an ever-increasing number of properties discovered to be species-specific rather than endlessly variable.

It may not be superfluous to stress that the recognition of the existence of many species-specific behaviour characters does not necessarily imply that all these characters are "innate" in the sense of ontogenetically wholly independent of the environment. It is true that this is often assumed in many ethological publications, and I shall have to return to this when I discuss behaviour ontogeny, but this point is irrelevant to us here. LORENZ's emphasis on the fact that so much in behaviour mechanisms is species-specific remains as fruitful as ever.

(2) LORENZ's emphasis on the complexity of behaviour phenomena (which is only seemingly contradictory to his inclination towards simplifying physiological *explanations*), seems to me still to be of the greatest importance, even though we now take this complexity for granted. Lack of appreciation of this point seems to me to have been one of the most important reasons for

the lack of co-operation between physiologists and ethologists. The magnitude of the gap between the phenomena studied by ethologists and those studied by neurophysiologists has been underrated by both parties. The early ethologists underrated the complexity of behaviour mechanisms in various ways, as was evident from our early attempts at "physiologising". One example of this is the lack of any provision for negative feedback in LORENZ's original "psychohydraulics" model (1950); another is provided by my own sketch (1951) of the organisation of the hierarchy in behaviour mechanisms; another again can be found in the original explanation of "displacement activities" (compare, for instance, TINBERGEN 1940, ROWELL 1961 and SEVENSTER 1961). Ethologists are now increasingly avoiding such over-simplifications, without however giving up the application of strictly analytical procedures which were started by LORENZ's work. A corollary of this is the development of concepts suited to the stage of analysis, concepts (and terms) which avoid implying physiological explanations — VON HOLST's (VON HOLST and v. ST. PAUL 1960) "*niveau-adäquate Terminologie*" — without becoming enslaved by such terminology and shutting the door to further analysis. Until recently neurophysiologists, concerned with the analysis of relatively simple processes, were either not considering the more complex phenomena, or were too ready to assume that combinations of the basic phenomena they knew would some day be found to account for behaviour of the intact animal. A striking example of the latter attitude was quoted by VON HOLST and MITTELSTAEDT (1950) in their analysis of the way in which an optomotor response was found not to interfere with "spontaneous" locomotion. Until these authors checked by a simple experiment whether it was true that, under such circumstances, the optomotor response was inhibited (and found that this was not so) this unproven hypothesis seems to have been taken for granted.

The situation is now changing rapidly. The "no-man's land" between Ethology and Neurophysiology is being invaded from both sides. While ethologists are making progress with the "descending" breakdown of complex phenomena, neurophysiologists are "ascending", extending their research to phenomena of greater complexity than was usual 20 years ago. To what extent the latter development has been influenced by Ethology is difficult to say, for who can trace the origin of new fashions in a science? While I am convinced that it would have happened anyway, I am equally convinced that the growth of Ethology has speeded up the process. The *rapprochement* between the two fields has gone so far already that it begins to be difficult, and in some cases even impossible, to say where Ethology stops and Neurophysiology begins. Are DETHIER and ROEDER ethologists or neurophysiologists? And where to put VON HOLST, MITTELSTAEDT and HASSENSTEIN? Several of my colleagues are still inclined to draw a sharp line between the two fields, and to deny some of these workers a place among the physiologists, mainly, I understand, because the mechanisms they describe cannot yet be expressed in physico-chemical terms. I believe that this view is a denial of the fact that much which is conventionally called Physiology has not reached that stage either; or was accepted as part of Physiology before physico-chemical explanations were possible or even within sight. What happens throughout this entire field is that *achievements* of complex systems are, after a varying number of analytical steps, described in terms of *achievements* of component systems. If VON HOLST's work on the superposition effect (1937), HASSENSTEIN's work on the interaction of ommatidia responsible for the response to movement (1951, 1957), and VON HOLST's and MITTELSTAEDT's work on reafference (1950) is not Physiology, then why was SHERRINGTON's work Physiology? It

is, of course, in itself completely unimportant whether or not one calls a certain type of work by a special name, as long as one agrees that it has a place in the progress of science, but the issue has important implications. I believe that it is doing our science a great deal of harm to impose boundaries between it and Physiology where there are none, or rather where there is only a "cline" from behaviour analysis on the one extreme to "Molecular Biology" on the other. I believe that the only criterion by which these extremes and the intermediate fields can be distinguished is that of the level of integration of the phenomena studied. For an understanding of our aims it seems to me much more important to recognise that fundamental identity of aims and method unites all these fields. It is the nature of the question asked that matters in this context, and this is the same throughout. Co-operation between all these workers is within reach, and the main obstacle seems to be lack of appreciation of the fact that there is a common aim.

(3) LORENZ's third postulate, stressing the part played in the control of behaviour by internal causal factors, has also had, and is still having, an effect on analytical studies. Again, the earlier confident statements about the nature of these internal determinants were, in some respects, premature and were at best over-simplifications. Thus, we are now far removed from the simple idea that the effect of hormones on behaviour is no more than a simple, direct stimulation of target tissues in the c.n.s., for it is clear that roundabout effects — e.g. those mediated by hormone-induced growth processes in the sensory periphery (BEACH and LEVINSON [1950], LEHRMAN [1955], and receptor-mediated feedback phenomena (LEHRMAN [1961], HINDE [1962]) enter into the causation of hormone-controlled behaviour. Nor do we believe any more that a complex behaviour system serving one major function, such as nest building in birds, should necessarily be controlled by one single, compact "centre" in the c.n.s. Yet it is surprising to see how interest in "spontaneous" activity of nervous tissue, and in units controlling entire behaviour patterns has grown, and even how many of LORENZ's suggestions about central control of complex behaviour prove to have more than a core of truth in them. To take but one example, BLEST's work (1960) on the interaction between the tendency to fly and the antagonistic tendency to settle in *Automeris* moths, which by elimination of all the known or suspected alternatives was concluded to be due to direct interaction between parts of the c.n.s. itself, illustrates a trend which, I am sure, owes much LORENZ's approach.

These briefly mentioned samples do indicate, I believe, how analyses of behaviour mechanisms which were initiated in the earlier ethological studies are moving towards a fusion with the fields conventionally covered by Neurophysiology and Physiological Psychology. As far as the study of causation of behaviour is concerned the boundaries between these fields are disappearing, and we are moving fast towards one Physiology of Behaviour, ranging from behaviour of the individual and even of supra-individual societies all the way down to Molecular Biology. There ought to be one name for this field. This should not be Ethology, for on the one hand Ethology has a wider scope, since it is concerned with other problems as well; on the other hand, ethologists cannot claim the entire field of Behaviour Physiology as their domain, for they have traditionally worked on the higher levels of integration, in fact almost entirely on the intact animal. The only acceptable name for this part of the Biology of Behaviour would be "*Physiology of Behaviour*", and this name should be understood to include the study of causation of animal movement with respect to all levels of integration.

Survival value

Lorenz's thesis that behaviour patterns, i.e. their mechanisms, ought to be considered "organs", and to be studied as such, has also had a beneficial effect on the study of the survival value of behaviour. In the post-Darwinian era, a reaction against uncritical acceptance of the selection theory set in, which reached its climax in the great days of Comparative Anatomy, but which still affects many physiologically inclined biologists. It was a reaction against the habit of making uncritical guesses about the survival value, the function, of life processes and structures. This reaction, of course healthy in itself, did not (as one might expect) result in an attempt to improve methods of studying survival value; rather it deteriorated into lack of interest in the problem — one of the most deplorable things that can happen to a science. Worse, it even developed into an attitude of intolerance: even wondering about survival value was considered unscientific. I still remember how perplexed I was upon being told off firmly by one of my Zoology professors when I brought up the question of survival value after he had asked "Has anyone an idea why so many birds flock more densely when they are attacked by a bird of prey?"

LORENZ was never in danger of conforming to this fashion. He always was much too good a naturalist for this; he further had the good fortune of being taught by HOCHSTETTER, an anatomist with a wide grasp of what Biology is about; finally, he was himself too clear a thinker to confuse teleology with the study of survival value. To him an organ was something which a species had evolved as one of its means for survival, something of which, as a matter of course, both the contribution it made to survival and its causation had to be studied. He has always been equally interested in "What is this good for?" and in "How does it work?". It was partly through this interest in survival value, for instance, that he arrived at his important concept of "Releaser" — an organ adapted to the function of sending out stimuli to which other individuals respond appropriately, i.e. in such a way that survival is promoted. "Releaser" was defined along much the same lines as any other effector, say, a wing, which is an organ adapted to the function of flying, or an endocrine gland, which is a gland adapted to the function of shedding hormones which, by acting on equally adapted "target organs", contribute to the proper co-ordination of functions within the body. It is an illustration of the inability of many biologists to think in terms of survival value that the concept of Releaser as an *organ characterised by a function* is so often misunderstood and confused with "anything which provides stimuli", a confusion due to the failure to see the function of the releaser and to preoccupation with the causation of the behaviour of the reacting animal.

It is through LORENZ's interest in survival value that he appealed so strongly to naturalists, to people who saw the whole animal in action in its natural surroundings, and who could not help seeing that every animal has to cope in numerous ways with a hostile, or at least unco-operative environment. Incidentally, just because LORENZ's work has revived interest in the study of survival value, and because this is an aspect of Ethology which may well fertilise other fields of Biology (where survival value studies are being neglected) I think it is regrettable that his fine new Institute has been named „Institut für Verhaltensphysiologie“ — its field of research extends far beyond Physiology.

Being myself both a naturalist and an experimenter at heart, one of my primary interests has always been to find out, if possible by experimentation, how animal behaviour contributes to survival, and I shall therefore enlarge a little more on this theme than on the others.

I have always been amazed, and I must admit annoyed as well, when I met, among fellow-zoologists, with the implied or stated opinion that the study of survival value must necessarily be guesswork, and that exact experimentation on the problem is in principle not possible. I am convinced that this is due to a confusion of the study of natural selection with that of survival value. While I agree that the selection pressures which must be assumed to have moulded a species' past evolution can never be subjected to experimental proof, and must be traced indirectly, I think we have to keep emphasising that the survival value of the attributes of present-day species is just as much open to experimental inquiry as is the causation of behaviour or any other life process.

Our study always starts from an observable aspect of a life process — in the present case, behaviour. The study of causation is the study of preceding events which can be shown to contribute to the occurrence of the behaviour. In this study of cause-effect relationships the observable is the effect and the causes are sought. But life processes also have effects, and the student of survival value tries to find out whether any effect of the observed process contributes to survival if so how survival is promoted and whether it is promoted better by the observed process than by slightly different processes. It is clear that he too studies cause-effect relationships, but in his study the observable is the cause and he tries to trace effects. Both types of worker are therefore investigating cause-effect relationships, and the only difference is that the physiologist looks back in time, whereas the student of survival value, so-to-speak, looks "forward in time"; he follows events after the observable process has occurred. The crux is that both are concerned with a flow of events which can be observed repeatedly, and which thus, unlike the unique events of past evolution, can be subjected to observation and experiment as often as one wishes.

The fact that we tend to distinguish so sharply between the study of causes and the study of effects is due to what one could call an accident of human perception. We happen to observe behaviour more readily than survival, and that is why we start at what really is an arbitrary point in the flow of events. If we would agree to take survival as the starting point of our inquiry, our problem would just be that of causation; we would ask: "How does the animal — an unstable, 'improbable' system — manage to survive?" Both fields would fuse into one: the study of the causation of survival. Indeed, logically, survival should be the starting point of our studies. However, since we cannot ignore the fact that behaviour rather than survival is the thing we observe directly, we have, for practical reasons, to start there. But this being so, we have to study both causation and effects.

The widespread lack of interest in studies of survival value and the opinion that it can never move beyond the level of inspired guesswork are all the more puzzling because the literature contains quite a number of good experimental studies in which the survival value of behaviour has been as well demonstrated as anyone could wish. To mention just a few examples: MOSEBACH-PUKOWSKI (1937) has shown that the habit of crowding of *Vanessa* caterpillars has survival value in affording protection from insectivorous song birds: isolated caterpillars are eaten more readily than those living in a cluster. KRISTENSEN (TINBERGEN 1951) has shown that the "fanning" of male Sticklebacks has survival value by renewing the water round the eggs; if this is prevented the eggs die, and artificial ventilation saves them. BLEST (1957) has shown that sudden display of "eye spots" by certain moths scares away certain predators and thus saves lives. VON FRISCH's studies of the bee dance do

not leave doubt about the survival value of this behaviour; it does direct workers to rich food sources unknown to them and thus greatly increases the efficiency of feeding; as LINDAUER (1961) has demonstrated, the dance also plays a part in directing a homeless swarm to a suitable site. Such studies are generally considered both interesting and reliable, and this gives the lie to the argument that survival value cannot be studied experimentally. What then are the reasons for this problem being underworked to such an extent?

First of all, the survival value of many attributes, behaviour and structure alike, is so obvious as to make experimental confirmation ludicrous. One need not starve an animal to death to show that its feeding behaviour has survival value, nor need one cut off a Blackbird's bill to show that this organ is necessary for successful feeding. But one of the reasons why ethologists are so much concerned with survival value is that the "use" of so many behaviour patterns is still completely unknown.

However, the quest for survival value involves, of course, much more than the demonstration that the Blackbird's bill is indispensable to it; one wants to know whether a bill of this size and this shape is best suited to feeding in the environment in which the Blackbird lives; similarly, one needs to understand in detail the suitability of every aspect of its feeding behaviour one sees, and this, of course, is very far from obvious. To think that we understand survival value completely in such cases is to think that, once it is obvious that sex hormones control mating behaviour, we need not inquire into the way they do this, nor into the interaction between various endocrine processes that are involved.

Another important reason for the lack of interest in survival value studies is a practical one. The method to demonstrate survival value of any attribute of an animal is to try whether or not the animal would be worse off if deprived of this attribute. This is easy with structures. For instance, BLEST could compare the effect of normal "eye spot"-bearing moths on song birds with that of moths whose eye spots were brushed off. In this test moths without eye spots could safely be regarded as differing from the controls in just this one respect. Similarly, HOOGLAND, MORRIS and TINBERGEN (1957) could show that Sticklebacks without spines were eaten more readily by small Pike than normal Sticklebacks. But how does one make an experimental animal which lacks just one behaviour pattern and is otherwise normal? How, for instance, to make a male bird which does not show aggressive behaviour, or lacks one of its threat postures, while in all other respects behaving normally?

This difficulty can in many cases be overcome, but one has to be aware of many pitfalls. Much of our evidence can come from systematic comparison of the success of animals at times when they do show a certain behaviour and the lack of success when they do not perform it. Thus, if a territory of a male bird is not invaded as long as it fights off intruders, but is invaded when, later in the day, his aggression wanes though he is still there and shows a variety of other behaviour, one has a good indication that it was the aggressive behaviour which kept the territory clear. Or, to take another example, if one can show that a motionless twig caterpillar is not eaten by birds while it is snapped up as soon as it moves (DE RUITER 1952) one can be pretty confident that immobility in this species has survival value.

Yet it is, of course, true that in such "natural experiments" one does not control the feature studied — one never knows which unknown aspect of the animal may have varied with the character studied; the aggressive bird may

have made an ultrasonic sound; the moving caterpillar may have given off a scent. Therefore the method of studying the survival value of behaviour is to use dummies and to control their "behaviour". For instance, when a dummy of a male stickleback is either ignored, or merely approached, by a ripe female when moved at random, but elicits following and even the movements of creeping into the nest whenever it is made to move like a "nest-showing" male, even in the absence of any nest, then one has demonstrated the effect of nest-showing and, since eggs not laid in the nest are eaten or abandoned, one has shown that the male's nest-showing contributes to, and is even indispensable for successful reproduction. Of course, an experiment such as this is but the first step, for one needs to know the full story of the cause-effect relationship which makes the female respond the way she does; also, one wants to know not merely whether absence of the behaviour studied has an adverse effect; one also needs to know what kind of deviations from the natural behaviour would reduce the effect — which includes the task of finding out whether the natural movement has the optimal effect and, if not (as is the case in supernormal stimuli) why the behaviour is not "better" — a question which will crop up again in evolutionary studies.

So far, we have only made the barest beginning with this task; there are even many behaviour patterns of which we do not even know the basic answer: has it any function at all? As an illustration let me mention the example of the "rocking" of certain cryptic animals. There are a number of animals which, either as an introduction to the change from motionlessness to movement, or from movement to immobility, perform a series of curious rocking movements. HEINROTH (1909) described these for the Nightjar, and mentioned that they are also found in *Phyllium* and in *Dixippus*. BLEST (1960) has shown that many Saturniid moths have a similar movement, usually preceding settling. Now these animals are all camouflaged; many of their behaviour characters (immobility by day, background selection, semi-closing of the eyes in the Nightjar, etc.) are obviously adapted to the function of avoiding detection by visually hunting predators. In view of this the habit of rocking seems very strange indeed, for movement in general is a stimulus to which visually hunting predators react, and which these cryptic animals are for the rest at such pains to avoid giving. Therefore the fact that these movements occur in such different animals suggests that they have survival value and are somehow connected with camouflage. I believe that a testable hypothesis can be formulated. DE RUITER (1952) has shown that European Jays ignore twig-shaped caterpillars as long as the latter stay motionless. However, this was only true of Jays which had grown up in a normal environment, and in particular those which had had the opportunity of discovering, by trial and error, that real twigs are inedible. Hand-raised Jays which had not "played about" with twigs took up and tried out twigs and caterpillars alike. We know that many young birds have, at the start, a very "open mind" with regard to food; they respond to an enormous variety of objects, edible and inedible alike, and learn to confine themselves to those they find edible. My suggestion is that we have as yet no more than the faintest idea of the kinds of things such birds learn when young. HEINROTH (1909) already suggested that the rocking movements of *Phyllium* might well be harmless because predators might recognise them as passive movements of a leaf slightly moved by the wind. It seems to me quite possible that many young birds actually do learn that certain types of movements are passive, and not indicative of animal prey, and that it might not only be harmless for certain cryptic animals to perform these movements but that it might be

definitely beneficial to them because it might ensure that a predator sees them and concludes that they are just vegetable matter. A motionless cryptic animal "hopes to be overlooked"; a rocking cryptic animal makes sure that it is seen and ignored — which means survival.

Critical, scientific zoologists had a way of applying the term "armchair science" to such ideas; yet it is becoming increasingly clear that it was the critics who judged such issues without investigation and even without knowledge of the real events; it is obvious that a well planned study of the ontogeny of the feeding behaviour of certain predators, combined with an accurate study of these rocking movements and the passive movements of inanimate objects could prove the hypothesis to be right or wrong.

Of course, in selecting this example I have applied "shock tactics" by taking a very exceptional type of behaviour. However, I would like to submit, first that we know so little about behaviour that new, equally strange behaviour patterns could well be discovered in large numbers; second, that the problem of survival value applies equally to every detail of behaviour and structure, however self-evident or insignificant it might seem at first glance. For instance, the fact that the Godwit walks differently from the Lapwing would seem too trivial to pay attention to, yet KLOMP (1954) showed that these differences are adaptive: Godwits lift and fold their feet much more than do Lapwings and thus avoid getting their toes caught in the tall grass in which they breed. Lapwings avoid habitats with tall vegetation. A parent Kittiwake does not produce a sound when it is about to feed its young but other gulls do; the Kittiwake is the only species of gull whose chicks stay on the nest and therefore have not got to be called to food (E. CULLEN 1957). HEINROTH (1928) suggested that Starlings and Partridges show remarkably little inhibition from trying to walk or fly straight through the thin metal bars of bird cages because they are adapted to living among grass rather than trees, and grass gives way. The writings of the good naturalists are teeming with such hints, arguments, and occasional demonstrations of the functions of a multitude of aspects of species-specific behaviour. It is also the experience of every good naturalist that the longer one studies a species, the more adaptive aspects of its behaviour one becomes aware of. The phenomena are countless, the field is practically unexplored, and yet without exploring it systematically we cannot hope to understand how behaviour helps animals to survive.

How can we tackle this immense task and catch up with the backlog? Hypotheses can be arrived at in various ways. LORENZ himself has pointed out one which he derives from his particularly fruitful method of raising and keeping animals in freedom, yet in partly artificial surroundings. Under such conditions one observes a number of behaviour patterns which "misfire". The observer's reaction is: "This seems ill-adapted; but it must be good for something" and this makes him try to see the behaviour in its proper context.

The naturalist who studies animals in their natural surroundings must resort to other methods. His main source of inspiration is comparison. Through comparison he notices both similarities between species and differences between them. Either of these can be due to one of two sources. *Similarity* can be due to affinity, to common descent; or it can be due to convergent evolution. It is the convergences which call his attention to functional problems. This method has been applied beautifully by VON HAARTMAN (1957) in his study of adaptations in birds hole nesting. The *differences* between species can be due to lack of affinity, or they can be found in closely related species. The student of survival value concentrates on the latter differences,

because they must be due to recent adaptive radiation. An example of this procedure is E. CULLEN's elegant study (1957) of the peculiarities of Kittiwakes as compared with other gulls.

Such hypotheses can be made highly probable even without experimentation. E. CULLEN's report contains hardly any experimentation, yet her conclusion that, for instance, immobility of the young, their "facing-away" gesture, the tameness of the adult Kittiwakes while on their cliff, their mud-trampling before nest building, and the absence of an acquired attachment to their own young are all adaptive corollaries of cliff-breeding carries conviction because this interpretation is the only one which fits into our general picture.

However, such studies are no more than a beginning; they can be extended and intensified in several ways.

First, as one becomes better acquainted with a species, one notices more and more aspects with a possible survival value. It took me ten years of observation to realise that the removal of the empty eggshell after hatching, which I had known all along the Black-headed Gulls to do, might have a definite function, and that even the length of delay of the response, which varies with the circumstances, and which is on the average longer than that found in the Ringed Plover, may be adaptive (TINBERGEN et al. 1962).

Secondly, hunches about survival value must, where possible, be strengthened by experiment. This meets with obstacles of a practical nature, but once the need is obvious, ways can often be found. Thus when one sees that the breeding season of the Black-headed Gulls is much more synchronised than that of Gannets, and one notices at the same time that the late broods of Black-headed Gulls seem to be less successful than the majority; when one further has indications that such late broods perish through heavy predation, one can first systematically compare predation of late and "peak" broods, and ultimately design an experiment to find out whether or not synchronisation has survival value as an anti-predator defence.

Thirdly, the experimental demonstration of survival value involves quite a number of steps. Much of the experimental evidence is not complete, because it has (often of necessity) been done in a situation which differs essentially from the natural context. In order to study the survival value of egg-shell removal in the Black-headed Gull, my co-workers and I demonstrated that gulls' eggs, laid out well scattered over the hunting area of Carrion Crows and Herring Gulls, were found more readily when they had an empty egg-shell at 4 inches distance than when no egg-shell was added (TINBERGEN et al. 1962). However, before we can conclude from this that egg-shell removal reduces predation, we have to consider whether in the natural situation this is its only effect. When a gull removes the egg-shell it leaves its brood unguarded for a few seconds. This, we know, can be critical: neighbouring gulls or Crows sometimes snatch up an egg or a newly-hatched chick in a second or so. It clearly depends on the balance of advantage and disadvantage whether the response is on the whole useful or not. The strict test for this would be a comparison of breeding success of a population of gulls which remove the shell with that of a population which do not, though in all other respects identical to the shell-carrying population. It is just because this is impossible that we have to be content with less good evidence. There are several indications that the advantage outweighs the disadvantage. For instance, whenever a Crow is in sight, the tendency of the gulls to attack it and drive it off dominates that of removing the shell; also, the danger caused by leaving the nest for a few seconds might well be less than that caused by the presence of the tell-tale

shells for a long time. It remains true, however, that the ultimate test of survival value is survival itself, survival in the natural environment. This ultimate test has been carried out in very few cases only; a good example, involving a colour adaption rather than a behavioural one, is supplied by the work of KETTLEWELL (1955, 1956) on differential survival of white and black mutants of *Biston betularia* in two different environments: one which favoured the white form, and one which favoured the dark form.

I have argued that survival value has to be studied in its own right, but there are two additional reasons. First, Zoophysiology derived, and again derives much of its inspiration and guidance from knowledge or hunches about survival value. Experiments on the external control of respiration often concentrate on the effect of varying oxygen and CO₂-content of the medium or in the blood; this is because one starts from the knowledge that it is oxygen the animal requires, and CO₂ it must get rid of. The work of VON FRISCH and his school on colour vision in the Honey Bee was set off by VON FRISCH refusing to believe that the colours of flowers had no function; our knowledge of the ability of Arthropods to register the plane of polarisation of light is due to VON FRISCH wondering about the exact function of the bees' dance.

Secondly, the part played by natural selection in evolution cannot be assessed without proper study of survival value. If we assume that differential mortality in a population is due to natural selection discriminating against the less well-equipped (the less "fit") forms, we have to know how to judge fitness, and that can only be done through studies of survival value.

To those, however, who argue that the only function of studies of survival value is to strengthen the theory of natural selection I should like to say: even if the present-day animals were created the way they are now, the fact that they manage to survive would pose the problem of how they do this.

Ontogeny

A newly-hatched Herring Gull pecks selectively at red objects (GOETHE 1937, TINBERGEN & PERDECK 1950) but a human being has to learn to stop when the traffic lights turn red. We have to learn the intricately co-ordinated motor patterns of speech, whereas a Whitethroat raised in isolation produces the complicated normal song of its species (SAUER 1954). It is the contrast between man and animals in the ways they acquire either "knowledge" or "skill" which arouses in most of us an interest in the ontogeny of behaviour. As we all know, the systematic study of behaviour ontogeny has had a slow start, and for a long time was heavily weighted, but differently so in different groups of researchers. While animal psychologists explored the ways in which various types of learning might account for behaviour ontogeny, ethologists emphasised the unlearnt character of many aspects of animal behaviour. Ontogeny was, for a long time, and to a certain extent still is, a field in which there is a real clash of opinion. All concerned agree that a complete understanding of behaviour requires an understanding of its ontogeny, just as morphologists agree that it is not sufficient to understand the adult form, but also the way in which this develops during ontogeny. But there is no agreement about the nature of the problems involved, and while the methods applied by psychologists and ethologists begin to resemble each other so closely as (in some instances) to be indistinguishable, the interpretation of the results gives rise to much discussion.

I believe that this discussion has been and is still being bedevilled by semantics, and that it would be helpful if, instead of discussing the justifica-

tion of the use of words such as "innate" and "acquired", of "instinct" (and "instinctive") and "learning" we could return to a statement of the phenomena to be understood and the questions to be asked — indeed I think this is imperative.

I should like to characterise the *phenomenon* as "change of behaviour machinery during development". This is not, of course, the same as a change of behaviour during development; when in spring we see a thrush pick up and smash a snail for the first time in months, this change in feeding behaviour may be due to snails having reappeared for the first time after winter. We can conclude that the thrush itself, i.e. its behaviour machinery, has changed only if the behaviour change occurred while the environment was kept constant. It should be pointed out in passing that systematic descriptions of behaviour ontogeny are still rare and fragmentary.

When we turn from description to causal analysis, and ask in what way the observed change in behaviour machinery has been brought about, the natural first step to take is to try and distinguish between environmental influences and those within the animal. It is about this very first, preliminary step that confusion has arisen.

As in studies of the cyclical behaviour of adult animals, external influences have been studied most, for the simple reason that they are so much more easily manipulated. It is also important to realise that, in ontogeny, the conclusion that a certain change is internally controlled (is "innate") is reached *by elimination*. This is not, of course, a reflection on the validity of a classification — one can perfectly well dichotomise any group of phenomena into one group possessing the character A and the rest not possessing A — but it does reflect on the justification of lumping all examples for which not all environmental influences have been eliminated into a class called "innate", thus suggesting a positive statement where merely a negative statement would be in order. And I submit that most statements about "innateness" of behaviour are based on the elimination of one or some out of several, perhaps many, possible external influences. I am again criticising myself just as much as others, for I am now convinced that I have helped to perpetuate the confusion. If we raise male Sticklebacks in isolation from fellow members of its own species, subject them as adults to tests with dummies, and find (E. CULLEN 1961) that they attack red dummies just as selectively as do normal males, we are entitled to say that exposure to red males cannot be responsible for the development of this selectiveness of response. We cannot, however, say anything about the problem whether or not interaction with the environment during "practising" has influenced the form of their fighting movements. When GROHMANN (1939) showed that the incomplete flying movements which young pigeons make while growing up (and which might be interpreted as providing "practice") did not influence their flying skill (birds that were prevented from flapping on the nest flew as well as controls on their first attempt), he eliminated a different form of interaction with the environment than CULLEN did with her Sticklebacks.

It is not helpful and even wrong to apply to both behaviour patterns the term "innate", because in each case only one out of various environmental effects was excluded, and these were different in each case. The conclusion can only be formulated correctly in negative terms, in describing which environmental aspect was shown *not* to be influential.

There is, in addition, another reason for not applying the term "innate" to the fighting behaviour of the Kaspar Hauser Sticklebacks. KNOLL (1953) has shown that the rods of tadpoles raised in darkness do not function pro-

perly; exposure to light is required to allow them to become fully functional. We have no information about this problem in Sticklebacks, and this means that, in the absence of evidence with respect to either rods or cones in Sticklebacks, we must allow for the *possibility* that light — an environmental property — is required for the proper “programming” of part of the Stickleback’s behaviour machinery. This brings me to another point which I consider important: the term “innate” whether applied to characters, or to differences, or to potentialities, or to developmental processes, is not the opposite of “learnt”; it is the opposite of “environment-induced”.

These few considerations seem to me sufficient to conclude that the application of the adjective “innate” to behaviour *characters*, and to do this on the basis of eliminations of different kinds is heuristically harmful.

If I were to elaborate this further I should have to cross swords with my friend KONRAD LORENZ himself — both a pleasure and a serious task requiring the most thorough preparation — but this is not the occasion to indulge in swordplay, and I prefer to continue with my sketch of the procedure which seems to me more fruitful. This seems justified by the fact that the practice of ontogenetic research is not so much dependent on the background of the experimenter as the semantic and theoretical disagreements would lead one to suspect. The difference, for instance, between RIESS’S (1950) and EIBL-EIBESFELDT’S (1956) work on the ontogeny of nest building in rats is due just as much to a difference in the extent of knowledge of the Rat’s normal behaviour as to the theoretical attitudes of the investigators.

A central issue in behaviour development studies seems to me the question raised by the fact that so many behaviour patterns can be said to be at the same time innate and learned, or partly innate and partly learned. EIBL-EIBESFELDT (1955) showed that nut-cracking in Squirrels consists of a series of component acts (manipulating, gnawing, and cracking) each of which develops in naive individuals which have not been able to practice; yet the adaptive integration of the acts into an efficient total pattern has to be learnt. Many similar cases are known, and it was a definite step forward when LORENZ (1937) coined the term „Instinkt-Dressur-Verschrankung“ indicating that learning processes were often, so-to-speak, intercalated by non-learnt parts of a behaviour chain. This has given rise to the idea that, if one could only split up behaviour chains in smaller and smaller components, one could always reach a state where some components could be labelled as innate, others as learnt or acquired. I maintain that this may well be unhelpful, since many interactions with the environment which result in increased efficiency are *additive* to some machinery that was already functional. For instance, WELLS (1958) found that a naive young *Sepia* can perform the movements by which it catches *Mysis*, but that both the delay of the “attack” and the selectiveness of the response to stimuli decrease as a result of “having performed”. In the sphere of conditioning — to mention a different form of environmental control of ontogeny — something similar is true: the animal is already selectively responsive (in other words it has an “IRM”) before it has been conditioned; the conditioning changes a connection that was already present. The story of song development in Chaffinches as revealed by THORPE’S work (1962) shows something very similar in the development of motor patterns: there is a definite pattern in the song of naive birds. I cannot see how, in view of such facts, it can be fruitful to look for innate and learned *components*, however small.

It seems to me that, if we return to a description of the phenomenon and the formulation of relatively simple questions, our course is laid out clearly.

The phenomenon (change in behaviour machinery) has to be described; the problem is, how are these changes controlled? As a first step one distinguishes between influences outside the animal and internal influences. External influences are usually detected by manipulating the environment during development, and the way in which such external agents influence the development can be studied along rather conventional lines, although it is obvious that, even in this relatively easier part of our task, we may well be in for some surprises, such as discovering that "rewards" may be of many more different types than known at present. One receives the first indications of *internal* control from demonstrations of the ineffectiveness of certain environmental properties, but the ultimate demonstration of internal control must come from direct interference with internal events. For instance, the development of successful ejaculation in Rats is, as BEACH and LEVINSON (1950) have shown, influenced by sex hormones which promote the growth of sensory papillae on the glans penis. Further insight into the internal control of growth of neural machinery is provided by the fascinating work of SPERRY (1959), particularly by his transplantation of peripheral „Anlagen“ before their innervation has been completed.

This general procedure, when applied at various levels of integration — to complex patterns, single acts, and even smaller components of the total behaviour machinery — seems to me much more fruitful than either basing a conclusion about innateness on elimination of part of the environmental properties, or proceeding on the assumption that all adaptedness of behaviour is acquired through interaction with the environment. It has been pointed out repeatedly (see PRINGLE 1951, LORENZ 1961) that there are two methods of "programming" the individual: the evolutionary trial-and-error-interaction with the environment which results in the specialisations of the genetic instructions, and the ontogenetic interaction between the individual and its environment — which, incidentally, takes the form of trial and error only where evolution has not given precise direction to the ontogenetic process.

I believe that such a procedure is in line with that widely applied in experimental embryology, which after all is the science concerned with exactly the same problem with reference to structure. And this takes me back to my starting point: by insisting on a biological approach LORENZ has influenced this aspect of Ethology as much as other aspects, even though his evaluation of the part played by internal determinants may have been on the optimistic side.

I admitted above that in speaking of "the four problems of Biology" we apply a classification of problems which is pragmatic rather than logical. This is true of ontogeny in two respects at least. First, I have so far been speaking of the causation of ontogeny only, and it is clear that we must apply the question "what for?", the question of survival value to ontogeny as well. That is, we need to ask what the survival value is of the many different types of ontogenetic control that our analysis brings out. As yet we have only a hint of what is in store if we were to apply this question consistently. For instance, it is in some cases easy to see why the control in certain behaviour patterns is largely internal, and why in others interaction with the environment is advantageous. Thus a young Gannet, which has to jump off a high cliff, would be poorly off if he had to acquire the basic pattern of flight the way we acquire a skill such as writing. Similarly, the selective responsiveness to rival males in territorial species might well have to be unconditioned so that it can function at once when a male starts its first breeding cycle. Young song birds on the contrary, which begin by responding to a very wide range of objects when they start feeding independently and gradually learn to take

only what has proved to be edible, are by this very "open-mindedness" able to adapt to many different habitats, and learn to select the most abundant food in each, however different this food may be in different habitats.

The study of ontogeny also overlaps, but in another way, with that of causation of cyclical or recurring behaviour in the adult. Some learning processes can occur all through the life of the individual, even though their impact decreases with age. (So do, of course, certain physiological changes, such as the formation of antibodies, or of pigmentation of the skin.) In this respect too ontogeny can be said to continue beyond the period of growth to maturity and the causation of the behaviour of the adult animal therefore grades into that of the phenomena usually classified under ontogeny; the distinction is partly one of the time scale involved. Yet there is sufficient justification to distinguish between the two sets of processes; as is obvious from the fact that one can say that a man is afraid of a flying plane "because he sees it" but also "because he has been bombed out as a child". The main point is to recognise that both statements may be true, that each covers part of the total causal chain involved, and that the question "what made him behave the way he did?" requires a complete answer in which both partial answers are contained.

Evolution

The fact that behaviour is in many respects species-specific, and yet often similar in related species has been recognised by many workers before LORENZ, and the natural conclusion to be drawn from this, namely, that behaviour should be studied comparatively just as structures, with the ultimate aim of elucidating behaviour evolution, had also been drawn. WHITMAN's work (1898, 1919), and that of HEINROTH (1911), HUXLEY (1914, 1923) and VERWEY (1930), preceded LORENZ's contributions. While WHITMAN can be said to have concentrated on questions of homology or common descent, HUXLEY's interest was focussed on the task of testing the theory of natural selection. In a sense, however, all these important studies can be said to have been preliminary, preparatory to a concerted attack on problems of behaviour evolution which has gradually developed since LORENZ (1937) began to emphasise the need for systematic comparative studies.

In this field, too, research began in a rather intuitive way, guided by trends of thought which have been gradually made explicit and which have become increasingly similar to general evolutionary thinking. In this respect, too, Ethology is being incorporated into general Biology.

In some respects the evolutionary study of behaviour suffers from handicaps not met to that extent in that of structure. It needs no repeating that direct documentary evidence in the form of "fossil behaviour" is hardly available. The exploration of behaviour ontogeny as a tool does not seem to be very promising either. This, however, is not a serious handicap in view of the controversial nature of this tool in the study of structural evolution. In other respects ethologists are perhaps better off than students of structure: through their familiarity with the behaviour of many animals in their natural surroundings their attention has been drawn more readily to questions of survival value, and through these to a consideration of the effects of natural selection. When I say that ethologists were "better off" in this respect, I feel I should add in fairness to ourselves that this is due to our own efforts in creating a better opportunity; it is, in principle, easier to experiment on the survival value of structure than on that of behaviour, and the truth is that ethologists, by being in general good naturalists, deserved their good luck.

Evolutionary study has, of course, two major aims: the elucidation of the course evolution must be assumed to have taken, and the unravelling of its dynamics.

The first task is being pursued mainly through comparison of groups of closely related species. This limitation to closely allied forms is necessary because it is only here that conclusions about homology (i.e. common descent) can be drawn with any degree of probability. It is due to this restriction that what evidence we have applies to microevolution, particularly to adaptive radiation of relatively recent origin. As I have discussed elsewhere (TINBERGEN 1959), the trend here is to apply very much the same methods as those employed by taxonomists: we judge affinity by the criterion of preponderance of shared characters, particularly of those which we consider non-convergent. Once we have hardened the conclusion, often already reached by taxonomists, that a certain group must be monophyletic, we judge the degree of evolutionary divergence by the degree of dissimilarity of those characters that must be considered highly environment-resistant ontogenetically — we try to exclude from our material such differences as are the direct phenotypic consequence of different environments, such as an individually acquired darkening of external coloration under the immediate influence of a moist environment (which, of course, is very different from differences in *ability* to respond to the environment).

The comparative procedure has now been applied to a number of groups and one of the encouraging outcomes is that classifications based on behaviour taxonomy have, on the whole, corresponded very closely to the already existing classifications. Minor differences were found — but these often concerned matters which taxonomists considered not quite settled. I think it is worth emphasising this correlation between the two sets of results because it is again a striking justification of treating behaviour patterns as “organs”.

The work on evolution *dynamics* can be said to consist of two major parts. First, the genetic control of species-specific behaviour, about which we know so much less than about that of species-specific structure, is now being studied with all the methods available in genetics; differences between species, subspecies and strains raised in identical environments are registered; the effect of mutations on behaviour are beginning to be explored, and controlled cross-breeding is being done. There seems little doubt as to the general outcome: individuals and populations differ as much in their hereditary behaviour “blueprints” as in their hereditary structural blueprints. The genetic variation on which natural selection can act is there.

The second major task is the study of the influence of selection on behaviour evolution. This task is being tackled in two different ways. One is the study of survival value of species-specific characters, the other is the direct application of a controlled selection pressure and its results over a series of generations.

The study of survival value receives its inspiration from the study of convergencies, and of divergencies within a taxonomic group; hypotheses about survival value are derived from these studies; they can be tested in experiment. The interpretation of the results is worth detailed scrutiny. When one finds that a certain characteristic has survival value — when it has been shown that various deviations from the norm lead to a lower success rate — one can draw one firm conclusion: one can say that one has demonstrated beyond doubt a selection pressure which prevents the species in its present state from deviating. One has really demonstrated the part played by selection in *stabilisation* of the present state. However, the conclusion that this same

selection pressure must have been responsible in the past for the *moulding* of the character studied is speculative, however probable it often is. One can support such a conclusion by marshalling supplementary evidence, such as arguing that the environment which exerts the selection pressure must be assumed to have remained constant in this respect for a long time, or showing that the species is even now slightly variable according to area. Thus, E. CULLEN's demonstration of the adaptive nature of many of the Kittiwake's peculiarities (1957) can be used as a pointer to past selection pressures by arguing that the species has probably a fairly long history of cliff-nesting behind it. An example of the second line of argument is BLAIR's demonstration (1955) of the fact that the mating calls of two species of *Microhyla* are more distinct in the areas where they overlap (and where selection against cross-breeding must be assumed to have favoured inter-species distinctness) than in the areas where either species occurs alone.

All I have said above about the study of survival value for its own sake is relevant again here, but I should like to re-emphasize one point. For an assessment of what selection can be assumed to have contributed to the present state of species it is important to realise that selection rewards or penalises isolated bits of animals through rewarding or penalising animals, or breeding pairs, as wholes. Since studies of survival value show us that there are often direct contradictions between different selection pressures, the animal that survives best must be a compromise, and it must be one of our main tasks to try and find all the pressures — favourable and unfavourable alike — that can have affected any character we select for study. In general, we should not only try to pinpoint isolated selection pressures, but study their interaction as well.

In spite of the fact that we shall never be able to prove directly which contributions selection has made in the past, and that therefore any conclusion about the way interaction with the environment has moulded present-day species must remain tentative and, as such, different from conclusions drawn in the field of Physiology, Ontogeny and Survival Value, the ethologist feels that this is no reason to dismiss evolutionary study as just speculation. I believe that this developing branch of Ethology may well have effects on general biological thinking.

The direct application of selection pressures will, with increasing precision of description and measurements, give us an increasing amount of real demonstration of the potentialities of selection. With the growing trend towards experimentation it is important, however, to point out that even the most perfect experiment of this kind does not give us direct proof of what selection has done in the past. The interpretation of such experiments as contributions to evolution theory will always include an extrapolation: while they demonstrate what selection can do, the best they can tell us is that selection can have happened in the way demonstrated, and that the results obtained are not contradictory to what other indirect evidence has led us to suppose. They really deal merely with "possible future evolution", and only indirectly with past evolution. For instance, CROSSLEY's demonstration (1960) that 40 generations of antihybrid selection in partially interbreeding populations of ebony and vestigial mutants of *Drosophila melanogaster* change aspects of mating behaviour of both males and females of both populations does not directly prove that such selection *has* contributed to speciation, but it is in line with ideas developed before these experiments were done. This is, of course, not at all to belittle the relevance of such experiments, but merely to assign them their proper place in the total body of evidence.

Conclusion

I have tried in this paper to give a sketch of what I believe modern Ethology to be about. I have perhaps given Ethology a wider scope than most practising ethologists would do, but if one reviews the various types of investigations carried out by people usually called ethologists, one is forced to conclude that the scope is in fact as wide as I have indicated. This sketch is not meant to be balanced or comprehensive; I have allowed myself to enlarge a little on special issues — on “bees in my bonnet” — such as the relations between Ethology and Physiology; the need to spend more effort on studies of survival value and methods to be employed in such studies; problems and methods of behaviour ontogeny; and the nature of arguments used in the study of evolution — all issues which require further discussion. I have also tried to assess KONRAD LORENZ'S contribution to modern Ethology, and have argued that I consider his insistence that behaviour phenomena can, and indeed must, be studied in fundamentally the same way as other biological phenomena to be his major contribution. LORENZ can with justification be said to be the father of modern Ethology — even though he has had his forerunners; there is nothing amazing about every father having had a father.

The central point in LORENZ'S life work thus seems to me his clear recognition that behaviour is part and parcel of the adaptive equipment of animals; that, as such, its short-term causation can be studied in fundamentally the same way as that of other life processes; that its survival value can be studied just as systematically as its causation; that the study of its ontogeny is similar to that of the ontogeny of structure; and that the study of its evolution likewise follows the same lines as that of the evolution of form. Moreover, in all these fields LORENZ has done concrete research which demonstrated the great heuristic value of his approach. Yet, although his concrete, factual contributions have been considerable, the impact he has made is due to his sketch of a type of approach, and to new and original hypotheses rather than to the experimental testing of such hypotheses. This is why recent changes of concepts and terminology, revisions of hypotheses, and the reporting of results which are sometimes different from LORENZ'S earlier conclusions, have little relevance to the question of the value of his work.

One of the measures of this value which I will mention in passing is the fact that students of human behaviour are showing a growing interest in ethological methods.

Finally, I should like to touch briefly on a matter of terminology. It will be clear that I have used the word “Ethology” for a vast complex of sciences, part of which already have names, such as certain branches of Psychology and Physiology. This, of course, does not mean that I want to claim the name Ethology for this whole science, for this would be falsifying its history; the term really applies to the activities of a small group of biologists. What I have been at pains to develop is the thesis that we are witnessing the fusing of many sciences, all concerned with one or another aspect of behaviour, into one coherent science, for which the only correct name is “*Biology of behaviour*”. Of course this fusion is not the work of one man, nor of the small group called ethologists. It is the outcome of a widespread tendency to apply a more coherent biological approach, which has expressed itself in what may well have been quite independent developments within sciences such as Psychology and Neurophysiology. Among zoologists and naturalists, it is LORENZ who has contributed most to this development, and who has more than any other single person influenced these sister disciplines in this particular way. Finally, the comprehensive view of the aims of the biological study of

behaviour has grown more rapidly in Ethology than in any of the other sciences. Yet, in view of the confused "public image" called up by the word Ethology it might well be advisable not to overdo the use of the word. What does seem to me to matter is the growing awareness of the fundamental unity of the Biology of Behaviour, and the realisation that "Ethology" is more than "Physiology of Behaviour", just as "Biology" is more than "Physiology".

Zusammenfassung

Ich habe in diesem Aufsatz kurz anzudeuten versucht, was meiner Ansicht nach das Wesentliche in Fragestellung und Methode der Ethologie ist und weshalb wir in KONRAD LORENZ den Begründer moderner Ethologie erblicken. Hierbei habe ich vielleicht das Arbeitsgebiet der Ethologie weiter gefaßt, als unter Ethologen gebräuchlich ist. Wenn man aber die vielartige Arbeit jener Forscher übersieht, die sich Ethologen nennen, ist man zu dieser weiten Fassung geradezu gezwungen. Ich habe in meiner Darstellung weder Vollständigkeit noch Gleichgewicht angestrebt und, um zur Fortführung des Gesprächs anzuregen, ruhig meine Steckenpferde geritten, vor allem das Verhältnis zwischen Ethologie und Physiologie, die Gefahr der Vernachlässigung der Frage der Arterhaltung, Fragen der Methodik der ontogenetischen Forschung, und Aufgaben und Methoden der Evolutionsforschung.

Bei der Einschätzung des Anteils, den LORENZ an der Entwicklung der Ethologie genommen hat und noch nimmt, habe ich als seinen Hauptbeitrag den bezeichnet, daß er uns gezeigt hat, wie man bewährtes „biologisches Denken“ folgerichtig auf Verhalten anwenden kann. Daß er dabei an die Arbeit seiner Vorgänger angeknüpft hat, ist nicht mehr verwunderlich, als daß jeder Vater selbst einen Vater hat.

Insbesondere scheint mir das Wesentliche an LORENZ' Arbeit zu sein, daß er klar gesehen hat, daß Verhaltensweisen Teile von „Organen“, von Systemen der Arterhaltung sind; daß ihre Verursachung genau so exakt untersucht werden kann wie die gleich welcher anderer Lebensvorgänge, daß ihr arterhaltender Wert ebenso systematisch und exakt aufweisbar ist wie ihre Verursachung, daß Verhaltensontogenie in grundsätzlich gleicher Weise erforscht werden kann wie die Ontogenie der Form und daß die Erforschung der Verhaltensrevolution der Untersuchung der Strukturevolution parallel geht. Und obwohl LORENZ ein riesiges Tatsachenmaterial gesammelt hat, ist die Ethologie doch noch mehr durch seine Fragestellung und durch kühne Hypothesen gefördert, als durch eigene Nachprüfung dieser Hypothesen. Ohne den Wert solcher Nachprüfung zu unterschätzen — ohne die es natürlich keine Weiterentwicklung gäbe — möchte ich doch behaupten, daß die durch Nachprüfung notwendig gewordenen Modifikationen neben der Leistung des ursprünglichen Ansatzes vergleichsweise unbedeutend sind.

Nebenbei sei auch daran erinnert, daß eine der vielen heilsamen Nachwirkungen der LORENZschen Arbeit das wachsende Interesse ist, das die Humanpsychologie der Ethologie entgegenbringt — ein erster Ansatz einer Entwicklung, deren Tragweite wir noch kaum übersehen können.

Am Schluß noch eine Bemerkung zur Terminologie. Ich habe hier das Wort „Ethologie“ auf einen Riesenkomplex von Wissenschaften angewandt, von denen manche, wie Psychologie und Physiologie, schon längst anerkannte Namen tragen. Das heißt natürlich nicht, daß ich den Namen Ethologie für dieses ganze Gebiet vorschlagen will; das wäre geschichtlich einfach falsch, weil das Wort historisch nur die Arbeit einer kleinen Gruppe von Zoologen kennzeichnet. Der Name ist natürlich gleichgültig; worauf es mir vor allem

ankommt, ist darzutun, daß wir das Zusammenwachsen vieler Einzeldisziplinen zu einer vielumfassenden Wissenschaft erleben, für die es nur einen richtigen Namen gibt: „*Verhaltensbiologie*“. Selbstverständlich ist diese synthetische Entwicklung nicht die Arbeit eines Mannes oder gar die der Ethologen. Sie ist die Folge einer allgemeinen Neigung, Brücken zwischen verwandten Wissenschaften zu schlagen, einer Neigung, die sich in vielen Disziplinen entwickelt hat. Unter den Zoologen ist es LORENZ, der hierzu am meisten beigetragen und zudem manche Nachbardisziplinen stärker beeinflußt hat als irgendein anderer. Ich bin sogar davon überzeugt, daß diese Einwirkungen auf Nachbarwissenschaften noch lange anhalten werden und daß die Verhaltensbiologie erst am Anfang ihrer Ontogenie steht.

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