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Essay on Contemporary Issues in Ethology

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On the Problems Studied in Ethology, Comparative Psychology, and Animal Behavior

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Abstract

I review TINBERGEN's "four problems of biology," their antecedents, and their subsequent development in the hands of other writers. As they have been developed from writer to writer the "problems" have been transformed and altered in subtle ways, some of which appear counterproductive. I suggest that the divisions of the problems in terms of "proximate-ultimate" and "how-why" have had unfortunate consequences and I suggest a modest revision so that problems are considered in relation to the genesis, control, and consequences of behavior.

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The core of any discipline concerns the problems studied and questions asked by its practitioners. TINBERGEN's (1963) formulation of the four problems addressed in the study of animal behavior has served to organize the discipline for many years. I review that formulation, as well as its antecedents and subsequent variations on it. I suggest a modification of the structure of these problems that I believe lies in the spirit of TINBERGEN's proposals and is clearer.

Two matters of style and approach should be addressed briefly. First, as will be seen, these four "problems" have been given different labels by different authors. I call them "problems" in an effort to retain the sense of TINBERGEN's usage. Second, in the interest of clarity of presentation we must distinguish between the problems studied and the ways in which the problems are grouped: the two issues will be addressed sequentially.

4. Consequence or Cause?

Perhaps the most pivotal issue under recent discussion has been the issue of whether studies of function are to be considered as causes or as consequences of behavior. It will be recalled from above that TINBERGEN (1963) was clear that studies of function (i.e., survival value) were to be distinguished from those of causation. However, in more recent literature functional explanations have been treated as answering problems of causation, particularly stemming from their classification as "ultimate causation."

Both FRANCIS (1990) and ARMSTRONG (1991) have argued convincingly, as was clear to TINBERGEN, that studies of the consequences or function of behavior should not be interpreted as causal. Events cannot be causes of events that precede them. To go from a consequence of behavior observed at the present time to the conclusion that similar consequences may have shaped the evolution of the behavior in the past requires an inductive leap. The justification for this inference must be made explicit and examined critically. Rarely is this done.

A Proposed Reformulation

The simplest solution to some of the problems just discussed is to drop the proximate/ultimate distinction and provide a new means of grouping the problems. The how/why distinction is of little help, as various of TINBERGEN's four problems can be framed so as to fit legitimate uses of "how" or "why," as for example in HINDE's (1959) "three whys." ARMSTRONG's (1991) proposal is centered on the differentiation of different consequences of behavior and is presented in a complex diagram that appears too awkward to have great impact on the field; the beauty of TINBERGEN's proposal and some of its refinements lies in its simplicity. I propose a more modest revision of the four-problem approach, as presented in Table 3. It was developed prior to and independently of the published work of FRANCIS and ARMSTRONG (e.g., DEWSBURY 1992). I divide the problems studied into three major headings, each of which can be sub-divided: the study of the genesis, control, and consequences of behavior.

I recognize that there are some gray areas between these categories, as there are between virtually all such categories. Indeed, I am tempted to propose as a universal law in the study of animal behavior that all distinctions that are initially proposed as dichotomies are destined to become continua.

1. Genesis

The study of the genesis of behavior concerns the influence of past events on the unfolding, over reasonably long time spans, of the behavior under study. This includes evolutionary, cultural, and developmental factors. I use the term "genesis" in the broadest sense to mean all relevant, antecedent events from the past that influence the behavior in question. The emphasis is on historical influences, but they are conceived dynamically.

a) Evolution

Problems of evolution concern the phylogeny of the behavior in question and relate to the past action of natural selection and other processes that influence gene frequencies as they have affected the phenomenon under study. Both the evolutionary origins and the subsequent evolutionary pathways are included, and could be treated as second-level sub-categories.

b) Culture

Problems of culture concern cross-generational, non-genetic transmission, as discussed in the context of the TINBERGEN problems approach by HAILMAN (1982) and JAMIESON (1986). Such formulations as that of the ontogenetic niche (WEST & KING 1987) would be included here.

c) Development

Problems of development concern events beginning with the conception of the individual and ending prior to the time of occurrence of the behavior under study. These concern events in the lifetimes of individual organisms that are on a relatively long time line. Genetic factors generally are treated here. Development is a dynamic process of the continuous and mutual interactions of the organism, its genotype, and the environment.

The most fundamental aspect of this category is the unification of concepts that are essentially historical, whether they be phylogenetic or ontogenetic. This linkage represents a return to the older usage of "genetic" in a broad, traditional sense. Thus, for example, BALDWIN (1901) defined genetic psychology as "psychology in so far as it concerns itself with questions of mental evolution, development, and growth." This also preserves the insight from HAILMAN's double partitioning, that linked ontogenetic and phylogenetic problems as problems of genesis.

2. Control

Problems of the control of behavior concern the short-term regulation, or causation, of behavior. This includes events immediately preceding and occurring concurrently with the behavior under study. As with previous proposals, it is admittedly impossible to define precisely the line between problems of development and control. Further, the time spans on which animals operate may vary across taxa, so that, for example, events that span hours may be pragmatically treated as "control" for a human, but as "development" for a protozoan. In practice, however, this distinction has generally proven both workable and useful in many areas of biology and psychology.

a) External Control

Problems of external control relate to events outside the skin of the animal under study. Relevant environmental events include influences from inanimate objects, effects of animals of other species, social influences, and, indeed, the effects of all stimuli impinging on the animal.

b) Internal Control

Problems of internal control concern those within the organism, problems of mechanism. Generally, these concern physiological, endocrinological, and related internal events. SHERMAN's (1988) category of mental events would be included within internal control. The distinction between internal and external events captures some of the differentiation suggested in the five causes and origins of HAILMAN (1964) and was also suggested by TINBERGEN (1963, p. 426).

3. Consequences

The consequences of behavior concern the full range of effects that are contingent on behavior, including effects on the organism and its fitness, other organisms, and the physical environment.

a) Consequences for the Organism

As a result of engaging in behavior and interacting with the environment, the organism is changed. It may learn, be injured, or be altered and affected in any of a large number of ways. Such consequences may be short-term or long-term.

b) Consequences for the Environment

There are many consequences of behavior for objects and organisms outside of the organism. In this category I include effects on other organisms of both the same and different species and the environment as a whole. Obviously, this category can be further divided as proves useful. An especially penetrating analysis of some environmental consequences can be found in R. DAWKINS' (1982) "The Extended Phenotype."

c) Consequences for Differential Reproduction

This includes all consequences of behavior for the inclusive fitness of the organism displaying the behavior.

Events may have consequences that fall into all three classes. Changes in the organism or its environment, for example, often, but not always, have consequences for fitness.

4. The Loop from Consequences to Evolution

The loop is completed as the consequence for differential reproduction feed back to affect future evolutionary change. This is the essence of natural selection. This is the step that often is implicit in alternative formulations.

5. Some General Comments

By dropping the terms "proximate-ultimate" and "how-why" one can escape many of the difficult issues of causation and the implication that consequences of events are causal to the event under study. The consequences of behavior may be of considerable significance for future events and present events may have been precisely shaped by past contingencies; however, consequences cannot be causal of contemporaneous events.

With this system I attempt to build solutions to many of the problems that have arisen in recent literature without making the system too unwieldy.

Although grouping the problems, this system is intended as a return to TINBERGEN's (1963) system in which all problems in the study of behavior were valued equally, in contrast to recent systems in which the ultimate has been valued more than the proximate. TINBERGEN also was clear about separating causation from function.

The problems of the evolution and present adaptive consequences, if any, of behavior are clearly differentiated. Present adaptive functions should often be suggestive of past adaptive functions, but this need not always be the case. The loop from consequences for differential reproduction to evolution completes a circle and renders this a somewhat complete system.

Use of the Proposed System

A few examples will help to clarify how the proposed system will work in practice.

1. Mammalian Copulatory Behavior

I will work through the logic of the system summarized in Table 3 with patterns of mammalian copulatory behavior. With regard to genesis with respect to evolution, one can study the phylogeny of patterns of copulatory behavior as did LANGTIMM & DEWSBURY (1991). Cultural influences on copulatory patterns are apparent in many differences among human societies. In regard to development, there have been many analyses of genetic, early experiential, and aging effects on patterns of copulatory behavior. Together, these analyses present a complete and dynamic picture of the historical factors leading up to a behavioral pattern.

With respect to control, social environment, time of day, and characteristics of the partner all have important influences acting externally. Studies to internal factors include those of hormones, drugs, and neural mechanisms. Both internal and external influences are important in the analysis of control.

Consequences for the individual female often include pregnancy; for the male, copulation often produces surges of hormones that can lead to enlargement of hormone-sensitive structures, such as the accessory glands. From the standpoint of a male, the female's pregnancy can be viewed as an environmental effect and as an effect on his fitness. There are other consequences for the environment, such as damage to branches and the substrate and the deposition of odors. Working on the beaches of Florida, BLAIR (1951) suggested that the circular patterns of footprints found in the sand on some mornings suggested sexual activity by beach mice, *Peromyscus polionotus*. The consequences of copulatory activity for differential reproduction hardly require elaboration. However, an important point apparent from Table 3 is that the leap from present consequences of copulatory behavior for differential reproduction to inferences that similar consequences prevailed and shaped these patterns in the past is made explicit.

2. Bird Song

The most commonly used example in illustrating TINBERGEN's four problems s is bird song (e.g., SHERMAN 1988). I will not take space to go through the entire e exercise. In the present system, questions of evolution, development, and control l are exactly as in the TINBERGEN and other formulations. They are grouped i somewhat differently, in part to reveal the commonalities between evolutionary y history and developmental history. With the new system there is a tidy place in n which to accommodate cultural evolution, such as the dialects in bird song. Also, the need to analyze both internal factors (e.g., hormones, brain structures) and i external factors (e.g., weather, presence of conspecifics) as part of the analysis of f control is made explicit.

The revised analysis of consequences accommodates some interesting factors. Singing has consequences for the individual. In the classic model of MARLER (1970), the animal must sing and hear itself sing in order to perfect song against a hypothetical template. The animal is thus changed as a result of feedback from its behavior. This particular example concerns a process usually conceptualized as developmental; however, it is now apparent that song learning in white-crowned sparrows, for example, can take place even in adults (PETRINOVICH 1990) and thus the process is general. There are many consequences of bird song for the other animals in the environment, including males, females, and predators. For example, a devocalized bird soon finds intruders in his territory. The consequences for the environment are less obvious than such examples of the extended phenotype as nests and other artifacts (see R. DAWKINS 1982). It is notable that when one animal influences another, with respect to the actor, these are environmental consequences of the behavior. With respect to the receiver, however, these concern external control of behavior.

Table 3: Proposed structure for the problems addressed in the study of behavior