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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.

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TINBERGEN's Four Problems and Their Impact

TINBERGEN's formulation was presented in his classic "On aims and methods of ethology" (1963). After discussing the nature of ethology and the importance of observation and description, TINBERGEN delineated the "four problems of biology" (p. 426) as applied to behavior; he called these causation, survival value, ontogeny, and evolution. In discussing causation, TINBERGEN related his approach to LORENZ's contributions and clearly was thinking primarily of physiological mechanisms. In discussing survival value, TINBERGEN made it clear that he was discussing the effects of behavior, rather than its causes:

> "The study of causation is the study of preceding events which can be shown to contribute to the occurrence of the behaviour. . . . 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 . . . we have to study both causation and effects." (p. 418).

Elsewhere, TINBERGEN used "function" as essentially equivalent to "survival value." In discussing ontogeny, TINBERGEN concentrated on the nature-nurture problem, which was an important issue separating some ethologists and psychologists at the time. Within the study of evolution, TINBERGEN delineated two major aims: "the elucidation of the course evolution must be assumed to have taken, and the unravelling of its dynamics" (p. 428). Studies of the genetic control of species-specific behavior would be included in the study of evolution.

A number of aspects of this formulation are notable. First, the four problems of biology are presented ungrouped. TINBERGEN tried to show relationships among the four problems, but did not propose any firm grouping among them. Nor was any hierarchy of importance developed. Second, TINBERGEN used the word "cause" in association with the short-term regulation of behavior and clearly contrasted it with the other problems. Problems of function, for example, were clearly differentiated from cause. Third, the term "ultimate" was used only in a very different context from recent usage and "proximate cause" was used only to contrast causal analyses from teleology in its crude forms.

Some authors have noted that TINBERGEN also delineated these four problems on the first two pages of "The Study of Instinct" (TINBERGEN 1951), where they were treated as causal structure, ontogeny, function, and evolution. However, because they were not emphasized and the implications of the four problems were not explored, this 1951 formulation had much less impact than that of 1963.

In the period since this formulation, the "four problems of TINBERGEN," transformed into various contexts and guises, have become the guiding principles for the study of behavior, especially for North American workers. Textbook authors (e.g. ALCOCK 1975; DEWSBURY 1978; KLOPFER & HAILMAN 1967) and authors of other influential works (e.g., LEHNER 1979) have relied upon TINBERGEN's formulation. However, in the process of this popularization, the "problems" have been transformed in ways that appear in some ways inconsistent with TINBERGEN's aims and that may be detrimental to the development of the balanced science of animal behavior that I envisage.

The "Problems" before TINBERGEN

Differentiation among different kinds of causation (i.e., material, formal, efficient, and final causes) can be traced at least to ARISTOTLE. I will not discuss these distinctions further, however, because MAYR (1974) and HAILMAN (1982) have already discussed the links between the biological problems and Aristotelian causes and they are not immediately germane to the approach taken here.

The direct predecessor acknowledged by TINBERGEN was HUXLEY (1942), who delineated "three aspects of biological fact:"

> "Every biological fact can be considered under three rather distinct aspects. First, there is the mechanical-physiological aspect: how is the organ constructed, how does the process take place? Secondly, there is the adaptive-functional aspect: what is the functional use of the organ or process, what is its biological meaning or value to the organism or the species? And in the third place, there is the historical aspect: what is the temporal history of the organ or process, what has been its evolutionary course?" (p. 40).

A similar approach was taken by ORIANS (1962, p. 261): "It is becoming increasingly apparent that a complete answer to any question should deal with physiological, adaptational, and evolutionary aspects of the problem." It was TINBERGEN who added ontogeny and converted the "aspects of biological fact" to "problems."

The Role and Changing Views of HAILMAN

Jack HAILMAN was important in popularizing the use of the four problems (e.g., HAILMAN 1964, 1967, 1977, 1982; KLOPFER & HAILMAN 1967, 1972a, b). Indeed, HAILMAN (1967) believed that he had developed the four problems independently of TINBERGEN. HAILMAN's conceptualizations changed over time; the various versions are summarized in Table 1.

For HAILMAN (1967) the four causes and origins of behavior were the biological function (or selective advantage), the population history (including cultural transmission), control, and ontogeny. Thus, he introduced to formulations of TINBERGEN's problems the issue of nongenetic intergenerational transmission, an issue ignored within the context of the problems of ethology by most other writers.

In the formulation of HAILMAN (1964), there were five causes and origins of behavior. He divided the problem of the "causation" of behavior into two categories: "physiological-anatomical" mechanisms and "causation" or "control." The latter had two aspects: "prediction of behavior from the state of the environment. . . ." and "from the immediate past actions of the behaving organism." (p. 4). This formulation has not generally been adopted.

For KLOPFER & HAILMAN (1967) there were four causes and origins, each of which was framed as a question:

1. How is behavior maintained in a population?
2. What is the history of behavior in a population?
3. How is behavior controlled?
4. How does behavior develop ontogenetically?

Table 1: A selection of alternative names for the problems studied in animal behavior

Reference	Name	Causation	Ontogeny	Survival value	Evolution
HUXLEY (1942)	aspects of biological fact	mechanical-physiological	—	adaptive-functional	historical
TINBERGEN (1963)	problems	causation	ontogeny	survival value	evolution
HAILMAN (1964)	causes & origins	2: causation/control & physiological-mechanical	developmental history	biological function/selective advantage	evolutionary history
HAILMAN (1976a)	causes & origins	dynamic control	ontogenetic development	adaptive function	phylogenetic origin
HAILMAN (1977)	behavioral determinants/classes of models	dynamic control	ontogenic development	preservation	phylogeny
HAILMAN (1982)	classes of behavioral determinants	control	ontogeny	perpetuation	phylogeny
HINDE (1959)	whys	causal	—	functional	historical
HINDE (1966)	main kinds of problem	causal analysis	ontogeny	consequences of the activity	—
BEER (1963/1964)	—	proximate causation	—	biological utility	phylogeny
BURGHARDT (1973)	—	control (causation)	ontogeny	function	evolution
DEWSBURY (1978)	questions	immediate causation	development	function	evolution
LEHNER (1979)	areas of study	control (causation)	ontogeny	function	phylogeny (evolution)
ALCOCK (1975)	questions	immediate or proximate cause	genetic & developmental bases	function or ecological significance	evolutionary history
SHERMAN (1988)	levels of analysis	mechanisms	ontogenetic processes	functional consequences	evolutionary origins

In his next papers HAILMAN (1976a, 1977) made some changes in the labels he attached to the various problems (see Table 1). The most notable departure was that HAILMAN (1977) used "phylogeny" in a broad sense, so as to include culturally transmitted behavior.

In his most extensive treatment of these issues, HAILMAN (1982) discussed the history and nature of these problems and again changed his terminology. Clearly, the nature of the four problems changed over time, even in the view of one writer as he developed his ideas on the subject.

Variations on Themes

Over the years in which the basic framework of the "four problems" has been extended and applied, the names applied to both the collection and the individual problems have changed as each author has applied labels with which he or she feels most comfortable. Some of these are summarized in Table 1.

Although many of the differences revealed in Table 1 are primarily in the labels applied, there were some substantive shifts as well. Whereas TINBERGEN (1963) placed the study of genetic influences on behavior within the problem of evolution, most authors have treated them as problems of development. HINDE (1959, 1966) and BEER (1963, 1964) recognized three classes, though the nature of the three varied from time to time. ARMSTRONG (1991) has been especially concerned with the multiplicity of effects of behavior, not all of which are obviously subsumed under the rubric of "function." For ARMSTRONG, there are effects of behavior on the actor, other individuals, populations, communities, and the physical environment. SHERMAN (1988) appears unique in wishing to separate cognitive processes as a sub-category separate from physiological processes within his category of mechanisms. This has metaphysical implications that may be undesirable.

The naming of the problem of "function" has been especially variable. TINBERGEN's "survival value" would not suffice, because it is the cross-generational consequences, rather than survival of individual organisms, that required emphasis. PITTENDRIGH's (1958) "teleonomy" appeared to be a useful alternative, but did not gain widespread acceptance. "Adaptiveness" has different connotations and has not been widely used in this way (see Table 1). Although "function" is among the most complex terms in biology and is loaded with multiple meanings (e.g., RUCKMICH 1913; HAILMAN 1976b), it seems to have become standard.

In a similar manner, there has been great variance in what the "four problems" have been called, with "causes and origins," "behavioural determinants," "areas of study," and "questions" being among the labels used. All appear roughly equivalent in treating four distinctive problem areas except SHERMAN's (1988) use of "level of analysis," which implies a hierarchy, with some levels higher or lower than others.

The Grouping of TINBERGEN's Problems

In his original formulations, TINBERGEN (1951, 1963) treated his four problems as equal. Although he tried to show how they might be interrelated, he did not present them in a clustered organizational framework. Contrary to the assertion of SHERMAN (1988), TINBERGEN did not suggest that global categories should be grouped under the rubrics of "proximate" and "ultimate" (cf. SHERMAN 1988, p. 616; HAILMAN 1982, pp. 137—138). Most subsequent authors have done so.

1. Proximate and Ultimate; How and Why

Credit generally is given BAKER (1938) for introducing the terms "proximate" and "ultimate" in the study of biological phenomena. However, he did this in passing, rather than as a deliberate attempt to organize the material of the field:

"There is, of course, no reason to suppose that the particular environmental conditions favourable to the young are necessarily the one or ones which constitute the proximate cause and stimulate the parents to reproduce. . . . In the wet tropics it is very hard to assign any ultimate cause for a breeding season, for there is no regularly recurring period of food-shortage or cold." (p. 162).

BAKER's approach was accepted and applied by LACK (1954) and it was probably LACK who established the terms in wider use. WILSON's (1975) use surely extended the popularity of this formulation.

It was MAYR (1961) who, though citing neither BAKER nor LACK, self-consciously developed a taxonomy of causes and problems. MAYR stressed the dichotomy between functional biology and evolutionary biology. He used the terms "proximate cause" and "how" questions in relation to functional biology and "ultimate cause" and "why" questions in association with evolutionary biology. MAYR further linked proximate causes to the responses of individuals and organs and ultimate causation to the evolution of DNA codes. MAYR's how-why and proximate-ultimate distinctions have become commonplace. The four kinds of causation he proposed (ecological cause, genetic cause, intrinsic physiological cause, and extrinsic physiological cause), however, were not widely adopted by animal behaviorists.

BEER (1963, p. 174) adopted a similar use of the proximate-ultimate distinction:

"Though much of this new information could be explained in terms of ultimate causes — biological utility and phylogeny — there remained the questions of proximate causation — the factors and mechanisms acting here and now which directly determine what an animal is doing."

2. The Hierarchical Grouping of TINBERGEN's Problems

Although Baker, Lack, Mayr, and Beer introduced the how-why/proximate-ultimate dichotomy, they did not link it to TINBERGEN's four problems; the puzzle of that origin remains. One important step occurred when KLOPFER & HAILMAN (1972a, b) issued two volumes of readings in ethology, one dealing with the "Function and Evolution of Behavior" and the other with the "Control and Development of Behavior." This two-way grouping became widespread, although, at this point, the groupings were still unnamed.

Perhaps the first explicit pairing of the four problems with the how-why/proximate-ultimate dichotomy was in ALCOCK's (1975) textbook. However, although his four categories clearly are those of TINBERGEN, ALCOCK did not cite or even mention TINBERGEN in his section on how and why questions. In any event, it would appear to have been ALCOCK who was the first to link these two developing traditions and classify and name problems of immediate causation and development as how/proximate and of function and evolution as why/ultimate.

Numerous authors adopted this hierarchical grouping, with problems of immediate causation and development classified as proximate causation and those of evolution and function as ultimate causation (e.g., DEWSBURY 1978; KREBS & DAVIES 1987; WITTENBERGER 1981; SHERMAN 1988). SHERMAN's use of the hierarchical schemas was diagrammed by ARMSTRONG (1991). Indeed, ARMSTRONG ignores much previous work to credit SHERMAN with the synthesis of the proximate/ultimate distinction with TINBERGEN's four problems.

3. A Double-Partitioning of the Four Problems

HAILMAN (1976a, 1977) proposed a double partitioning of the four problems, with level of action (individual versus population) and type of determinant (cause versus origin) as the two factors producing the double partitioning (see Table 2). This system was adopted with modification by LEHNER (1979), though without citation of HAILMAN.

The system has the advantage of highlighting an affinity between evolutionary history and ontogeny as relating to the genesis of behavior. However, in the process, functions must be treated as causes. These issues are discussed below. The double-partitioning approach has not been widely adopted.

Table 2: Double partitioning of the four problems as presented by different authors

a) HAILMAN (1976):		
	Individual	Population
Causes	dynamic control	adaptive function
Origins	ontogenetic development	phylogenetic origin
b) HAILMAN (1977):		
	Immediate cause	Antecedent origin
Individual organisms	control	ontogeny
Population of organisms	preservation	phylogeny
c) LEHNER (1979):		
	Level of individual/ "Proximal causation"/ "How questions"	Level of individual or population/ "Ultimate causation"/ "Why questions"
Origins	ontogeny	phylogeny (evolution)
Causes	control (causation)	function

4. The Ascent of Function

In either the simple hierarchical form or the double-partitioned form, the grouped four problems became a standard means for organizing the study of animal behavior. However, since the publication of WILSON's (1975) "Sociobiology," the study of function has received exceptional emphasis, to the detriment of studies of the other three problems (see BARLOW 1989; M. S. DAWKINS 1989; SNOWDON 1990; ARMSTRONG 1991). When a volume of papers was published in

honor of TINBERGEN it was significantly entitled "Function and Evolution in Behaviour" (BAERENDS et al. 1975).

Recent Controversy

Several controversies focused about these four problems have emerged in recent years. The preceding historical analysis may shed some light on these controversies.

1. Cultural Inheritance

JAMIESON (1986), following GOULD & LEWONTIN (1979) and HAILMAN (e.g., 1982), emphasized the view that the four problems are noninclusive. He pointed out that behavioral patterns can be "induced environmentally without a change in the genotype, and they can be learned and transmitted culturally as well as genetically" (p. 206).

Although environmental induction is fairly easily handled via development or immediate causation within the "four problems" structure, the problem of cultural inheritance is not. The latter point resembles one that HAILMAN has made several times which led him to an atypical definition of phylogeny:

> "To contemporary biologists the word phylogeny is nearly synonymous with evolutionary history, but I use the term in its older and wider sense of simply the history of the population. Therefore, phylogenetic considerations include the origins of culturally transmitted behavior and hence complete a comprehensive albeit general scheme for investigating behavior." (HAILMAN 1977, p. 12).

Complete, the scheme may be, but it creaks from being forced into the Procrustean bed of the four problems. The study of cultural inheritance is a legitimate enterprise, even if careful analysis sometimes reveals modes of transmission different from those of first appearance (e.g., GALEF 1990). HAILMAN's use of "phylogeny" is not widespread, as he points out, and is not always obvious to the reader. Some revision of the system seems appropriate.

2. The Clitoris Debate

Another issue in recent literature concerned the evolution of the clitoris, but spilled over to include other phenomena, such as helping behavior in birds. It entailed two pairs of combatants: GOULD (1987a, b) versus ALCOCK (1987) and SHERMAN (1988, 1989) versus JAMIESON (1989). The basic question concerned the function of the female clitoris. Whereas ALCOCK contended that the clitoris has functional consequences that are subject to natural selection, GOULD maintained that there need be no fitness consequences for the clitoris; it may have evolved as a secondary consequence of the evolution of male penile structure just as male nipples may be a result of a single male-female developmental body plan.

SHERMAN (1988) suggested that the confusion arose from a failure to distinguish problems of "evolutionary origins" from those of functional consequences. However, JAMIESON (1989) contended that the issue did not concern the investigation of different problems, but rather two parallel questions: (1) whether the past selective pressures acted directly on clitoral evolution or only secondarily via penile evolution, an evolutionary question, and (2) whether or not there are presently functional consequences of the clitoris that produce differential fitness, a question of function.

It must be remembered that there are at least three aspects to the evolution of a behavior in a population: the original source of the trait, the past history of selection (if any) as the trait evolved further, and the present fitness consequences (if any). All three are legitimate areas of study. However, the TINBERGEN problems structure was not designed primarily to clarify this particular set of potential confusions. It seems reasonable to include problems of the original sources and past history of a trait within the study of evolutionary history and the study of consequences for the organisms presently available for study within function. Problems of evolutionary history concern all aspects of history prior to the lifetimes of the individuals under study.

SHERMAN's term "evolutionary origins" is not incorrect; however, it can be confusing if it is read as implying only one aspect of the past history of a trait in a population, its origination. I see no purpose for the term "origins" in SHERMAN's formulation. However, there are more important problems with the formulation. One is the implication of different valuation for different levels. A second is the treatment of consequences as causes; events cannot cause events that precede them. Both of these problems and the issue of the function of the clitoris are discussed below.

3. The Mischief of "Ultimate"

Although the proximate-ultimate distinction has become generally adopted in biology, it is fraught with hidden traps. The main one lies in the surplus meaning carried by the term "ultimate." The usual opposite of proximate, or proximal, is distal, not ultimate. As noted by ARMSTRONG (1991), "ultimate" can convey a sense of distance, a final aim, or that something is fundamental and incapable of further analysis. Although probably unintended when the terms were coined, it is easy to slip from the meaning of "ultimate" as "distal" to that of "more fundamental." This makes explanation in terms of "ultimate" causes seem more basic and important than explanations in terms of proximate factors. Such an approach would be difficult to defend and certainly runs counter to TINBERGEN's intentions in proposing the four problems.

It is this excess baggage inherent in the term "ultimate" that leads to the slippage from four "problems" to that of four "levels," again with the hidden implication that some explanations lie on a more important and satisfying plane than do others. If the term "proximate" is to be retained, it is more neutrally opposed by "distal" than by "ultimate." As noted by FRANCIS (1990, p. 404), "Granted, 'distal' lacks some of the connotations of 'ultimate', but it is meaning well lost." The use of "levels" in this context should be dropped. This should not preclude the use of the term to refer to "levels of analysis" (e.g., cell, organ, individual, group), which is quite different.

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 functions 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 is bird song (e.g., SHERMAN 1988). I will not take space to go through the entire exercise. In the present system, questions of evolution, development, and control are exactly as in the TINBERGEN and other formulations. They are grouped somewhat differently, in part to reveal the commonalities between evolutionary history and developmental history. With the new system there is a tidy place in 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 external factors (e.g., weather, presence of conspecifics) as part of the analysis of control is made explicit.

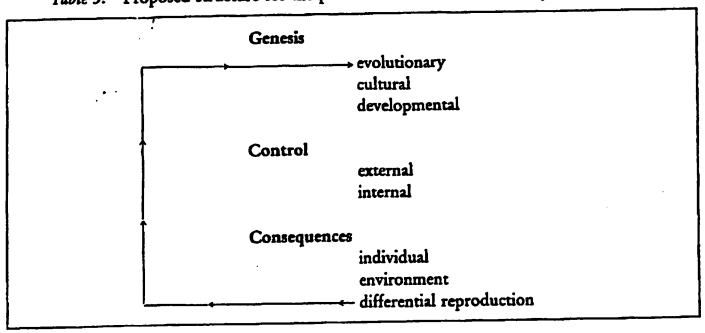
The revised analysis of consequences accommodates some interesting factors. Singing has consequences for the individual. In the classic model of MARLER (1970), the animal must sing and hear itself sing in order to perfect song against a hypothetical template. The animal is thus changed as a result of 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.

3. The Clitoris Debates

We can now return to the recent controversies concerning the function of the human clitoris. In the present perspective, ALCOCK and GOULD appear to be talking past each other. ALCOCK (1987) rejects GOULD's parallel between male nipples and the female clitoris, arguing that "male nipples do not do anything" (p. 4), whereas the clitoris does. In essence, ALCOCK argues that the clitoris has consequences and that we can study its consequences in relation to testable predictions. This is a reasonable argument. If possession of a clitoris has consequences and male nipples do not, it is these consequences that allow us to reject GOULD's analogy.

However, GOULD (1987b) is also making an important point which was emphasized above. He notes that his major complaint about adaptationism is "its *logically* incorrect equation of current utility with reasons for historical origin." (p. 4). The choice of the word "origin" is especially unfortunate. In essence, GOULD argues that there is a whole range of possible consequences of the possession of a character and the fact that it has demonstrable consequences need not necessarily mean that it has consequences for reproductive success. This is made explicit in Table 3. Further, the fact that there may now be consequences

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



need not necessarily imply that we can draw the loop back to evolutionary history. Indeed, even if there are fitness consequences at present there is no guarantee that they are the same as those that may have prevailed when the character was shaped. But GOULD (1987a) goes too far asserting that "female orgasm is not an adaptation at all." (p. 17). We need to study the consequences of orgasm for differential reproductive success and then determine whether a plausible case can be made for drawing the loop from present consequences to the past history of natural selection. These need to be studied, not asserted or denied a priori.

The SHERMAN (1988, 1989) — JAMIESON (1989) controversy follows that between ALCOCK and GOULD and has a similar resolution. The 4-problem structure lacks the flexibility to handle the questions with which these authors deal. There really are three questions that they consider: (1) What was the phyletic origin of the trait? (2) What selective pressures led to the evolutionary paths that led to the current form of the trait, and (3) What are the current consequences of possession of the trait? Again, it is common to use evidence from question (3) to draw conclusions regarding question (2). This often is justified. However, the inferential nature of this step needs to be made explicit. I bring out the distinction between questions (1) and (2) in my text above, but not in Table 3. Although I prefer not to make the Table too complex, the distinction is an important one.

Has the "Problems" Formulation Outlived its Usefulness?

During the classical period of ethology when TINBERGEN formulated his "four problems," the differentiation of research programs addressed to different problems was clear. Some researchers were more interested in function and others in causation. With the advent of the sociobiological approach there was an increased emphasis on problems of adaptive function and the gulf between students of adaptive function and other students of animal behavior was widened. In recent years, however, various animal behaviorists have recognized the inter-

dependence of studies of function and other aspects of behavior (e.g., DEWSBURY 1990; SNOWDON 1990). For example, in studies of sperm competition there is a fine line between problems of the mechanisms and dynamics of interaction between the sperm of two males and their fitness consequences. Increasingly, problems of learning are being studied with concern for the consequences of learning as they may relate to consequences that could affect fitness (e.g., HOLLIS 1990). There also is a thin dividing line between function and mechanism for studies of foraging and optimal foraging strategies (e.g., KAMIL & CLEMENTS 1990).

The interdependence of research in different problem areas has been cited repeatedly in literature in ethology. For example, TINBERGEN (1963, p. 426) noted that "we must apply the question 'what for?', the question of survival value to ontogeny as well." HAILMAN (1982) conceptualized the study of development in terms of changing patterns of dynamic control (i.e., immediate causation).

Although the increased attention by individual researchers to multiple problems is a welcome and healthy sign, I believe that the distinctions posed by TINBERGEN and others remain as important today as when they were first proposed. It remains easy for students and even experienced researchers to confuse these problems. It is especially common for students asked to provide an immediate cause of a behavior to respond with a function (e.g., the immediate cause of an animal's eating lies not in external influences and internal mechanisms, but because it needed food in order to live). In the cases cited above we can still differentiate problems of the dynamic control of behavior from those of consequences, even where the dividing line is thin, where more than one question is addressed within a single laboratory and research program, and even where we recognize the interdependence of our answers. It is important that we do so.

William JAMES (1890) noted that:

> "Not one man in a billion, when taking his dinner, ever thinks of utility. He eats because the food tastes good and makes him want more. If you ask him *why* he should want to eat more of what tastes like that, instead of revering you as a philosopher he will probably laugh at you for a fool (p. 386). To the animal which obeys it, every impulse and every step of every instinct shines with its own sufficient light, and seems at the moment the only eternally right and proper thing to do." (p. 387).

JAMES clearly understood the distinction between causation and consequences and regarded it as the "psychologist's fallacy" to assume that the behavior of the subject was governed by processes apparent to the observer. That distinction is no less important today than it was 100 years ago. Even as more people consider the functional consequences of their diets, and thus make knowledge of probable consequences a factor in causation, we must keep differentiated the problems of control and consequences.

However, we must not ignore any of these classes of problems. Albeit from an evolutionary bias, MAYNARD SMITH (1992, p. 36) put it nicely on learning that Harvard University is dividing the sciences into the "experimental-predictive" and the "historical:"

> "If they are not careful at Harvard, they will finish up training a lot of molecular biologists who do not know what the right questions are, and a smaller number of biologists who know the questions, but have not the knowledge to answer them."

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Note added in proof:

Julian HUXLEY (1916) clearly distinguished between "immediate cause" and "ultimate cause" (p. 161). (J. S. HUXLEY: Bird-watching and biological science. Auk. 33, 142—161 + 256—270).