

## CLASSIC ETHOLOGY REAPPRAISED

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**ABSTRACT:** I analyze the theoretical tenets of early ethology and the criticisms leveled against it from comparative psychology. Early ethology had a clear research object, the study of behavioral adaptedness. Adaptedness was explained by the functional rules and programs that underlie the relation between a given organism and its natural environment (the function cycle). This research object was lost during the redefinition of ethology that took place after the Second World War, a redefinition that led to an emphasis on physiological and evolutionary explanations instead of functional ones. This loss happened because early ethologists did not make their aims sufficiently clear and because of fundamental epistemological and semantic misunderstandings between ethologists and comparative psychologists. I argue that the behavioral explanation of adaptedness is different from both physiological and ecological research and that it needs functional concepts similar to the ones of early ethology. I defend the idea of function cycles and causal centers defined in terms of perceptual selection and behavioral response tendencies and I try to show that these functional concepts may be fruitfully combined with learning theories. I suggest calling this line of research Comparative Behavioral Ethology.

*Key words:* classic ethology, Umwelt; organism–environment interaction; Uexküll, Lorenz, Tinbergen, Lehrman

Wilson's (1975) *Sociobiology: The New Synthesis* advanced a dreary prognosis for Ethology and Comparative Psychology: they would progressively melt between behavioral ecology and neurophysiology. Even if it can be argued that ethology is an active field of research, it is true that the fields of behavioral ecology and physiology (neuroethology) are more important than strictly behavioral research. This may seem a natural development of early ethology: Tinbergen's interest in ecology and Lorenz's interest in releasers are being continued by behavioral ecology and neuroethology. However, I will maintain that something very important was lost in modern ethology—namely, a theory for the study of behavioral adaptedness and the functional logic linking a priori structures and environment, as in Uexküll (1921; Uexküll & Kriszat, 1956) and Lorenz (1961, 1965).

In this paper I will try to show that Lorenz's ethological approach was not exhausted and that most criticisms of it throw out the baby with the bath water. I

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will also try to show some possible developments that stem naturally from early ethological theory, but first I briefly unravel the conceptual network of early ethology and its critique by comparative psychologists.

### **Genesis of Ethology**

It is usual to mark the beginning of ethology by reference to the work of Konrad Lorenz and Nikolaas Tinbergen. While acknowledging that the systematization of “behavioral comparative studies” into “ethology” is the result of the joint efforts of Lorenz and Tinbergen, I think it is important to mention, first and foremost, the work of Jakob von Uexküll. As I will show, the core of Uexküll’s thinking exactly corresponds with Lorenz’s theories at the time Tinbergen came under the influence of Lorenz. In fact, Lorenz’s arguably most important paper—the 1935 Kumpan paper in which ethology’s early theoretical elements were developed—was written when he was under the influence of Uexküll’s ideas and was dedicated to Uexküll.

#### ***Jakob von Uexküll and Umwelt Theory***

Uexküll claimed that any significant biological research ought to strive to understand the connection between organism and environment. This connection could be morphological (the way a tree grows) or behavioral. When it was behavioral, it was broadly described as the function cycle, the cycle that begins with the perceptual selection of environmental stimuli, continues with the apperception of the selected stimuli, and ends with the behavior activated by the apperception. Uexküll stressed the importance of researching the stimuli to which the animal responds and the behaviors that comprise its response. In this way the investigator could objectively determine the animal’s Merkwelt (perceptual space) and Wirkwelt (action space) and how the two were linked through the Innenwelt (inner organism). Merkwelt and Wirkwelt would create the animal’s specific environment (Umwelt). It is important to stress that, to a certain extent, Merkwelt, Innenwelt, and Wirkwelt match the sign stimuli and releasers, the Innate Releasing Mechanisms (henceforth IRM), and the fixed action pattern (henceforth FAP), respectively. It is also important to stress that Uexküll thought that each particular combination of stimulus and response (the Funktionskreis, or function cycle) could be connected to other such combinations. The result would be the animal’s adaptedness to its environment (e.g., the stickleback’s behavior chains described by Tinbergen, 1951).

Adaptedness is the central point of Uexküll’s theory. He calls it Bedeutung (meaning), but operationally it corresponds to adaptive function: meaning is understood when the researcher explains, in terms of inputs and outputs, the survival function of a given behavior cycle.

Although Uexküll was a physiologist by training, he considered that physiological explanation was different from explanation of adaptedness. Physiology might explain behavior and perception, but it would never explain

adaptedness because organism and environment form a system that cannot be predicted from the workings of the nervous system alone. Adaptedness was explained by the unraveling of the function cycle in terms of what was perceived and how it was acted upon. This is a purely functional approach.

### *Lorenz's Ethology*

Because Konrad Lorenz is the acknowledged founder of the discipline (Tinbergen, 1963), the analysis of his thinking is necessary to trace the genesis of ethology. I submit that there are four main ideas that Lorenz tried to combine and that shaped the development of the field.

The first idea is that behavior patterns are species-specific in exactly the same way that the structure of a wing or a bill is (Lorenz learned this from Heinroth, although Whitman had independently said it before; see Burkhardt, 2005). To be species-specific a behavior pattern must be genetically transmitted and not learned. Heinroth (see Burkhardt, 2005) performed deprivation experiments to determine whether a given behavior pattern was innate. By describing the various innate behaviors it was possible to know the set of innate patterns that characterize a species, the ethogram. Moreover, describing the species ethogram was considered the equivalent of describing the species anatomical structure and might lead to studies of comparative phylogeny in which behavior patterns are used as the diagnostic character (Lorenz, 1941).

The second idea came from Wallace Craig. Both Craig and Lorenz accepted that behavior could be described in terms of the ethogram; however, not all behavior consists of fixed action patterns. Craig first and Lorenz next (Lorenz, 1935, 1937) suggested that instinctive behavior could be divided into two phases, consummatory and appetitive. The consummatory phase consisted of a fixed behavior pattern that was not modifiable; the appetitive phase comprised the search for the occasion to perform the (consummatory) fixed action pattern and was open to learning (much as in conditioning, in which behavior can be shaped by a given reinforcement contingency, although Lorenz did not stress the parallel). Thus, behavior was described in terms of sequences of alternating learned and innate elements.

The thresholds for releasing a FAP were variable in time, and Lorenz hypothesized "Stimmungen" (moods) caused either by internal physiological factors or by external factors.

The third idea came from Jakob von Uexküll. Although in Lorenz's (1931) paper on crows Uexküll's influence is already detectable, nowhere is that influence clearer than in Lorenz's (1935) "Kumpan paper," arguably his most important work. In it Lorenz reformulated fixed action patterns as function cycles with a perceptual field that selected environmental cues and a behavioral field that consisted of the "instinctive" blocks of behavior. Thus he described what was later called the Innate Releasing Mechanism (IRM).

The fourth idea came from physiology, chiefly from Erich von Holst. When searching for an explanation for the fixed action patterns, Lorenz first thought they

were reflex chains. Later, and under the influence of Holst, Lorenz claimed that fixed action patterns were caused centrally, and he went on to describe the causation using a well-known analogy, his “hydraulic model” (Lorenz, 1950a). For Lorenz, the explanation of the behavioral patterns was necessarily physiological (1950b, 1958, 1961, 1965, 1978).

### ***Tinbergen and Motivational Hierarchy***

It was in this general framework that Tinbergen became acquainted with Lorenz’s ideas. After “converting” himself to Lorenzian ethology (see Tinbergen’s 1976 letter to Thorpe, quoted in Burkhardt, 2005, p. 199), Tinbergen’s major contribution was the concept of the hierarchical organization of instinct (Tinbergen, 1942 [in 1951]). This idea was first presented in Baerends’s (1941) work on the brood care of the wasp *Ammophila campestris*, a work supervised by Tinbergen. The idea behind the concept of hierarchy is that elementary behaviors are organized into functional–causal units which, in turn, organize themselves into higher units or centers (Tinbergen, 1951). Causation was represented by energy flowing from higher to lower centers and finally to FAPs.

The hierarchical model accommodated all the findings of previous ethological work: the IRM, FAP, appetitive and consummatory behavior, and “mood” (“Stimmung,” or motivation) changes. It was explicitly a functional model, but Tinbergen tried to link it to physiological research.

An important point is that Tinbergen’s model actually tries to capture the successive functional tasks the animal has to deal with in the environment. The idea of successive functional tasks had been proposed by Uexküll’s celebrated example of the tick (e.g., Uexküll & Kriszat, 1956). In this example a series of different function cycles come successively into play to solve different problems posed by the environment.<sup>1</sup> More than Lorenz, Tinbergen stressed the importance of the IRM in linking the animal to its environment.

From the preceding summary it may be argued that ethology was an extension and updating of the earlier Umwelt theory. Ethology’s starting point is adaptedness and its aims are the unraveling of the perceptual and behavioral means by which adaptedness is achieved.

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<sup>1</sup> The stimuli for the tick’s behavior are light, the odor of butyric acid released by mammals, and the body heat of the host animal. The tick being photopositive after fertilization, light stimulates it to ascend to a bush. The tick can stay perched for years until a mammal passes by. In response to butyric acid, the tick releases its grip and drops from the bush. If the tick lands on the mammal, the skin warmth stimulates the insertion of the proboscis and the sucking of blood. If it lands on the ground, photopositive responses come into play and the tick will again climb to a bush. In this way three function cycles occur in succession to ensure adaptedness.

## The Comparatist's Critique and the Founders' Reaction

### *The Critique*

Lehrman published his *Critique* in 1953. In the year after, two important meetings discussed the critique, the first held in Paris (Fondation Singer-Polignac, 1956) and the second held in New York (Schaffner, 1955). Lorenz's final reaction is represented by a long paper (1961) which was later translated into a book (1965). For Tinbergen's reaction we have to analyze his "four whys" paper (Tinbergen, 1963) and a later text (Tinbergen, 1969). Taken together, these sources illuminate the differences between the two fields and the effects of the critique.

Apart from the emphases on environmental explanations, the most influential aspect of the critique is the importance of explaining behavior through development and physiology rather than functional analysis. Lehrman argued that the fact that a given behavior is species-typical and that it appears despite deprivation experiments does not warrant the conclusion that the behavior is innate because development is a process of interrelationships between internal and environmental information, and regardless of how resistant to change a particular behavior may be, it always depends on external factors. The difference between the two viewpoints is not only a matter of abstract principle (Hinde, 1970) but also of empirical consequences. Because behavior cannot develop in vacuum, both Schneirla (1956, in Fondation Singer-Polignac, 1956, pp. 69-70) and Lehrman (1953, in Fondation Singer-Polignac, 1956, pp. 445-446, in Schaffner, 1955, pp. 136-139) thought that research on the integration of behavior through development was mandatory. Such research involved the study of internal factors, defined in terms of inner physiology, and their interplay with the environment.

Furthermore, the deprivation experiment was said to be useless because it showed only that the specific environmental factors withheld from the animal are not relevant. Before calling a behavior innate it would be necessary to show that its development was not influenced by *any* factor—obviously an impossible task. A related, but slightly different point is that the use of the term "innate" hinders research because it does not encourage the investigation of how all the developmentally relevant factors interact.

A very important point is that the approach of comparative psychologists did not start with the description of adapted behavior. Indeed, Schneirla (1956, Schneirla in Schaffner, 1955, p. 94) did not even endorse the idea of adaptedness, which he considered to be dangerously close to vitalism and dependent on observation bias. The emphasis was on physiology, not on function (see, for instance, Schneirla's discussion with Lorenz in Schaffner, 1955, pp. 82-85).

The importance attributed to physiology manifested itself in the rejection of functional concepts such as releasing mechanisms or sign stimuli. According to both Schneirla and Lehrman (Lehrman, 1953; Schneirla, 1956), the use of the same term (e.g., IRM) across widely different species implied that very different physiological processes were lumped together. This lumping, they claimed, was an obstacle to causal research because instead of investigating the actual processes

ethologists simply labeled them. The IRM or instinctive act as well as the concept of innate were said to be nothing but detrimental labels.

### *The Founder's Reaction*

At first Tinbergen (1955) seemed to accept the critiques while maintaining that there were aboriginal perceptual and motor systems. He accepted that these systems ought to have been studied developmentally, but he pointed out that his level of research was different from the physiological one and that the idea of causal and functional systems of behavior (hierarchy) was important. Later (Tinbergen, 1963) he would come closer to Lehrman and say that the level of perceptual and behavioral organization is just description and that truly causal studies were physiological (including developmental). Therefore it seems that Tinbergen accepted most of the comparatists' critique but tried to salvage the view of behavior as adaptation. He suggested that if adaptedness is accepted as the starting point of research, both physiological causation and selective pressures could be causal studies of behavioral adaptedness. In other words, the starting point of ethology would still be adaptedness through behavior. However, this starting point is conceived of as "description," not explanation, the latter consisting of either the identification of selective pressures for behavior or physiological causes of behavior. Even if ethology's concepts were not abandoned, they were demoted to mere description.

Later yet, Tinbergen (1969) seemed to be even more concerned with description and adaptedness. He said it was important to investigate behavior in terms of hierarchies of causally and functionally homogeneous systems of action and perception, and he claimed that the previous notion of causally functional systems was "sound." He went even further and equated causal-function systems with the function cycle.

Tinbergen's (1969) work did not seem to influence research, and perhaps because of that he grew increasingly uneasy with the direction ethology was taking; he wanted to maintain the adaptedness of organisms through behavior as an important point. In this he was only partly successful, for if, on the one hand, behavioral ecology is often said to stem directly from his later work (see Kruuk, 2003, for analyses of Tinbergen's legacy), on the other hand behavioral ecology has been concerned mostly with identifying selective pressures for behavior adaptedness and not with the analysis of adaptedness per se.

Lorenz's reaction was different. He acknowledged that Lehrman's approach to development was useful, but he maintained the importance of the concept of innate. According to Lorenz, the fact that development needs an environment does not contradict the fact that there are very rigid innate instructions for development. Speaking of "innate behavior" might be wrong—the "genetic blueprint" for development was innate, not the behavioral result—but the term captures the existence of species-typical differences in behavior and perception that are crucial to adaptedness and that appear from the start. He also denied that instinctive behavior could be anything but centrally coordinated, for otherwise it would not be

species-typical. In two places (Lorenz, 1956, p. 67; Lorenz in Schaffner, 1955, p. 171) he accepted the charge that he relied only on behavioral data, but subsequently (e.g., Lorenz, 1965, 1971) he rejected the purely behavioral approach: the ethologists' work should be to push analysis downwards into physiology. Lorenz was convinced that this analysis would show the integration of the instinctive movements to be akin to the central pattern generators described by Erich von Holst.

Lorenz (1956) admitted that his concept of development (the study of innateness or of how innate instructions direct learning) was different from the comparatists', but he stressed the importance of the deprivation technique as a prerequisite to discovering where the information for adaptedness comes from—genes or environment. This means that to predict behavior in natural conditions it is necessary to know what the animal's innate perceptual and behavioral instructions are (as in Uexküll). In the same spirit, he claimed that without the notion of innate blueprint it would be impossible to study learning (Lorenz, 1965; Lorenz in Schaffner, 1955, p. 144). His argument is that stimulus association needs a releaser to which a conditional stimulus can be associated, and that random response variation alone is improbable because learning almost always results in adaptedness. There are, therefore, innate teaching mechanisms, but what these mechanisms are is not clearly stated.

Lorenz stressed the importance of behavioral description in natural conditions as a fundamental basis for inference, but (as with Tinbergen) he always considered physiology and not ethological functional concepts to be the explanation. Therefore, in the same way as Tinbergen, Lorenz seems to conceive of early ethological research as "preliminary description" to be subsequently explained by physiology.

Lorenzian ethology continued, but its aims were never stated clearly. Eibl-Eibesfeldt (2004), a close disciple of Lorenz, argued that ethological research ought to proceed in a series of steps: 1) ethogram establishment through observation; 2) correlation studies such as those performed by Baerends to establish motivational structure; and 3) physiological studies of innate releasing mechanisms. Again, there is no reference to behavior–environment dovetailing, even if this was always performed by the Lorenzian school. The closest definition Eibl-Eibesfeldt gives of ethological specificity is when he defends that physiology cannot explain the kind of behavior ethologists are after. He speaks about a level of integration that differs from that studied by physiologists and to which physiology has no access. This is, again, a definition by exclusion: ethology is what physiology is not, but as the aim of ethology is said to be the physiological explanation of behavior this is tantamount to saying that ethology's aims *are* and *are not* the study of the physiology of behavior.

### *Analysis of the Arguments*

The kernel of early ethology seems clear. According to the motivational state, the releasing configurations are sought by the animal; they are abstracted from the

environment by some sort of neural filtering process and they release a fixed action pattern that integrates with the environment. This conception can be seen as a refinement of Uexküll's function cycle: the focus of analysis is adapted behavior (function cycles) achieved by *Merkwelt* (perception), *Wirkwelt* (action), and *Innenwelt* (motivation and IRMs).

Early ethologists further claimed that this organization was innate because it was species-typical and because it was shown to appear independently of early experience. Because it was innate in this sense, ethologists made an empirically unsupported claim—that the function cycle was to be explained by physiology, and that this explanation ought to be sought in the central nervous system.

Lehrman and Schneirla attacked this unsupported claim. They were physiologists of ontogeny and justly remarked that it is unwarranted to claim that because behavior is species-typical and environmentally stable it is centrally coordinated and independent of experience. Also, they were much more interested than the ethologists in environmental influences. This, I think, is the anatomy of the discussion opposing both groups.

The most straightforward way to settle the dispute is to accept Uexküll's claim that causation is not a substitute for function and that the aim of behavior theory is to unravel function. In order to unravel function it is necessary to capture the relation between organism and environment. This relation can be expressed only by concepts that describe perceptual and motor biases when the animal is confronted with a given environmental situation. Such concepts are at a different level of integration than physiology, for the latter explains behavior and perception but does not explain the actual interaction with environment. Therefore, physiology explains behavior and perception, but behavior and perception explain adaptedness. To explain adaptedness the functional concepts do not have to be explained by physiology. In other words, even if it is possible to explain some adaptive concepts physiologically, as neuroethology has done (e.g., Huber, 1983), physiology and behavioral adaptedness are logically independent.

The crux of the problem is this: Lorenz and Tinbergen never said that ethology's concepts should be evaluated by their capability to predict environment-organism interaction and not by their capability to explain behavior in terms of its physiological substrate.<sup>2</sup>

The founders never accepted that what they were doing was independent of physiology. This may have been because of physiology's prestige or because of the need to root ethology in biology (see Burkhardt, 2005). However, the refusal to accept the non-physiological nature of ethology had a much more serious consequence. When functional models were attacked because they lacked physiological bases and even plausibility, Lorenz maintained that the IRMs were

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<sup>2</sup> It is perhaps interesting to note that, during the Macy conferences, Mayr countered Lehrman, stating that selection acts on functions regardless of their physiological substrate (Mayr in Schaffner, 1955, p. 140). Significantly, neither Lorenz nor Tinbergen elaborated on this important remark. They tacitly accepted that ethology was the physiology of behavior.

explained in terms of Holst's theory. He had no data on which to support this claim, and perhaps for that reason his claim did not convince the scientific community. It is true that Tinbergen (1955, pp. 104, 108, 114-115) seems to have realized the error of the comparatists when he accused them of not understanding biological functional concepts; however, he never made the additional step of defending a functional definition of ethology.<sup>3</sup>

From then on, the study of adaptedness became the study of the selective pressures for behavior strategies, and a causal behavioral approach almost ceased. Without functional models ethology could no longer study the behavioral organization of adaptedness, and it therefore lacked what was its chief initial concern. As adaptedness lost its primary status (Hinde, 1970, pp. 430, 676) animal behavior studies were progressively incorporated into mainstream biological approaches such as ecology and physiology.

### *Consequences for Ethology*

Without functional models ethology's specificity is just description, and it seems that this was how subsequent students of behavior viewed strictly behavioral research. For instance, in an influential book, Huntingford (1984, p. 49) wrote that the "behavioural level [is] merely a stepping stone on the way to physiological explanation." More recently, Kruuk (2003, p. 184), a disciple of Tinbergen, wrote that functional concepts are just labels that suggest similarity of mechanism due to similarity of behavior (this argument is exactly the one the comparatists used in their early critiques). Therefore, a shift to "hardware" instead of "software" explanations took place (Tinbergen, 1963, 1969; see also Griffiths, 2004, and *in press*). For instance, Bateson and Klopfer (1989) said that classical ethology had ceased to be important by the end of the 1950s. Zippelius (1992) said the same thing, adding that Lorenz's concepts were physiologically and evolutionarily wrong. The perceptual and behavioral account of adaptedness of behavior was no longer an essential issue.

I think that Lorenz and Tinbergen were wrong when they claimed that causal analysis must be physiological. Their empirical work captures a different level of integration, that of developing predictive concepts for understanding how behavior is functionally organized into stable systems of exchange with the environment. Since these concepts are defined in terms of behavior and make only behavioral predictions, they could never have been criticized in terms of physiology. Neither can they be criticized in terms of principle—as Hinde (1970) has done—because their adequacy value is first and foremost an empirical, not a philosophical issue.

I therefore defend that it is necessary to posit the characterization of the organism–environment exchange systems as the main object of ethological

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<sup>3</sup> In contrast, Baerends (1941, 1970, 1976, 1984), who was conceptually very close to Tinbergen, never abandoned purely behavioral studies. In fact, he maintained that a strictly behavioral approach was essential and that behavioral and physiological levels were to be researched independently (1976, p. 208). Although recognized as important (Hinde, 1982), Baerends' approach was not taken up by other ethologists.

research. In this I rank with Uexküll rather than with Lorenz or Tinbergen, which does not imply that I accept Uexküll's non-Darwinism.

I conclude that, despite the founders' unwillingness to defend a purely functional approach, classical ethology was never validly rejected theoretically or empirically.

### **Important Concepts for the Study of Adaptedness**

The Umwelt is the most important concept I want to maintain from early ethology because it allows us to capture the idea that animals and environments are two parts of the same phenomenon: adaptation. An animal without an environment is impossible, but an environment only exists when there is an organism to interpret it. The concept of Umwelt does not imply that the entire life cycle of the species be known. What we consider to be our study is defined only by function and the researcher may specify the function he is interested in. For instance, he may want to study the full parental behavior in a given species, but he can also concentrate in less ambitious functions and study only how an animal builds a nest or even how it selects nest material. The common ground of all these studies is that the researcher begins with adapted behavior, that is, with function. This is important because we are studying not arbitrary chunks of behavior defined by the researcher's whim but naturally occurring behaviors that demonstrably have a function in adaptedness. In this way we do not run the risk of studying problems that are important to us but not to the species.

I do not think the concept of IRM, defined by one sign stimulus and one fixed action pattern, is sufficient to capture the Umwelt in all its aspects. Some fixed action patterns tend to occur together, which implies the existence of higher-order causal factors (for instance, there are many IRMs in predatory behavior, but all tend to co-occur). We also know that many learning occasions modify the IRMs and perhaps even higher systems (for instance, in cats hunger is linked to predation through learning; see Leyhausen, 1965). The structure of adaptedness therefore implies more concepts than just IRMs.

I will review some of the concepts that I deem important, but I do not pretend to be exhaustive. On the contrary, I think that much empirically anchored conceptual work needs to be done. The main question asks how animals and environments connect and whether there are identifiable but distinctively different types of interaction. Some tentative answers follow.

When certain configurations are present in an animal's environment, the animal reacts. What this reaction is must be discovered through observation and experimentation. To illustrate, when a cuttlefish faces a small, shrimp-like configuration for the first time and before the "learning parts" of its brain develop, it responds with predatory behavior; if the shrimp is shown repeatedly behind a glass, the cuttlefish will fail to learn that it cannot reach it and will die of exhaustion and lesions to the tentacles (Hanlon & Messenger, 1988, p. 465). This is an example of what I would call an innate response. In this case the function cycle is based only on a pre-wired instruction.

There are cases of information gathering that seem to depend entirely on innate processes. For instance, the wasp *Ammophila pubescens*, studied by Baerends (1941, 1959), digs a pit in which she puts a paralyzed caterpillar. She lays an egg on the caterpillar and then closes the nest. Later she will inspect the nest and gather information on the development of the larva, which influences what she will do next: either bring in more caterpillars or close the nest definitively. The wasp is receptive to signals emitted by the larva only during the inspection visit; when she enters the pit to put caterpillars in it she is not receptive. How the wasp “knows” when to gather information is not known, but it could certainly be studied. There are other cases of selective information gathering (in bees, e.g., Menzel, 1990; in ants, e.g. Hölldobler, 1980). The well known work of Aronson (1971) on *Bathygobius saporator*, a fish that learns the depressions on the ground of the intertidal zone and uses this knowledge to accurately jump from one pool to another when the water level is low, may be described in this way. In all these cases the main research question asks: what information is actually collected and what circumstances prompt the collection?

The preceding cases do not seem to involve any modification of innate mechanisms; however, such modification is evident in most cases of IRM-like behavior.

### ***Behavior Modification***

Behavior modification must be inferred from either perceptual or behavioral selection or by behavioral alterations in the FAPs. I will consider the two cases separately.

In many cases animals are not born with a complete perceptual picture of the key stimulus. Instead, they seem to possess a general configuration that matches many outside stimuli (for examples, see Sá-Nogueira Saraiva, 2003; for a review, see Curio, 1976). Lorenz himself admitted that the learning of sign stimuli is more the rule than the exception (Lorenz, 1935). What actually triggers learning is not always clear. For instance, Curio and his team (Curio, 1978; Curio, Ernst, & Vieth, 1978; Vieth, Curio & Ernst, 1980) showed that if the European blackbird (*Turdus merula*) listens to the mobbing response of conspecifics while it is shown a new avian configuration, then it learns to emit mobbing to that configuration. Therefore, it seems that there is a specific situation (listening to mobbing sounds while viewing a new avian configuration) that triggers learning. The features of the target of learning were not identified, nor was there any discussion of a learning trigger, but learning was significantly more effective to an unknown stuffed bird than to an unknown brightly colored bottle. It is entirely possible that the specific kind of learning that was activated includes a template of, or an instruction about, what must be learned.

The type of study initiated by Curio was later pursued by Csanyi (e.g., 1988) with the sun fish *Macropodus opercularis*. Any new configuration present during tissue destruction (e.g., by a bite or an electric shock) was subsequently avoided provided the configuration had “eyes” and was not a conspecific. Therefore, tissue

destruction seemed to trigger the learning of a specific configuration that must have certain features and not others.

This type of learning new releasers is very frequent. For instance, in cats, any general configuration that moves and has a certain size is pursued and “tested” by pawing and biting, but a new stimulus configuration becomes a learned sign stimulus only if the animal senses that it is edible (Leyhausen, 1965). Again, the precise triggers and targets remain to be studied.

The foregoing cases seem to be the ethological equivalents of classical conditioning. There is, however, a difference. In classical conditioning a new stimulus (the conditional stimulus to be) comes to release the conditional response after being paired with an unconditional stimulus. In the cases I mentioned earlier, the conditional and unconditional stimuli may co-occur and be part of the same stimulus complex. Thus, a new prey-like configuration “contains” the unconditional stimulus (the releaser) and the conditional stimulus (the characteristics that make this new prey-like configuration different from other already known prey).

Let me now turn to the modification of action patterns. The simplest example is the adjustment of FAPs. For instance, a squirrel “knows” that a nut is to be gnawed, but it must learn how to direct the bites and with what force. More complex processes are known. Often an animal will have a set of responses to a given releaser and will try them more or less in sequence. To take an example from my research (Sá-Nogueira Saraiva, 1995), the first behavior that a cuttlefish directs to a prey item seems to be the tentacle attack: the animal positions its arms like a cone and projects the tentacles toward the prey. If this behavior fails, after some trials the cuttlefish shifts to the open-arm attack, in which the prey item is approached with open arms and grabbed. The well-known principles of operant learning might explain the response selection process (see also the work by Chichery and his team, e.g., Darmaillac, Chichery, Poirier, & Dickel, 2004; Darmaillac, Chichery, Shashar, & Dickel, 2006; Duval, Chichery, & Chichery, 1984).

In the case just mentioned there are two general FAPs, but with other species there may be more. Leyhausen (1965, 1973) and Baerends-van Roon and Baerends (1979) studied response variation in cats. Both teams identified a series of movements that are available when a young cat is confronted with a new prey. The most effective behavior patterns are selected for each prey; the cat will paw, grab, angle, bite, and so on, the prey, and the faster a behavior pattern allows for prey catching, the stronger that pattern will become in the presence of the same prey. Also in cats, Leyhausen (1965, 1973) noted that in experienced hunters the particular motor patterns for a given prey species vary across cats and contain elements that are very different from the innate FAPs. However, should the atypical patterns cease to be effective (e.g., the cat is bitten by the prey), the innate FAPs come into action again.

In these cases the causal center seems to have at its disposal, so to speak, a certain number of innate behavior patterns to deal with a particular kind of releasing stimulus. The outcomes of the behavior patterns are compared with a

template such that the patterns that result in stimulation closer to the template are strengthened. In the case of cats, another mechanism seems to inhibit the “wrong” patterns and, under some circumstances, bring the innate FAPs into action again. It is also important to note that behaviors that are not part of the causal centre may be incorporated into the final coordination. The extent to which this occurs might profitably be studied.

### ***Behavioral Plasticity***

In the case of perceptual learning, there are usually limits to the stimuli that may be associated with a given causal centre (e.g., Domjan, Cusato, & Krause, 2004; Hinde, 1973). In the case of motor learning, there is usually a set of behaviors that are innately emitted in the presence of a given releaser. These behaviors may be modified by selection, but the modifiability of the behaviors varies. Many predators, after grabbing prey in their mouths, give it a shake (the “death shake”), which has the function of stunning or even killing the prey. Ewer (1968, p. 38) fed jelly to Tasmanian devils. The animals never ceased to emit the death shake, despite the fact that doing it threw most of the jelly out of their mouths. Apparently there is a set of behaviors that is activated when feeding is activated and that cannot be suppressed easily. This result seems related to the Brelands’ well-known work on instinctive drift and to negative automaintenance in autoshaping (Breland & Breland, 1961; Schwartz & Williams, 1972).

Other cases such as the already mentioned predatory behavior of cats (*Felidae*) are more flexible; there are more behavioral elements, the non-IRM motor actions may organize into a functional reaction, and innate reactions may be inhibited (see chiefly the work of Leyhausen). Therefore, upon activation of predatory behavior cats are able to vary their behavior and thereby learn a rich repertoire of hunting patterns.

There are cases in which almost any behavior may be linked to a given reinforcer. Tool use in primates may be one such case. Capuchin monkeys seem to approach a feeding situation with every possible combination of actions (e.g., Visalberghi & Limongelli, 1994). Effective actions are retained, whereas ineffective ones are eliminated. The degree of behavioral variability displayed by the capuchin monkeys may be an extreme case of what happens in cats. Recall that in cats the final predatory behavior may include elements that do not belong to the innate prey-catching repertoire. This means that, behaviorally, the causal center for hunting may be enriched with behaviors that do not originally belong to it. What happens with capuchin monkeys is, perhaps, a rather extreme case of the same phenomenon. This kind of progressive integration of different behavioral elements into a functional whole is also found in chimpanzees learning to use a hammer and an anvil to break hard nuts open (Matsuzawa, 1994; Matsuzawa et. al., 2001). These cases suggest that variation and selection of behavior play a far greater role than whatever innate responses are present. However, the concept of Innate Teaching Mechanisms (Lorenz, 1965) is useful in this context: species that have many non-IRM-related behavioral elements (e.g., scratching, touching, tooth

handling, pounding) may vary a great deal when faced with a reinforcer that is not easy to reach. What actually varies—and how—would be important to know.

I hope the preceding analyses will have shown that a function cycle approach to behavior is entirely compatible with learning studies. Researchers of classical and operant conditioning have made similar claims (e.g., Shettleworth & Juergensen, 1980; Staddon 1983, 1988; Timberlake, 1993, 1994).

### *The Deprivation Experiment*

If we want to know the Umwelt of a given species we must establish, as Lorenz claimed, from whence the information for adaptedness comes. This is possible only through the deprivation experiment, which I analyze below.

Using cats as an example, if we hypothesize that mouse recognition needs (or does not need) learning, we must see if the first encounter with a mouse releases predatory behavior that is different from the typical adult behavior. However, to ensure that we are dealing with the first encounter, the only possibility is to withhold mouse-like configurations from the cat (i.e., to isolate the animal from that critical information until data collection begins). Recall that comparativists claimed that this technique showed only that the factors being withheld were unimportant for development—but this remark carries little weight because it might be applied to any experiment: we only test the effect of the hypothesized factors.

It is important to stress that there is nothing wrong in asking if a given factor has no effect on development. It is virtually the same thing as asking if the factor has an effect. To illustrate, consider the work of Hübner and Wiesel. The authors asked if vision developed in isolation, and having seen that it did not they proceeded to show how experience was influential. Had they asked if visual stimulation is not important, the result would have been the same because methodologically the two questions (i.e., does experience play a role or not?) entail the same experimental procedures. The results of visual deprivation show that early stimulation is important for normal vision. Having established that, Hübner and Wiesel asked what kind of information was important. This is exactly how the Lorenzian school proceeded (for representative work see Apfelbach, 1973; Curio, 1975; Eibl-Eibesfeldt, 1963; Scherzinger, 1970; Schleidt, Schleidt, & Magg, 1960).

Another good example of the value of the deprivation experiment occurred in the study of birdsong development (Hultsch & Todt, 2004; Kroodsma, 2004; Marler, 2004a, 2004b). What initiated the research was the observation that chaffinches do not all develop the same songs. Therefore, researchers hypothesized that environmental factors play a role. In order to test this hypothesis it was necessary to further hypothesize which factors might be important. Thorpe's first hypothesis was imitation from adult males (Thorpe, 1961). Using the deprivation technique, the hypothesis led to the identification of a "vocal template," that is, an endogenous pattern of behavior that resulted in a particular type of sound

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patterning, and a “neural template,” that is, a set of filters that allowed only certain environmental inputs to affect behavior.

The main point to be stressed here is that it is necessary to establish what the innate perceptual and motor instructions are, what releases them, and how they combine with patterns of environmental stimulation. The deprivation experiment seems not only useful but inevitable when studying development.

### Conclusion

Based on the first part of this paper I suggest that the rejection of early ethology was due to semantic misunderstandings, for neither the comparatists nor the ethologists were clear about what was to be explained. It seems that for comparatists it was behavior and for ethologists it was adaptedness.

What I am proposing is not a new theory. The idea that drive centers have preferential connections with certain patterns of behavior and stimulus configurations is well known (see the concept of behavioral systems, Timberlake, 1993, 1994, and the concept of behavioral inference, Staddon 1983, 1988). Also, research that fits into what I am proposing is being done, although atheoretically (e.g., Amo, López, & Martín, 2006; Brown, 2003; Dalesman, Rundle, Coleman, & Cotton, 2006; Pongrácz & Altbäcker, 2000).

What is new is the proposal to take Uexküll’s function cycle concept further. The aim is to study how adaptedness is achieved through perception and behavior. There are concepts that may complete the idea of the IRM. Some of them come from the ethologists themselves while others come from learning theorists, but new concepts must be discovered by empirical studies and by the integration of ethology with learning theories. Should this approach be accepted, I propose to call it comparative behavioral ethology.

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