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## Biology of Learning in Nonmammalian Vertebrates Group Report

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### INTRODUCTION

The study of nonmammalian vertebrates, especially birds, has been a rich source of material not only for the student of animal learning, who is interested primarily in the mechanisms (causation) of behavior in laboratory environments, but also for the ethologist, who is interested in causation, function, evolution, and development of behavior in more natural settings. In this report we consider reconciliation of these two approaches by discussing a) the inevitable problem with "unnatural" categories of learning, b) productive efforts at the interface between traditional psychology and ethology, c) the apparently "special" processes of birdsong learning and imprinting, and d) how little we know about the perception of complex stimulus patterns. Finally, we e) comment on the potential productivity of a new behavioral biology.

### CATEGORIES OF LEARNING

The taxonomies of learning in use today are not necessarily helpful in identifying important psychological processes. The diversity of organisms in the world can be classified according to their phylogenetic histories, and a variety of characteristics, including morphological, behavioral, and cellular features, can be used to construct such evolutionary histories (43); however, there are no currently accepted "natural" organizing

principles upon which to base a taxonomy of learning (Holland et al., this volume).

A taxonomy based on laboratory operations, such as a) mere repetition of an event, stimulus, or a setting, b) exposure to relations between stimuli, or c) exposure to relations between stimuli and responses, may be convenient for textbook headings, but such a classification is relatively arbitrary and may lead to apparently different phenomena being classified together (e.g., imprinting with habituation). A considerable improvement on a procedurally based system might be to classify learning via a functional approach, i.e., how learned behavior reflects increases in an animal's fitness, or reproductive success. Categories based on behaviors in nature might involve abstractions such as prediction, control, familiarization, imitation, and so forth, or immediate functional contexts such as feeding, detection and avoidance of danger, finding mates, or parental care.

Although taxonomies aid in organizing a diverse world and "natural" taxonomies are useful in making predictions, they can also prejudice the direction of research. Classification of imprinting or song learning as a special process, for example, may have prevented a closer examination of the processes involved and their relation or similarity to psychological studies in the laboratory. Furthermore, taxonomy is constantly in a state of flux. This is true not only for phylogenetic classifications of organisms (49), but also for taxonomies of learning. The old distinction between classical and operant conditioning is no longer considered very useful in the sense of characterizing fundamental categories; most, if not all, situations involve some stimulus, a response, and an unconditioned stimulus (or reinforcer), so separation of the categories is always problematical anyway. Likewise, taxonomies once used by ethologists included taxes and releasers, and while these are still heuristically useful, they should not be considered rigid categories (18).

One additional category of behavior, "unlearned" or innate responses, also needs clarification. The term has a variety of meanings (Bateson, this volume), and conclusions from all relevant experiments tend to rest on plausibility or negative evidence. Ethologists using the comparative approach use the term "innate" to designate behavioral differences which depend on a genetic difference. Although an organism can never be isolated from itself, and animals often bring into play backup mechanisms for developing a behavior, rearing individuals of different populations

or closely related species under very similar environments can yield valuable data on "innate behavioral" differences between groups (39).

### PRODUCTIVE INTERDISCIPLINARY ENTERPRISES

There are, of course, many natural situations in which birds and other nonmammalian vertebrates show learning. One that has received a great deal of recent attention involves searching for food. MacArthur and Pianka (37) argued that success in foraging is so crucial to an animal's survival that animals should evolve to become optimal foragers within the environment to which they have adapted - i.e., foraging behavior should be perfectly adaptive, or optimal.

There are three ways in which optimal foraging requires animals to learn. First, the forager must learn the locations in which prey are to be found ("patches"). Second, it must learn the densities of prey in each patch. Third, it must constantly update its estimates of prey density, because these are likely to change as a result of its own or other animals' foraging efforts.

Working from the general principle of optimization, behavioral ecologists have established quantitative generalizations to describe foraging behavior. These models can be applied to behavior observed in the wild (12, 17), but they can also be tested in laboratory experiments (28). Such experimental methods correspond to standard procedures used in operant conditioning, in which quantitative generalizations about relations between response output and reinforcement frequency are a contemporary topic of lengthy discussion ((8, 19); see also (51), Ch. 9). The parallels were quickly noticed by a number of authors (e.g. (33, 50)), and a fruitful area of interdisciplinary interaction arose. For such work, ecologists have gained access to the precise techniques and substantial accumulations of data of the operant psychologist; operant psychology has gained both a sense of ecological relevance and an impetus to study new species, new situations, and new problems - notably the problem of schedule transition, taken up in several recent theoretical papers (25, 35). Both fields have gained a more precise understanding of the operation of decision rules in a wider range of situations. Further collaboration at this interface between two traditional fields can only benefit both.

From the psychological point of view, the interdisciplinary study of foraging is part of a general attempt to understand natural behavior in terms of the components of learning that can be studied using

conditioning procedures (Hollis, this volume). Animals in the laboratory learn relationships between events during classical or operant conditioning, and animals in nature undoubtedly use what they have learned in order to predict future events. However, conditioning studies restricted to the study of causation are bound to remain incomplete. They must be extended to the study of function. Understanding the relationship between events in nature is of interest, but it is also important to understand how the relative fitness of the organism is affected by these behavior patterns.

### **BIRDSONG LEARNING AND IMPRINTING: SPECIAL PROCESSES?**

One of the crucial questions that arises repeatedly is whether or not birdsong learning and imprinting are really "special processes." Do the generalizations that derive from the study of conditioning in conventional laboratory preparations (e.g., CER conditioning, autoshaping, classical conditioning of reflexes (eye blinks, salivation, etc.)) allow us to understand or make sense of the properties of birdsong learning and imprinting? Addressing this issue requires a full understanding of the attributes of both song learning and imprinting, and hence we first discuss more thoroughly the characteristics of these two phenomena before returning to the question of special processes.

#### **Imprinting**

The characteristics of imprinting are discussed in greater detail by Bateson and Immelmann (both this volume). One of its most distinctive features lies in the way it restricts the range of stimuli that elicit behavior after imprinting has taken place. Preferences become restricted to those stimuli that have been experienced in the course of imprinting. Establishment of this restriction ends the developmental phase when the preferences in question are sensitive to influences from the external world. The self-terminating characteristic of imprinting can in certain circumstances be overridden so that further plasticity of preferences occurs later in development (21), but in general, once formed, the preferences are remarkably stable (6). In this respect, then, imprinting seems to demand special-purpose neural machinery even if the process of storage is the same as in other learning processes (but compare Immelmann, this volume).

Other aspects of imprinting invite comparisons with less specialized mechanisms. Some components of stimuli used in experiments on filial imprinting in chicks and ducklings are powerful attractors (e.g.,

movement), whereas others are initially neutral. What happens when the neutral stimulus is paired with the initially attractive one and then a bird's responses to the unpaired neutral stimulus alone are subsequently measured? The answer is clear. The birds approach and are pacified by the now familiar but initially neutral stimulus (for review see (21)). So far so good, but the following experiment has yet to be done. Using three different neutral stimuli, A preceding the initially attractive stimulus, B occurring at the same time, and C following it, which stimulus does the bird learn most about? If imprinting works in the same way as typically observed in classical conditioning, the predicted levels of post-conditioning response should be highest for A and lowest for C. At least one biologist's hunch, however, is that B would elicit the most social behavior with C coming next and A last, the reasoning being that when a bird's attention has been attracted by a moving object, the bird continues to gaze at the object once it has stopped moving (Bateson, personal communication). If the hunch turns out to be correct, then the underlying process is likely to be different from those indicated by Pavlovian experiments (though see (24) for an example of "backward conditioning"). The difference might be small and could involve small variations in the parameters influencing when a neutral stimulus can be associated with an initially effective one to produce imprinting. Once again, though, the implication is that special neural machinery would have to be dedicated to imprinting and the behavior it affects. The expectation is strikingly confirmed by the neuroanatomical studies of the systems involved in imprinting (Bateson, this volume).

A further complication that generates frequent misunderstanding involves the fact that imprinting is not "unitary" but is probably subject to a variety of neural and hormonal factors, as well as processes of growth and differentiation. The process which has been studied most intensely is filial imprinting, and the majority of references in the literature refer only to the "following reaction." However, just as interesting is the establishment of sexual and other social preferences (i.e., sexual imprinting), and there are other "imprinting-like phenomena" such as the acquisition of habitat, locality, and food preferences, or perhaps the learning of particular star patterns as a target for homeward orientation in migratory birds (Immelmann, this volume). These processes all share to some degree the two main characteristics of imprinting, namely, its phase specificity, and a certain degree of selectivity about the stimuli that are most effective in achieving stable results (23). The learning processes involved in imprinting, however, might be different

from one case of imprinting to another. Filial imprinting, in which immediate reward is available, may be more akin to various conditioning phenomena than, for example, learning of a particular star pattern, which may be closer to what has been called perceptual or exposure learning.

It seems possible that the "special nature" of imprinting refers to the way information is protected from change in the central nervous system rather than to the way it is acquired (10, 22). The discovery of temporal correlations between sensitive phases for imprinting and developmental processes (cell death, synaptogenesis) in certain areas of the brain may be a pointer, together with the anatomical specialization for the control of song, for directions which future research about the nature of both processes could profitably take ((52), and Bateson, this volume).

### **Birdsong Learning**

Selected aspects of birdsong learning have been discussed by Marler and Konishi (both in this volume). We here elaborate upon other factors which might facilitate the comparison of song learning with general psychological processes.

### **Seemingly trivial differences in experimental methods can affect results.**

As in the imprinting literature (5), experimental treatments and methods are rarely, if ever, replicated by other independent investigators or even the same investigator. Thus, data must be interpreted cautiously, and with careful attention given to experimental design. Several key treatment factors include the age at which birds are taken from the field (as eggs, nestlings, fledglings, juveniles, or adults), the treatments or experiences before and after tutoring, the age during which tutoring occurs in the laboratory, the means of presentation of the tutor sounds (e.g., via loudspeakers or live birds - see below), the amount of exposure to the tutor songs, the photoperiod on which the birds are maintained, and possible interactions among experimental subjects (30). There are many permutations and probable interactions of these different treatments, and lack of standardized procedures has undoubtedly contributed to some of the apparent differences (and perhaps even similarities) among species.

**"Song learning" usually means "vocal imitation."** A juvenile bird can be exposed to a number of songs during its sensitive phase, usually occurring during the first one to three months of life. After passing through stages of subsong, which involves a rambling series of more or less amorphous sounds, and plastic song, when one can begin to recognize

some of the sound patterns that will eventually emerge, the young (usually male) songbird finally develops its adult song when about a year old. Audio spectrograms of the tutor songs and those "performed" by the subject are then compared visually to determine if "song learning" has occurred.

**Song "performance" gives an incomplete picture of what is "learned."** In most studies, the performance of a song is the only reliable indication that a bird has imitated (i.e., learned) that particular song. This distinction between learning and performance is well-known to psychologists. Learning is the change in "internal state" brought about by some experience. Performance is the change in subsequent behavior shown as a consequence of some earlier experience. The effect of an earlier experience may or may not be revealed by a particular test situation or set of situations. Without a change of state, no subsequent performance difference is possible, but lack of a performance difference says nothing decisive about whether learning (state change) has occurred - it may just be that the appropriate conditions for performance have not been identified.

Birds can and do learn far more than is revealed in their vocal displays. For example, in the laboratory a non-singing female white-crowned sparrow (*Zonotrichia leucophrys*) will respond preferentially to songs heard during an early sensitive phase (2) indicating that even though the song is not imitated vocally, it can still be recognized, and that necessary aspects of the signal parameters have been "learned." Furthermore, Marler and Peters (41) have demonstrated that "sparrows learn adult song and more from memory," because in the developmental stage of plastic song juvenile males provide evidence that they have learned the characteristics of song types which never appear in the final adult repertoire of song types (Marler, this volume). Finally, as implied in the foregoing example, songs are usually committed to memory (i.e., "learned") well in advance of the time when the individual attempts to match its vocal output with the song pattern stored in memory. Hence, it may be useful to distinguish a sensory and a sensorimotor stage of learning with song development per se consisting of the second phase in which "errors" in vocal output are corrected by auditory feedback (26, 44).

**Songbirds preferentially learn songs of their own species.** Because the effects of perceptual choices are usually assessed only through motor performance (but see (14)), it is difficult to say whether the perceptual

or motor system is the primary determinant of predispositions in song learning.

As in imprinting, the association of a positive (i.e., conspecific sound) and otherwise neutral stimulus (heterospecific song) in time can lead to the learning of both (Marler, this volume). This observation has prompted several interesting observations and proposed experiments. For example, if A is the species song and B, C, and D are alien songs, A is typically preferred over B, C, and D in a free choice situation (playing back these songs in random sequence and with equal frequency). If during the sensitive phase birds are exposed to A first, the period terminates or shortens, but exposure to B, C, and D first does not block the acceptance of A. While it is tempting to try to interpret these findings in terms of overshadowing or blocking, both of these phenomena demand two stimuli, a "neutral" one (to-be CS) and a hedonic one (US), and the opportunity to learn a predictive relationship; it is unclear which vocal stimulus would be the US and which the CS, and what predictive relationship is to be learned. It is also possible that exposure to B, C, and D first might enhance the acquisition of A, but such studies have not been done. Still another interesting problem would be to see, after pairing stimuli A and B, where A is the appropriate positive stimulus (a "trigger" in the sense of Marler (this volume)), whether B could then serve as a "conditional" trigger of learning C or D. Demonstration of such a relationship would indicate that song learning shares some common properties with classical conditioning.

**Song learning may not require any external reinforcement**, but several studies now indicate that use of live tutors may enhance the learning process (4, 32, 48, 54). These live tutors may influence the size of the vocal repertoire learned, the acceptability of heterospecific songs otherwise rejected, and the duration of the sensitive phase for song learning. The nature of the interactions between the tutor and the subject have not been studied in detail, but these studies may open a new avenue for the introduction of paradigms like those used in the study of associative learning.

**Song learning demonstrates a remarkable capacity for memory.** In song learning the sensory and sensorimotor stages may be separated by several months during which birds need neither hear nor vocally rehearse the memorized song (42). Furthermore, once a song is crystallized (adult song is said to "crystallize" from the earlier developmental stages), it



remains unchanged from one year to the next, even though there are months during the intervening non-breeding season when the song is not rehearsed. Even after they are deafened, some species can reproduce the crystallized song every year (27).

**There are striking species, sex, and age differences in song learning.** Among species there is considerable diversity in the size of the learned repertoire (e.g., a male white-crowned sparrow develops one song, whereas California marsh wrens (*Cistothorus palustris*) may develop over two hundred (11, 39)) and in the variety of sounds produced (marsh warblers (*Acrocephalus palustris*) and northern mockingbirds (*Mimus polyglottos*) may mimic many species, whereas North American sparrows generally do not mimic alien songs (9, 15, 40)). In most temperate zone species only the male sings, though in tropical environments females frequently sing as well (16). Finally, one of the most characteristic features of song learning is the presence of a sensitive phase, a time usually early in life when the ability to learn songs is maximal (29, 39). Hence, there is considerable diversity in the ability and inclination to learn songs among different species, sexes, and ages, a fact that is challenging learning theorists who search for commonalities.

**The learning and recognition of large song repertoires** may provide interesting insights into the problems of stimulus generalization and/or categorization. For example, a male marsh wren in eastern Washington sings about 115 different song types, each of which is learned from other males in the population. These song types are performed in such a stereotyped sequence that a male wren, upon hearing one of his song types broadcast from a loudspeaker within his territory, will respond with the next song in the sequence (55). Why certain song types are associated with one another in these sequences (56), or how the birds recognize the different song types (which may number up to two hundred in some western USA populations (11)) is at present unknown.

One of the major limitations in the study of these and other forms of learning is that it is unclear how the outside world is represented in the brain. How many features of a stimulus must an animal attend to in order to classify a given sound, and what must be the nature of the neuroanatomical or biochemical changes that accompany learning of a song, surrogate mother, or any other stimulus? Until major advances are made in understanding the physiological bases of learning, many details here will remain a mystery (Konishi, this volume).

**A series of discrete brain nuclei** in the bird brain appear correlated with the ability to learn songs. These brain nuclei ((45), and Konishi, this volume) are involved in both the perceptual and motor pathways of song learning. The most significant features of this song control system is its apparent absence in birds incapable of vocal mimicry (e.g., New World flycatchers, representatives of the suboscine suborder of the order Passeriformes) and its presence in birds well-known for their vocal imitation and/or mimicry (e.g., parakeets of the order Psittaciformes and songbirds of the oscine suborder of the order Passeriformes) (1, 45). In addition to this presence/absence correlation, the volume of these song control nuclei in the brains of several songbirds is correlated with the size of the song repertoire ((11, 46), and Konishi, this volume). The hypothesis that the system of discrete brain nuclei has in fact evolved to accommodate vocal learning will have to be addressed through further comparative studies.

#### **Special processes?**

Because birdsong learning and imprinting have not been "explained" in terms of generalizations that derive from the study of conditioning in conventional laboratory preparations, it is tempting to conclude that these are indeed special processes. Most students of birdsong, though, are more interested in the functions or ecological relevance of the behavior (3, 9, 16, 31, 38, 42, 47, 53) than in trying to explain or understand the development of the behavior in terms of any "general processes" gleaned from laboratory studies performed by learning theorists. This fundamental difference in research orientation and interest is unlikely to change. The "special process" issue must be addressed in a direct manner, perhaps designing experiments after those outlined above, before the possible roles of conditioning processes in birdsong learning and imprinting will be clear.

In addition to the phase specificity and the preferential response to appropriate stimuli, birdsong learning and imprinting appear to be processed in discrete portions of the brain (see above, and separate contributions by Bateson, Immelmann, and Konishi, all in this volume). It is tempting to conclude that the anatomical specialization in the brain for both imprinting and song learning provides additional support for labelling these two phenomena "special processes." However, other forms of learning may also occur in functionally discrete but anatomically diffuse regions of the brain, and mere packaging of relevant brain nuclei into discrete and identifiable units is no indication that within these

areas typical conditioning processes are not involved (but see Bateson, this volume). Moreover, learning mediated by different parts of the brain is nevertheless likely to involve the same essential biochemical and neural processes.

### **PERCEPTIONS OF STIMULI**

We know that young songbirds identify conspecific songs during song learning, and that nidifugous chicks come to identify appropriate social partners during filial and sexual imprinting. But in many cases it is not clear either exactly what the stimulus identified is or how it should be characterized. The appearance of a bird from different viewpoints is very different (5) and the samples of song that a bird hears may be very diverse (30). Sometimes a consistent output is derived from this varying input. The problem is similar to that described by Lea (this volume) as involving "concept discrimination." The experimental work of Herrnstein and Loveland (20) and others therefore becomes relevant to this problem.

The work of Herrnstein and Loveland (20) initiated a provocative program of research on natural concepts in the pigeon. This research is interesting for what it might tell us about animal perception and the role of adaptive predispositions in perceptual categorization. At present, however, it is not clear what the results indicate about the level of perceptual analysis that mediates the pigeon's performance.

The results show that pigeons can learn to respond for food to each of a large set of photographic slides consisting of highly disparate exemplars of a natural category such as tree, person, or water, while responding less strongly to each of an equally large, heterogeneous set of slides which do not exemplify any category. They are slower to discriminate between randomly selected slide sets. Moreover, they can respond correctly to first presentations of new exemplars of a natural category.

One interpretation of these results is that the pigeons perceive the slides much as we would, namely, as depicting objects. The interpretation is implied by the claim that the pigeon's performance in discriminating between the category and noncategory slides, and generalizing to new instances, is mediated by a "natural concept."

There is, however, a rival hypothesis that has yet to be rejected. The performance could be the result of discrimination and generalization

based on a lower-level perceptual analysis of the slides as arrays of meaningless, or nonrepresentational stimulus features made up of color, brightness gradients, and shapes. It is conceivable that at the level of nonrepresentational features, the slides depicting a natural category exhibit a matrix of similarities that would account for more rapid learning to discriminate between a category and a noncategory set than between randomly selected sets. Moreover, generalization based on similarity of new exemplars to some subset of the previously trained category exemplars might account for better than chance performance on new exemplars.

Experiments are needed to provide information on the level of perceptual analysis of the stimuli in the natural concept experiments, but it is by no means clear how to construct those experiments. One would like to be able to remove the representational value of the slides without altering the similarity matrix at the level of nonrepresentational stimulus features, but it may not be possible to change one without the other. A more feasible, although perhaps less direct, approach would be to examine transfer between photographic representations and real objects, and vice versa. At present there are rather few experiments of this type. In addition to the light such experiments might throw on the hypothesis of natural concepts, they could provide new information about perceptual processing in birds.

Furthermore, "category discrimination" may be a safer term than "concept discrimination." The bird's mode of responding serves to organize the perceptual world into categories, but it is not clear how those categories are represented structurally. Perhaps only if abstract representational processes were demonstrated should we talk in terms of "concepts," and perhaps only if the concepts are demonstrably acquired should we talk of concept formation. However, these "semantic adjustments" still leave the empiricist groping for techniques. Although we can show by using artificial stimuli that pigeons can use more than one feature in making a category discrimination (36), this does not really solve the problem. With any real set of stimuli, our evidence that there is no single feature that could support the category discrimination is always negative; furthermore, why should we attribute concepts to a bird that uses several features to solve a category discrimination any more than to one that uses only a single feature? And this query still disregards the problems associated with defining what a feature is. What might be a feature to us might not be such to a pigeon, and vice versa.

Another problem lies in precisely what we mean by a natural category or a natural categorization. Is it one that divides the world neatly and easily ("carves nature at the joints"), presumably because the world of natural objects contains few things that fall near the inevitably fuzzy border between membership and nonmembership? Is it characterized by and limited to the set of phenomena dealt with by the organism in a single set of responses, distinct from the response set for other categories? Or is it one which the bird comes "naturally" well equipped to solve, either by possessing unlearned concepts corresponding to the categories concerned (13), or by being especially attentive to the features that are useful in discriminating them? And can these possibilities even be distinguished? There are needs for at least three new directions for research in this area.

First, more work needs to be done on the problem of finding metrics for expressing similarity between percepts of natural objects. However, opinions are divided about whether the outcome of such research would be the discovery of useful metrics or of a proof that they do not and cannot exist.

Second, more needs to be done, both in logical and experimental analysis, to find ways of determining whether animals develop concepts. Three proposals were considered: a) The "Clumping" procedure used by Bateson and Chantrey (7) in imprinting with chicks, in which stimuli that occurred in close contiguity during imprinting became hard to discriminate in a subsequent instrumental task. In unpublished work on category discriminations of letter by pigeons, Lea and Ryan have failed to obtain this result, though their procedures and subjects were so different from Bateson and Chantrey's that the two results do not really conflict. b) A technique involving transfer from a single instance to all members of a category, described by Lea (34); Lea and Ryan's unpublished data suggest that this effect may occur. c) Investigations of whether birds' discriminations of slides of objects involve them in perceiving these as objects in any sense. Although this third question might in the end be unanswerable, more data on problems such as transfer from slide discrimination to object discrimination, and vice versa, would undoubtedly give us a better feel for the interpretation of data in this entire field. In this connection, the use of naturally occurring category discriminations has potential advantages. Psychological experiments on category discrimination involve such extended training that they are only really practicable if they can be automated, and it is very hard to automate

the presentation of entire objects. Natural learning must necessarily be complete in a manageable period of time.

Finally, there is a need for comparative studies. Pigeons come in a variety of shapes and sizes, ranging from forest-dwelling species, to those that live in deserts, to large, ground-dwelling flightless species. If trees are in fact a natural category for "the" pigeon, closely related pigeon species living in an array of different habitat types should show corresponding differences in predispositions to recognize trees as a category. As stressed by Delius, however, concept learning experiments are often very fickle, and weak or negative results cannot be safely interpreted. Very small changes in procedures can lead to drastic though often inexplicable improvements. If different pigeon species were not equally tame in a laboratory setting, for example, results might be difficult to interpret.

In summary, "concept formation," like so many other psychological terms (e.g., learning, concept formation, perception, etc.), seems to be defined largely by exclusion. It may mean something like "the ability to recognize objects (in photographs) with an accuracy comparable to that of human observers, with similar error patterns, and in a way that is not reducible to simpler mechanisms (such as single feature extraction) which all would agree are not concept formation." However, while there is agreement that some phenomena are not "concept" formation, it is not entirely clear that we know exactly what concept formation itself is.

#### **TO RECONCILE LEARNING THEORY AND NATURAL BEHAVIOR**

Learning theory has produced a body of knowledge gleaned from studies of a few animal species under laboratory conditions. The basic question, then, is whether we can apply generalizations derived from these sources to behavior occurring in the field. We believe that the answer is a qualified "yes."

Operant conditioning has contributed to our knowledge of decision rules made by foraging birds, and elements of classical conditioning can be applied to functional accounts of some species' behaviors. And perhaps conspecific song elements, or "triggers," can be tested to see if they are "conditionable." To the die-hard ethologist, though, some of these questions seem strained, perhaps because they appear aimed at merely labelling a behavioral phenomenon with some (un)familiar terminology from learning theory, or perhaps because they appear an attempt to infuse conditioning approaches with ecologically relevant paradigms.

Furthermore, the ethologist revels in the diversity of natural behaviors, often using them as a comparative tool in an approach to understanding innate contributions to development and the functions and evolution of those behavior patterns. The mere thought of reducing behavior patterns to combinations of blocking or overshadowing effects, for example, in an attempt to understand the underlying causation and to seek commonalities in the diversity seems at first heretical.

To gain greater relevance, the study of mechanisms should be extended to that of function, or how the fitness of animals is influenced (Hollis, this volume). Furthermore, a major need is to see clearly the difference between the procedures used in laboratory studies - operant and classical conditioning - and the processes that allow these procedures to have their effects. It is these processes that will generalize to natural behavior, phenomena such as song learning and imprinting, not simplistic accounts that assume something called "classical conditioning," which merely relabels the results of Pavlovian procedures. Progress is being made, and one hopes that these somewhat skeptical remarks only reflect healthy growing pains of an interdisciplinary approach to behavioral biology.

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