Contrasting approaches to a theory of learning

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Abstract: The general process view of learning, which guided research into learning for the first half of this century, has come under attack in recent years from several quarters. One form of criticism has come from proponents of the so-called biological boundaries approach to learning. These theorists have presented a variety of data showing that supposedly general laws of learning may in fact be limited in their applicability to different species and learning tasks, and they argue that the limitations are drawn by the nature of each species' adaptation to the particular requirements of its natural environment. The biological boundaries approach has served an important critical function in the move away from general process learning theory, but it is limited in its ability to provide an alternative to the general process approach. In particular, the biological boundaries approach lacks generality, it is in some respects subservient to the general process tradition, and its ecological content is in too many cases limited to ex post facto adaptive explanations of learning skills. A contrasting, ecological approach to learning, which can provide a true alternative to general process theory, is presented. The ecological approach begins by providing an ecological task description for naturally occurring instances of learning; this step answers the question: What does this animal learn to do? The next step is an analysis of the means by which learning occurs in the course of development, answering the question: How does the animal learn to do this? On the basis of such analyses, local principles of adaptation are formulated to account for the learning abilities of individual species. More global principles are sought by generalization among these local principles and may form the basis for a general ecological theory of learning.

During the first half of this century, psychologists invested an enormous effort in the search for a general theory of learning. Underlying that effort was the belief that all forms of learning could be explained in terms of a fairly small set of general principles. A variety of such principles was proposed, and although their respective merits were widely debated, there was no serious disagreement with the view that some set of general principles existed that would eventually explain all of the phenomena of learning. The general learning theorists of that era held not only that there is a set of general principles applicable to all learning, but also that all examples of learning are manifestations of an underlying general process. That is, they believed that whenever animals learn, not only can we always account for what they do in terms of the same set of principles, but we will also find that they are doing the same sorts of things (e.g., forming stimulus-response associations).

In recent years, a number of authors (e.g. Seligman 1970; Bolles 1970; Rozin & Kalat 1971; Shettleworth 1972; Hinde 1973) have taken issue with the general process approach to the study of learning, arguing that many instances of learning provide evidence of rather specialized processes — adaptations to the specific demands of the environments inhabited by different animals. This view, which is discussed in more detail below, has been dubbed the "biological boundaries approach" to the study of learning. Its proponents have provided a number of important criticisms of the general process tradition, but it will be argued in a later section that their contribution is limited in the extent to which it can offer an alternative to that tradition. In particular, the biological boundaries approach has, in many of its formulations, denied the possibility of general principles of learning with the same vigor that it has denied the existence of general processes. Yet the search for general principles must surely be one of the most important aspects of any scientific endeavour. Any denial of their existence in a particular field of inquiry should be accepted only after all possible alternatives have been explored.

This paper discusses one approach to the study of learning that may be a viable alternative to both the general process tradition and the newer biological boundaries approach. It is an ecological approach to the study of learning — one that seeks its general principles in the relationships between animals and their natural environments, rather than in the characteristics of animals alone. The ecological approach will be contrasted with both the biological boundaries approach, from which it differs in the importance attached to the search for general principles of learning, and the general process tradition, from which it differs in the importance attached to ecological considerations in the study of learning.
discussion of the theory that underlies the ecological approach has been published elsewhere (Johnston & Turvey 1980).

Some terms and distinctions

A few terms should be defined at the outset. The term "environment" will be used to refer to those aspects of the physical, biological, and social world with which an animal interacts (Mason & Langenheim 1957), rather than the location, or type of location, that it inhabits. Ecologists will recognize this usage as being closer to the concept of "niche" than to the concepts of "habitat" or "biotope" (Hutchinson 1967; Whittaker, Levin & Root 1973). While humans and rats may share similar habitats, such as cities and farms, they occupy very different environments within those habitats. The natural or "normal" environment of an animal will refer to that which it occupies by virtue of its phylogeny and species-typical ontology; statistically, one might define it as the modal [i.e. typical] environment of members of a species or population (Miller 1977).

When the unqualified term "environment" is used in this paper, the qualification "natural" will always be implied.

The emphasis here (and in other ecologically oriented discussions of behavior) on animals’ natural environments sometimes leads to misunderstandings. It is often thought, mistakenly, that any study that subjects an animal to conditions that deviate from its natural environment cannot qualify as "ecological." This belief misrepresents the role of the natural environment in ecological study, in which atypical or artificial conditions are often employed to advance our understanding of the relationship between an animal and its natural environment. Although the goal of ecological study is always to explain relationships with the natural environment, the experimental use of unnatural environments may be an important means of attaining that goal. This point will be elaborated later in this paper.

The distinction between general principles and general processes is also important to the arguments of this paper, and so I will briefly explain what is meant by it. Consider the following example, modified from Cabanac (1974). The thermal relationship between a homeothermic animal and its environment may be described by the following equation:

\[ Q_{\text{prod}} = Q_{\text{gain}} - Q_{\text{loss}} \] 

where \( Q_{\text{prod}} \) = metabolic heat production, \( Q_{\text{gain}} \) = radiative, convective, and conductive heat gain from the environment, and \( Q_{\text{loss}} \) = radiative, convective, conductive, and evaporative heat loss to the environment. [printing errors present in original PDF]

Equation 1 expresses a general principle about thermoregulation that is true for homeothermic animals over some range of environmental temperatures characteristic of each species. Under different thermal regimes, various physiological and behavioral processes are initiated so that the principle in Equation 1 remains true, but in different animals, and in the same animal at different times, different processes will occur. For example, with an ambient temperature of 40°C, the thermal balances of a man and a dog will both obey Equation 1, and both do so in part because of processes that increase evaporative heat loss. However, in man these processes include sweating (but not panting), whereas in the dog they include panting (but not sweating). By the same token, the man's thermal balance will also obey Equation 1 when the ambient temperature is 15°C, but now the processes involved will include shivering, which increases metabolic heat production, rather than sweating.

The distinction between the principle expressed in Equation 1 and the processes by virtue of which the principle holds may be made as follows. Processes are events or series of events that are said to occur, to terminate, or to be observed. Those associated with learning may usually be described in either behavioral or physiological terms; physiological descriptions are conventionally said to underlie or reduce behavioral descriptions. Principles, on the other hand, are formal or informal statements about processes, relations among processes, or relations between processes and sets of external conditions. We speak of principles as being true, as being violated, or as being formulated. The aim of theories is, in general, to explain or predict processes by means of principles.

The acceptance of a general principle such as that expressed in Equation 1 need imply nothing about the generality of the processes by virtue of which it holds. In the preceding example there are some thermoregulatory processes that are very general (such as vasoconstriction and vasodilation) and others that are restricted to only a single species (such as putting on warm clothing). In a precisely analogous way, the search for general principles of learning does not commit one to the view that all learning reflects a general process (such as the formation of associations), and doubts raised as to the purported generality of certain processes of learning need not lead one to question the possibility of finding general principles.

The ecological approach to learning discussed in this paper shows how a search for general principles of learning may be undertaken quite independently of any assertions as to the existence of general processes. As will become clear in the final sections of the paper, the nature of the empirical research mandated by the ecological approach is radically different from that currently being undertaken by the majority of workers in animal learning.

Contemporary approaches to the study of learning

To attempt anything like a comprehensive survey of the current state of the psychology of learning would far exceed the scope of this paper, and the following account is intended only to highlight certain trends in the field that are particularly relevant to my arguments in the remainder of the paper. The reader interested in a more thorough treatment of the issues is referred to Rescorla & Holland (1976) or Jenkins (1979) for a brief account, and to Bitterman, LoLordo, Overmier & Rashotte (1979) for a more comprehensive survey.

One of the primary differences among modern workers in the field of learning is in the importance
that they attach to ecological and evolutionary considerations for the study of learning. For many years, the study of behavior was strongly influenced by a tacit belief in the complete separability (both conceptual and experimental) of learning and instinct - a belief that had, and continues to have, profound and far-reaching effects in both biology and psychology (Kuo 1929; Lehrman 1970; Oppenheim, in press). On this view, instinct provides an animal with the capability of responding to situations that are typical of its natural ecology, whereas learning enables it to cope with atypical or unusual events. It is not surprising, given this conceptual position, that in the study of learning, little heed was paid to the subjects' natural ecology, and that subsequent development of the field left no room for ecological considerations to be taken into account.

I doubt that many modern students of learning would argue in favor of a learning-instinct dichotomy, but it can hardly be denied that the field as a whole continues to reflect the dichotomy, at least insofar as ecological considerations are denied any theoretical or methodological representation in the study of learning. Since about 1970, arguments have been presented against the ecologically arbitrary nature of work on learning, echoing the earlier concerns of such authors as Tinbergen (1951) and Lehrman (1962), and current opinion is clearly divided between those who argue that ecological differences among species are important to our understanding of their learning abilities and those who believe that such differences are of no great theoretical significance. Two current approaches to the study of learning that reflect these two points of view may be identified.

**Miniature theories of learning.** Most modern students of learning acknowledge that the concern of earlier theorists with large-scale theories, each of global applicability, was too ambitious. Attention has now turned to the construction of smaller-scale theories, each dealing with a restricted range of learning phenomena - a development that was anticipated by Tolman (1949). The work of Rescorla (1972; Rescorla & Wagner 1972) on classical conditioning, of Sutherland & Mackintosh (1971) on discrimination learning, of Kamin (1968; 1969) on expectancy theory, and of Bolles (1971; 1972) on avoidance learning, is representative of such miniature theories. With few exceptions, primarily Bolles (1970; 1971), the proponents of this approach have paid little attention to ecological considerations in their analysis of learning. The methods that they employ for the study of learning are ecologically arbitrary in just the same way as were those employed by the general theorists of a generation ago, and theoretical analyses continue to offer no recognition of the different ecological circumstances with which each animal species must deal and to which it has become adapted as a result of natural selection. If anything, there is perhaps less interest now than previously in using laboratory investigation to determine how animals learn about the world in which they live (cf. Hull 1937). Indeed, the major difference between those working on the development of miniature theories and the general learning theorists of the past would seem to be procedural rather than conceptual, as Revusky (1977, p. 2) suggests:

> "These students of learning typically believe in the general process approach in principle, but feel that the only practical methodology, at least for the time being, is to construct theories limited to narrow situations and effects."

Although these theorists are certainly aware of species differences in learning ability, it is unclear what role, if any, they expect such differences to play in the completed theoretical formulation. One prominent modern learning theorist, M.E. Bitterman, has devoted much of his research effort to an analysis of differences in learning ability among different animal species (Bitterman 1975; 1976; Bitterman & Woodard 1976). Of all the work being carried on in the tradition of general learning theory, Bitterman's comparative analysis is perhaps where one might most expect to find an interest in exploring the ecological correlates of learning, since few other investigators are so explicitly concerned with interspecies differences. That even his work reveals no such ecological content strongly suggests that the nonecological traditions of the field will not give way easily.

**Biological boundaries of learning.** Of more direct relevance to the present discussion is the second modern approach to the study of learning; the so-called "biological boundaries" approach. This approach draws its main support from various recalcitrant data, obtained in studies of conditioning, that appear to contradict several major assumptions of general process learning theory. The best known of these data is the finding of Garcia & Koelling (1966) that rats readily learn to avoid sweet-tasting water if its ingestion is paired with toxicosis, but not if ingestion is paired with foot-shock. By contrast, avoidance of water that is associated with an audio-visual stimulus can be learned by pairing its ingestion with shock but not with toxicosis. This result contradicts the principle of equivalence of associability of stimuli (Seligman 1970), according to which it is possible to pair any noxious US (unconditioned stimulus) with any CS (conditional stimulus) to produce aversion. Other findings (Garcia, Ervin & Koelling 1966) showed that delaying toxicosis for up to two hours following ingestion still resulted in learning to avoid the sweet-tasting water. Again, this contradicts the principle that the US and the CS must be temporally contiguous if learning is to occur (Seligman 1970).

Since the publication of Garcia's original findings, and of papers by Seligman (1970) and Rozin & Kalat (1971) emphasizing their theoretical significance, there has been a dramatic increase in the number of taste-aversion studies (see Riley & Baril 1976). These studies, taken together, strongly support the view that the avoidance of noxious foods is mediated by different cues in different species. Many of the results suggest that the nature of the effective cues is determined by the way in which food is typically selected by members of a particular species. Thus quail (Wilcoxon, Dragoin & Kral 1971) and vervet monkeys (Johnson, Beaton, & Hall 1975), which may rely on visual cues in food selection, are able to learn to avoid noxious food on the basis of visual as well as gustatory cues. For the rat, a nocturnal scavenger, presumably visual cues are rarely...
available in the context of food selection, and so the ability to associate such cues with subsequent illness has never been selected for in the evolution of this species (Rozin & Kalat 1971).

Although studies of taste-aversion learning have provided the bulk of the evidence in favor of the biological boundaries approach, substantial support has also come from studies of other forms of learning. Bolles (1970; 1971) has reviewed a wealth of evidence from the instrumental avoidance literature, which shows that rats will learn to make certain avoidance responses (such as running away or jumping out of the shock box) far more readily than others (such as turning a wheel or pressing a bar). Bolles proposes that each species possesses a limited number of species-specific defense reactions (SSDR's) that it uses under natural conditions to protect itself in any aversive situation, independently of any specific learning (see Bolles & Fanselow: "A Perceptual-Defensive-Recuperative Model of Fear and Pain" BBS 3(2) 1980).

Only if the instrumental response required in an experiment permits the subject to use an SSDR to escape or avoid shock will learning occur. Complementary data, using food reinforcement in an operant conditioning paradigm with hamsters, are provided by Shettleworth (1975). Certain responses, such as digging, rearing, and scrabbling, can be reinforced by food, whereas others, such as face-washing, scent-marking, and grooming, may actually be depressed under food reinforcement. Shettleworth argues that the responses that can be reinforced are those that would normally occur in the context of feeding behavior in this species.

There are many other examples of such biological boundaries to learning ability, for which the reader may consult Breland & Breland (1961), Seligman (1970), Seligman & Hager (1972), Shettleworth (1972), and Hinde & Stevenson-Hinde (1973).

Theoretical implications of the biological boundaries approach. At present there is no clear agreement on the implications of the biological boundaries criticism for the future development of learning theory. Some investigators (e.g. Bitterman 1975; Malone 1975) clearly feel that its impact on the general process view will be minimal. Others are more receptive but offer no very clear vision of the directions in which the psychology of learning should proceed. Thus Kimble (1973, p.12) acknowledges that "biological variables of many sorts have important messages for the psychology of learning," but he does not say what he perceives these messages to be, or how psychology should respond to them.

A few learning psychologists have responded more directly to the criticisms of the biological boundaries approach. Logue (1979) has reviewed the data from studies of taste-aversion learning and concludes that most require no radical reformulation of the accepted laws of learning, although some do require important quantitative modifications to those laws, especially in regard to the speed of acquisition and the long delay over which aversions may be formed. Logue concludes her review with a call for a more balanced approach to the study of learning: "This view recognizes the existence and utility of general laws of learning, but it also recognizes the necessity of acknowledging and investigating the dissimilarities in the learning of different species and the learning of different tasks. Otherwise we are likely to assume generality where none exists" (Logue 1979, pp. 290-91).

The heart of most current learning theory is associationism (Rescorla & Holland 1976; Jenkins 1979), and it is therefore not surprising to find a serious attempt being made, by LoLordo (1979), to defend the principle of equivalence of associability against the claim that some associations are more easily formed than others. LoLordo presents a careful methodological critique of many of the experiments on which the biological boundaries criticism draws. He concludes that very few of those experiments demonstrate the selective formation of associations, and that the selective effects that they do reveal may be attributed to nonassociative phenomena such as cue salience, attention, and differential response elicitation.

LoLordo’s analysis is especially interesting. If his defense of associative equivalence is correct, then it is possible to identify a wide range of selective nonassociative processes, of manifest importance to learning, that is unconvincing to dismiss as mere species-specific "contaminations" (Schwartz 1974). If these processes have a major influence on an animal’s ability to learn, as they apparently do, then our theories should reflect this fact and not view them as peripheral to “true” (i.e. associative) learning. It is, of course, quite legitimate for particular theories or investigators to focus their attention on associative rather than nonassociative phenomena, but if this is allowed to become the bias of the entire field of animal learning, then the theories that result are likely to be of rather limited explanatory scope (Rescorla & Holland 1976).

There is lack of agreement among the critics as well as the defenders of traditional learning theory as to what the biological boundaries criticism implies for the study of learning. Seligman (1970), for example, proposed a dimension of preparedness (similar to the notion of belongingness proposed earlier by Garcia & Koelling, 1966) for ordering associations according to the ease with which they may be formed. Somewhat arbitrarily, he delineates three types of association - prepared, unprepared, and contraprepared — and suggests that each type may have its own laws governing the formation of associations. The concept of preparedness is a purely descriptive one, since there is nothing to tell us which associations are prepared until after we have demonstrated a certain ease of formation (Schwartz 1974). Nor, having demonstrated this, and identified certain associations as prepared, is it clear that very much has been gained over the general process account. The most that the concept of preparedness seems to offer is an additional variable in the equations of learning (see Schwartz (1974) for further criticisms of preparedness). [See also Eysenck: "The Conditioning Model of Neurosis" BBS 2(2) 1979.]

Bolles’s (1970; 1971) concept of the species-specific defense reaction (SSDR) has already been discussed. Although it appears at first sight to refer to a restricted type of prepared association (i.e. that certain avoidance responses are learned more easily than others), the
SSDR concept is in fact somewhat more predictive than that of preparedness. We could, in principle, determine from naturalistic observation which responses an animal actually uses as SSDR's and then make predictions as to the ease with which various escape and avoidance responses could be acquired under experimental conditions. Although the applicability of the SSDR concept is limited to escape and avoidance conditioning, a similar concept could be developed for application to other forms of learning, such as that studied by Shettleworth (1975). In this case one would identify species-specific feeding behaviors, for example, and predict that these should be more easily reinforced by food than other, nonfeeding behaviors. However, the approach of testing predictions based on concepts like the SSDR has not yet been tried.

While Seligman and Bolles clearly hold out hope that some principles of learning, albeit of restricted generality, will be found to apply across species, other biological boundaries theorists seem much less optimistic. The dominant impression to be gained from the discussions of Hinde (1973) and Shettleworth (1972), for example, is that whatever principles of learning may be formulated, they are most likely to be limited in their applicability to one or a few species and situations. On this view, research inspired by the biological boundaries approach would consist largely in cataloging constraints on the learning abilities of each species of interest:

While it seems to be possible to delineate certain kinds of constraints on learning, it is probably not possible to predict where they will operate by translating directly from one case to another. However, as research in this area progresses, it may well become possible to characterize the constraints on learning and the cases in which they occur much more explicitly (Shettleworth 1972, p. 59).

Rozin & Kalat (1971) occupy a position that is much closer to that which I shall develop in later sections of this paper. They stress the importance of considering learning as a component of an animal's adaptation to the specific requirements of its environment, but they are also quite optimistic about the emergence of at least some generality from these diverse data:

Given the constraints on adaptation produced by basic properties of the nervous system, the cost of evolving specializations, and the fact that most species face a common set of problems, we doubt that a separate learning mechanism would exist for every situation, or that there would be separate laws for each species (Rozin & Kalat 1971, p. 481).

The view to be developed later in this paper is similar in spirit to that of Rozin and Kalat but, as will be seen, differs from it in some respects.

An important recent contribution to the biological boundaries debate has been made by Revusky (1977). Revusky is a strong proponent of general process theory who has met the challenge posed by taste-aversion studies head on. His own experimental work has focused on the long delay between stimulus (taste) and reinforcement (illness) over which taste aversions can be formed (Revusky & Garcia 1970; Revusky 1971), and he has attempted to show that this phenomenon is compatible with a general process account of learning, in contrast to the claims of uniqueness by Seligman (1970) and Rozin & Kalat (1971). Revusky (1977) is especially concerned, and rightly so, with the lack of any attempt by biological boundaries theorists to provide an alternative framework to general process theory within which we might search for general principles of learning:

The basic evidence used against general process learning theory seems to be lists of phenomena which do not fit into a known general process framework. Critics who use such "evidence," particularly Hinde (1973), do not seem disturbed by the fact that few of these phenomena can be explained by means of any other reasonably rigorous approach (Revusky 1977, p. 11).

Rozin and Kalat and other neoevolutionary [i.e. biological boundaries] learning theorists aggrandize minor science, the study of the particular, at the expense of extremely important science, the study of the general (Ibid., p. 10).

Like Logue (1979) and LoLordo (1979), Revusky is concerned to defend the assertions of general process theory by showing that many of the apparently contrary data may be accounted for in general process terms. An alternative response is to view the work of biological boundaries theorists not only in terms of the criticisms that it raises against general process theory, but also as suggesting an alternative approach to the study of learning that adopts a different point of departure from that of general process theory. Rather than starting from the position that the varieties of learning reflect an underlying general process, but one which may perhaps be modified in accordance with particular adaptive requirements, we might start with an explicitly ecological perspective on the problems of learning. In adopting such a perspective, we would be acknowledging the validity of the biological boundaries criticism, but using ecological considerations as a primary motivation in the study of learning rather than as a set of secondary, and largely peripheral, constraints. An approach of this kind would provide a framework that can motivate a search for general (ecological) principles of learning but that does not require allegiance to the associationist tradition, or to any other general process view. As these general principles become elucidated, we will be able to tackle the separate question of whether they reflect an underlying general process.

The question then arises whether the biological boundaries approach itself might not provide such an ecological alternative to the general process tradition. There are three main reasons for believing that it cannot, and these are discussed in the next section.

Limitations of the biological boundaries alternative to general process learning theory

Lack of generality. It may be the case, as many critics of general process theory imply, that there will be very few interesting generalizations to be made about learning, because of the wide diversity of phenomena that are revealed when learning is studied from a more
naturalistic standpoint. If that were to prove true, it would be extremely surprising, for there is a wealth of phenomena that have been studied from an ecological, naturalistic point of view and that have nonetheless yielded significant general insights. The literatures on population dynamics, predator-prey relationships, social organization, and evolution all show substantial theoretical development, based in large part on the study of particular, natural instances (see Mayr 1963; J. M. Emlen 1973; Alcock 1979). In some cases, general principles have been found to reflect general processes, and in others they have not. Given the primitive state of our knowledge about learning outside the general process tradition, it seems unduly defeatist at present to deny the existence of general principles. A far more productive strategy would be to admit that general principles may exist, although we cannot at present see what they are, and to consider how we might best go about searching for them.

In fairness to those whose work is being criticised, it should be admitted that part of the problem is to dislodge a weight of tradition that insists on the existence of general processes and to draw attention to adaptive specializations of learning that have been overlooked in the past. It is, however, much easier to dethrone a dominant paradigm, especially a long-lived one, if one has a viable alternative to offer (Kuhn 1962), and the biological boundaries theorists do not appear to have such an alternative.

Subservience to the general process tradition. Perhaps the greatest drawback to the biological boundaries approach is that it is less an alternative to general process theory than an addendum. As Revusky (1977, p. 12) points out, the very use of terms like "boundaries" and "constraints" implies that there is something (a general process?) that is being constrained. This is more than just a semantic observation: The two main theoretical proposals of biological boundaries theorists — Seligman's (1970) concept of preparedness, and Bolles's (1970) concept of the SSDR — look much more like supplements to the appropriate portions of general process theory than alternatives. A reasonable response by the general process theorist would be to continue the development of his general theory and to leave it to others to detail its application to particular species or ecological situations.

If the development of the poison-avoidance literature is a good indication of the kind of experimental work that is to support the biological boundaries approach, then we may also point to a methodological subservience to the general process tradition. Although some scientists may still believe in the conceptual neutrality of methodology (i.e. that "facts" exist to be "collected" by a convenient methodology, like collecting pebbles on a beach), this view has been almost universally abandoned, with good reason, by modern philosophers of science (see Kuhn 1962; Hanson 1969; Medawar 1969; Lakatos 1970). Methodology interprets the world, and it does so in terms of the theoretical predilections of its designers. Most of the experimental designs in the poison-avoidance literature are minor variants on themes developed by Pavlov, Thorndike, and their intellectual descendants. These designs were chosen for the study of learning precisely because they are biologically arbitrary (e.g. Thorndike 1911, p. 30) and to prevent the subjects from relying on "the helping hand of instinct" (ibid) in solving the problems posed. This is not to say that modern psychologists necessarily subscribe to a separation of learning and instinct; but in searching for an alternative to (rather than merely a criticism of) general process theory, it seems counterproductive to employ the methods that have been sanctioned by that theory. There is a very real danger that these methods force an interpretation of the world in the very theoretical terms to which we seek an alternative.

An illustration of the power of the general process tradition is provided by the introduction to a recent poison-avoidance study by Galef & Osborne (1978). They sought to investigate the hypothesis that apomatism (bright coloration) in many poisonous insects is an adaptation to the ability of potential predators to learn to avoid such prey, which implies that predators should indeed demonstrate the appropriate learning ability. Clearly that is just the kind of hypothesis whose investigation might promote a biological alternative to general process theory. Having presented their hypothesis, the authors discuss their choice of an experimental species:

The choice of a species in which to test the preceding hypothesis poses something of a problem. It might well be argued on ecological grounds that, given the rationale for the present studies, Rattus norvegicus would be a particularly inappropriate choice. Not only have we failed to find evidence in the literature that rats encounter apomastic prey in the wild, but in addition it is well established that rats feed most frequently in hours of darkness when visual cues are difficult to utilise. On the other hand, models of poison avoidance learning in the psychological literature most frequently treat the rat as representing the general mammalian case, from which, for example, one extrapolates to poison avoidance of humans or that of coyotes. The taste aversion learning of other species is by contrast viewed as, to some extent, idiosyncratic and specialized.

Thus the species chosen for the present work is necessarily undesirable from either the psychological or the ecological point of view. Because the work described below was more directly addressed to questions concerning the proximal causation of behavior than its function, we made the ecologically inappropriate choice of subject species (Galef & Osborne 1978, p. 908; emphases added).

Given the rationale for the study, the reference to "proximal causation" in the last sentence can only imply a belief in some general process underlying poison avoidance, which is equally well revealed by studying any form of poison avoidance in any species. Although this may be a somewhat extreme example, it illustrates the power that general process theory may have to constrain experimentation in the absence of any alternative theoretical framework.
Ex post facto adaptive explanations. It is extremely difficult to test hypotheses about the presumed adaptiveness of a biological trait, especially when it is not amenable to direct manipulation, as in the case of a learning ability. Unfortunately, it is very easy to think up plausible adaptive stories about almost any characteristic of an organism, and such stories tend to prevent any real ecological interpretation of the characteristic in question. This is widely recognized as a persistent deficiency in much evolutionary writing (Ghiselin 1974); in some areas, such as the rapidly developing field of sociobiology, it has reached epidemic proportions (Lewontin 1979). [See also Ghiselin: "Categories, Life, and Thinking" BBS 4(2) 1981 (forthcoming).]

A primary aim of the biological boundaries approach to learning is to offer an explanation of learning in terms of its contribution to an animal's adaptation to its environment — an aim that it shares with the ecological approach that is developed later in this paper. However, if such explanations are to be truly revealing, they must be based on analysis, not solely on conjecture (although conjecture may of course be a source of fruitful hypotheses), and such analysis has been lacking in the biological boundaries approach. Thus, while it may be reasonable to argue that primates can learn to associate visual cues with nausea because they normally select food on the basis of such cues (Johnson et al. 1975), in the absence of an empirical demonstration of how primates do in fact select food, this remains a hypothesis, not an explanation. Similarly, the fact that hamsters can be reinforced with food for digging, scrambling, and rearing may be due to the occurrence of such actions during feeding (Shettleworth 1975), but this needs to be demonstrated by observations of naturally occurring behavior.

It may be objected that the adaptiveness of such learning phenomena is either self-evident or readily apparent from casual observation, and that there is no need for detailed and time-consuming ecological analysis. Claims of self-evidence in science are of course best treated as hypotheses, since they often turn out to be false. Inferences about adaptiveness based on casual observation should likewise be treated with extreme caution, since it has proved difficult even to define criteria for identifying adaptive behavior (Hinde 1975; Lewontin 1978; Gould & Lewontin 1979; Glutton-Brock & Harvey 1979). The adaptiveness of Batesian mimicry, in which a noxious model is mimicked by a palatable species, might be considered "readily apparent," and yet, despite detailed ecological study (e.g. Brower, Cook, & Croze 1967), it is only recently that convincing evidence of that adaptiveness has been forthcoming (Jeffords, Sternburg & Waldbauer 1979). It is true that an experienced investigator can often make accurate inferences about the adaptive value of an animal's behavior, but the ease with which incorrect, though plausible, adaptive stories may be devised (Lewontin 1979) suggests strongly that such inferences should be framed as hypotheses rather than as explanations. As more complex forms of learning attract the attention of biologically motivated investigators, the dangers inherent in ex post facto adaptive explanations will increase.

A sketch of an ecological approach to the study of learning

If it is agreed that science should aim for generality of explanation, then, other things being equal, a single theory of learning is to be preferred over a variety of models of limited applicability. My aim in the remainder of this paper is not to attempt to formulate a general theory of learning, but rather to indicate how such a theory might be sought. My argument is that, to do this, we must follow the lead of those who claim that learning is to be understood in terms of adaptation. At the same time, we must avoid arguing, as some have done, that particularity of principle implies particularity of principle, as urged in the introduction to this paper. If we can do this, then we will be able to discover whatever general processes of learning may exist, but we will not overlook important adaptive specializations of learning, which is the major criticism voiced by biological theorists against general process learning theory.

The question of central importance in the ecological approach to learning is: What do animals learn and how do they learn it? The first part of this question (What do animals learn?) reflects a concern with the problems faced by animals in their natural environments; the second part (How do they learn it?), with the ways in which experience contributes to the solutions of those problems. The general process approach has concerned itself almost exclusively with the second part of the question. Anything that an animal can learn, regardless of whether or not it actually does learn such a thing under natural conditions, might be selected for study by a general process theorist; his choice would be constrained by convenience (Skinner 1950) and tradition, not by any consideration of whether the task is a natural one for the animal under study. A similar emphasis is evident in other fields concerned with the development of behavior. Gottlieb has remarked on . . . the banality of recurrent demonstrations of experiential modification or experimental modifiability, when these demonstrations are attended by a failure to relate the significance of such modifications to the normal (usual) route or outcome of species-typical development. . . . In the literature on this topic, there seems to be the tacit assumption that, if a given feature of neural or behavioral development can be shown to be susceptible to the influences of experience, then experience must normally play a part in its ontogeny. (Gottlieb 1976, pp. 48-49)

McCall (1977) expresses a similar point of view in regard to developmental psychology.

Gottlieb's caution applies equally to the study of learning: Simply showing that an animal can learn a particular task does not allow us to say that it actually does learn the task, or even any similar task, under natural circumstances. In order to be able to make this assertion, we must study the animal under natural conditions, or under some close approximation to them in the laboratory (Schneirla 1950; Miller 1977; Petrinovich 1979).
Some readers will no doubt object that psychologists are primarily interested in studying the mechanisms of learning, rather than the ways in which those mechanisms are employed under particular natural circumstances. It is frequently unclear what is to be understood by the term "mechanism" in this context. Not all persons who declare such an interest are concerned with the physiological bases of learning (one possible definition of "mechanism"), and the term requires some clarification before the strength of the objection can be properly evaluated. However, whatever interpretation is given, an important problem remains. The objection implicitly assumes that there is some underlying process (or processes) of learning that does not change as a function of what the animal is learning to do (that is, it assumes a fairly strong version of the general process view). Such an assumption is absolutely required of an argument which claims that "the mechanisms" of learning are equally well revealed by any one task situation, regardless of how closely it approximates one that is a natural task for the animal. This assumption is by no means logically necessary; in fact, it is a very strong empirical claim that surely remains to be demonstrated. While it may be true, it cannot be assumed to be true. In searching for a general theory of learning, we require an approach that can determine the truth or falsity of that claim, rather than assuming its truth.

If the assumption of a common mechanism underlying learning is mistaken, then a serious problem arises with any approach that assumes it — namely, the possibility of creating behavioral artifacts. The study of behavior is a part of natural science and, as such, is concerned with the explanation of natural phenomena. Distinguishing natural from artificial phenomena is frequently very difficult in practice, but in principle it is quite straightforward: Natural phenomena are those that exist independently of our investigations of them. When we make investigations, it is therefore important to determine which of our observations reflect the natural organization of the phenomena we are studying, and which are artifacts that reflect only the peculiarities of our investigative methods. When an anatomist studies the structure of a particular cell type, for instance, he may use various staining and fixing procedures to highlight certain aspects of structure and suppress others. It is well known to anatomists that the incautious use of many of these procedures produces artifacts that are highly reproducible and that can easily be mistaken for natural phenomena. The study of behavior, of course, carries with it no guarantee of exemption from this danger. The fact that an animal behaves in a regular and reproducible manner in an artificial laboratory environment does not mean that what we observe in such an environment necessarily demonstrates anything about the natural organization of behavior. The regularities observed may be imposed on the animal's behavior by the characteristics of the situation and may have nothing whatever to do with the regularities of natural organization that we seek to describe and explain.

This danger has been pointed out by Seligman (1970) and Petrinovich (1979), and the ecological approach strives to avoid it by ensuring that the phenomena of learning that we study are natural ones — that they do in fact exist independently of our investigations of learning. Such an approach therefore begins by analyzing each example of learning as an adaptation to a natural environment, rather than introducing adaptive considerations after the fact of laboratory studies (see the preceding remarks on ex post facto adaptive explanation).

The conception of adaptation. The concept of adaptation is central to any ecological study; it is a formal statement of the intuition that biologists have had since well before Darwin that animals are in general very well equipped to cope with the demands of their environments. In pre-evolutionary biology, that fact was seen as the result of providential design; since Darwin, it has been interpreted as the outcome of natural selection. Despite its importance in ecological study, and in biology in general, finding a broadly acceptable definition of adaptation has proven very difficult (see Bock & von Wahlert 1965; Dobzhansky 1968; Brandon, 1978; Lewontin 1978; Bock 1980). The most complete analysis of adaptation is that provided by Sommerhoff (1950; see Johnston & Turvey 1980).

In Sommerhoff's account, an animal's adaptation to its environment is expressed in terms of its ability to attain a set of goals in that environment. The nature of those goals depends, of course, on the animal under study; they might include orientation to a nest site, capture of a certain kind of prey, courtship of a mate, or defense against certain predators. In general, they comprise whatever states of affairs must be brought about, typically recurrently, in order that the animal may survive and reproduce. The animal's ability to attain those goals depends upon various physiological, anatomical, behavioral, and/or developmental characteristics that together constitute the biological support for adaptation, and the analysis of particular cases of adaptation involves the specification of the pertinent characteristics. The technical and conceptual difficulties involved in such endeavors are considerable and have been discussed by Hinde (1975), Lewontin (1978; 1979), Gould & Lewontin (1979), and others.

Two points that have been stressed by recent authors are particularly relevant to the present discussion. The first of these is that not all characteristics of an organism necessarily contribute to the biological support for adaptation, and those that do may not be optimally designed for the adaptive role that they play. Characteristics may be vestigial, such as the vermiform appendix in man, or they may show adaptively neutral variation, such as eye or hair color. Even in the case of adaptive characteristics, there may be internal constraints on development or on the organization of the genome that preclude selection of an optimal design in the course of evolution (Lewontin 1978). The ecological study of learning must therefore take very seriously the possibility that not all forms of behavior or behavioral change can be considered to be adaptive. The fact that an animal can learn to perform a task is no guarantee of an adaptive role for either the task or the learning ability.

The second point is that adaptation is an inherently relational concept: When we speak of some character-
istic of an organism as being adaptive, we necessarily imply an environment to which it is adapted. If we are to reach an understanding of learning as, or in terms of, adaptation, then we must pay close attention to the nature of the environments to which particular kinds of learning are adaptations (Slobodkin 1968; Slobodkin & Rapoport 1974).

The nature of the environment: task description. Like all other approaches to the study of learning, the ecological approach seeks an answer, or set of answers, to the question: "How do animals learn?" But from the ecological point of view, we see that the question cannot be answered in that form. Different animals have different adaptive relationships with their environments, and so the question must be broken down into two questions, to be answered separately for each animal species. The first of these takes the form: "What are the behavioral problems that this animal must solve in adapting to its environment?" The second question takes a more familiar form: "How does the animal learn to solve those problems?" Not only are questions of the first kind equal in importance to those of the second, they also clearly have logical priority. To draw an analogy, if we were to ask how to design a bridge, an engineer's first question, of necessity, would be: "What is it that you wish to bridge?" A question of this kind is a request for a task description, and task descriptions play an important and fundamental role in the ecological approach to the study of learning.

The term "task description" comes from the literature of artificial intelligence (e.g. Simon 1969). In order to write a program to solve a particular problem, one requires a detailed analysis of what the problem is. In many cases (for example: Compute 2 + 2) the task description is quite straightforward. In other cases (for example: Play a good game of chess) writing the task description may be a major part of the whole endeavour. The problem of writing task descriptions for learning is far more likely to resemble the latter of these two examples than the former (see further below).

The claim that descriptions of "What?" are logically prior to and as important as analyses of "How?" has been made by Gibson (1966) in his ecological theory of perception, and before him by Brunswik (1952). Gibson points out that, outside the psychological laboratory, animals (including humans) do not perceive brief, isolated flashes of light; rather, they perceive objects and events that are revealed by patterns of stimulation in a dynamically changing, richly textured optic array. He argues that it is surely an empirical question whether the means by which we perceive the former stimuli are the same as those by which we perceive the latter, and that in order to answer this question we need to know what is being perceived in the natural case. That is, we need a task description for the perceiving organism. [See also Ullman: "Against Direct Perception" BBS 3(3) 1980.]

My argument in regard to learning is similar to Gibson's in regard to perception. In order to answer the question "How does this animal learn?", we must first ask "What does it learn to do?" (see also Petrinovich 1979).

Task descriptions in the study of learning. It must not be supposed that the formulation of task descriptions for the study of learning will be an unproblematic enterprise. On the contrary, determining in useful detail what it is that animals learn is likely to require as much effort and ingenuity as that already devoted to the question of how they learn. Several authors have seriously addressed the issue of task descriptions (although not by that name) in their studies of learning, and a brief consideration of some of them will illustrate what may be involved.

Charlesworth (1976; 1978; 1979) has studied the nature of the problems typically encountered by young (2- to 4-year-old) children in their home environments. As part of a larger research program designed to analyze the "survival or adaptive value of intelligence" (Charlesworth 1979, p. 212), the description of those problems corresponds to the task-description stage of an ecological study of learning. It answers the question: "What are the problems that young children typically solve?" Further research will clearly be needed to determine how children learn to solve those problems, but Charlesworth's research already suggests that serious concern with task descriptions may lead to a picture of the child's intelligence rather different from that provided by the traditional approaches. For example, he notes that "very few instances of complex problems, such as those used in psychological testing or tool-using studies, were observed" (Charlesworth 1979, p. 214; emphases added).

The work of S. T. Emlen on the development of migratory orientation in the indigo bunting (Passerina cyanea) is perhaps a paradigmatic example of the ecological approach to the study of learning (reviewed by Emlen 1972; 1975). The first studies in Emlen's research program (Emlen 1967a; 1967b) involved the task-description stage; they answered the question "What behavioral problems are involved in migratory orientation for the indigo bunting?" The bunting is a nocturnal migrant; by placing mature, ecologically experienced birds under a planetarium dome during the normal migratory season, Emlen was able to arrive at a precise description of the orientation skill. Briefly, configurational information distributed over groups of stars, especially those within about 10° of the pole star, provides the basis on which the bird selects an initial migratory direction (Emlen 1967a; 1967b). Arriving at the task description required information on the species' habits and life history to determine what orientation cues might be available to it, together with experimental manipulation to determine which of those cues are actually used for orientation. On the basis of this ecological task description, Emlen was able to proceed with an investigation of the second question: "How is this orientation skill learned?" (see below).

It is interesting to contrast the ecological approach in the study of learned orientation in a particular species with that adopted by traditional learning theorists in the study of learned orientation as a general, supraspecific problem. When Small (1901) used mazes in his studies of rat learning, he did so on the plausible, though so far as I know undemonstrated, assumption that a maze is a close approximation to the burrow systems in which rats live — that is, he attempted to set up a task.
description for this kind of learning. Subsequent development of Small’s work eliminated most of the ecological content of the task description and reduced the problem to one of “behavior at a choice point” (Tolman 1938). The relation of the logical conclusion of this development (the T maze) to any problem actually faced by the rat is obscure and has certainly received no attention by general process theorists. The methodological trend in this area of learning research has been to emphasize the logical structure of the task to the complete exclusion of its ecological structure. That animals normally learn about logic is, I think, debatable, although if they learn anything at all, they must learn about their ecology. Since different species have different ecologies, they may well learn different things, even within the general domain of orientation. The orientation problems faced by a rat and by a migrating bunting are very different, and it is not clear that anything is gained by attempting to strip them of their ecological content and reduce them to problems of logic. My general point is supported by Lynch’s (1961) classic study of human orientation in cities, which demonstrated that the ecological structure of a city may be much more important than its geometric structure in determining how people find their way around. The geometric structure of a city is ecologically neutral in the same way the logical structure of a learning task is. [Cf. Olton: “Hippocampus, Space and Memory” BBS 1(3) 1979, and O’Keefe & Nadel: The hippocampus as a cognitive map, BBS 2(4) 1979.]

What general guidelines do these examples offer for the construction of task descriptions? It is of central importance that task descriptions start with the study of the animal’s behavior under natural, species-typical conditions, but it is unlikely that naturalistic observation can provide all the required information. In many cases, experimental study will be necessary, especially to determine the sources of information in the environment with respect to which the behavior of interest is controlled. Some readers may feel that the requirement of naturalistic observation limits the ecological study of learning to individuals who have the necessary training and interest in the field study of behavior; but, in fact, many of the data from which task descriptions could be constructed are already available in the ethological literature. In particular, the problems of orientation and feeding have long been the concern of behavioral ecologists, and numerous excellent studies of the ways in which these problems are solved in many different species have been published (see J.M. Emlen 1973; Brown 1975; Alcock 1979). The ecological study of learning need not be forestalled by any lack of data on which to base task descriptions.

Local principles of adaptation by learning. The provision of a task description for behavior is only the first stage, albeit a most important one, in an ecological approach to the study of learning. Having answered the question “What does this animal learn to do?”, we can approach the question that is of central importance to any student of learning: “How does it learn to do that?”

Generally speaking, the answer to this question involves a specification of the contributions of experience to the development of behavior (as given by the task description) and an analysis of the means by which such experience has its effects (ultimately, though not necessarily immediately, in physiological terms). More specifically, we might seek information on any of the following points (this is not an exhaustive list):

1. What are the necessary and sufficient experiential conditions for the normal development of this behavior?
2. Is the experience required, or most effective, at certain times if learning is to occur?
3. How do different experiences interact in the development of the behavior?
4. How does the development of one behavior interact with that of another?
5. In what ways does early learning constrain learning that is possible in later life? In particular, is the acquisition of certain behavioral skills necessary before others can develop?
6. What are the effects of experience primarily maintaining, facilitative, or inductive? (Gottlieb 1976).

Because the behavior whose development is being analyzed has been given an ecological task description (e.g. feeding in a certain manner on certain foods), the kind of analysis implied by the above questions is implicitly undertaken in an adaptive framework. The fact that these questions reflect an ecological/adaptive approach to the analysis of learning must not, of course, be taken to mean that their answers demonstrate the adaptiveness of either the behavior or the means whereby it is learned. Determining the adaptiveness of learning is an extremely difficult theoretical and experimental problem (Tinbergen 1963; Hinde 1975; Lewontin 1978) that will not be considered here. A partial treatment of this problem will be published elsewhere (Johnston, in press).

The kind of analysis implied by the six questions listed above, and others like them, deliberately blurs the distinction between development and learning (Johnston, in preparation). The concept of development as a passive unfolding or maturation under genetic control has been almost universally rejected on the basis of repeated demonstrations that nearly all development shows some important dependence on experiential factors (see Kuo 1922; Lehrman 1953; Schneirla 1956; Gottlieb 1976; Oppenheim, in press). In more recent usage, “development” has come to imply the ontogeny of species-typical behavior, whereas “learning” often refers to the acquisition of the highly artificial kinds of behavior studied within the general process tradition. (This is, of course, a question of emphasis rather than of definition.) If the ecological approach to learning is to be successful, it is clear that this distinction can no longer be maintained. Many of the phenomena traditionally analyzed as instances of “development” will undoubtedly turn out to have important implications for an ecological theory of learning and should not be excluded from the scope of such a theory by arbitrary definition (Johnston & Turvey, in press).

A few words should be said here concerning the methodological approach required for an ecological analysis of learning. There is nothing in the ecological attitude that precludes the use of artificial situations for
the study of learning. Indeed, without manipulating an animal's environment, it is clearly impossible to determine the role of various kinds of experience in the development of its behavior. The ecological approach does demand, however, that such artificial situations be used to test hypotheses about learning as it occurs naturally, rather than serving as objects of study in themselves. The insights to be gained from the use of artificial conditions depend on the contrast with development under normal circumstances, and the definition of normal circumstances must obviously be based on ecological description (Gottlieb 1976, pp. 48-9; Miller 1977).

The aim of the analyses I have been discussing is to provide a set of local principles of adaptation for each species' behavior. The ecological task description for each behavior of interest specifies the nature of the adaptation to be accounted for; it describes the way in which the animal solves a particular adaptive problem, such as feeding, orienting, or communicating with conspecifics. The aim of the analysis is to specify how this solution is reached in the course of development. The results of the analysis might be expressed as a model (not necessarily formal), which is an explicit statement of the principles by which the animal achieves its ontogenetic adaptation to some aspect of its environment. These principles are termed "local" because there is no way to determine, without further analyses of other species, whether they apply to more than the single species in which they are described. The problems of arriving at more general principles of learning are discussed in the following section.

A good example of the way in which the search for local principles of adaptation may be carried out is provided by Gottlieb's (1971) studies of the development of auditory species identification in ducklings. Space precludes a comprehensive review of these very extensive experiments; what follows is a selective account. Incubator-hatched, maternally naive Peking or mallard ducklings (Anas platyrhynchos) show a strong tendency to approach the mallard maternal call 24 hours after hatching, preferring that call to the maternal calls of other species (Gottlieb 1971). Selective approach to the conspecific call is clearly a skill of considerable adaptive importance to young ducklings, who rely on their mother for warmth and protection for some time after hatching (Collias & Collias 1956; Miller & Gottlieb 1978). Gottlieb's studies concern the role of prenatal auditory experience in the development of this species-typical auditory preference. Normal Peking ducklings start to vocalize in the egg at about 24 days of incubation, three days before hatching. Embryos that are surgically devocalized before that time fail to show the normal postnatal auditory preference for certain features of the maternal call, in particular for the species-typical repetition rate of 4 notes/second (Gottlieb 1978). Since the embryos show a selective response (diminution of bill-clapping; Gottlieb 1979) to the mallard call before the onset of self-produced vocalizations (at about 22 days of incubation), the role of those vocalizations is to maintain a preexisting auditory preference (Gottlieb 1976). If a tape recording of the embryonic call is played to devocalized embryos, the postnatal preference for the maternal call is reinstated (Gottlieb 1980), confirming the role of self-produced stimulation in the development of this adaptive behavioral skill.

Gottlieb's results do not reveal the kinds of processes that would be called "learning" by someone working within the general process tradition, but they are the kind of finding with which an ecological approach to learning must be prepared to deal, since they demonstrate an important role for experience in the development of an adaptive behavioral skill.

A second example of the search for local principles of adaptation comes from the work of Emlen (1972) on the development of migratory orientation in the indigo bunting (discussed earlier). Emlen (1969) found that when young birds were prevented from viewing the night sky in their first year (prior to the onset of any migratory tendency), no directional preference was exhibited in the following migratory season — an example of an inductive effect of experience (Gottlieb 1976). Further study (Emlen 1970) showed that exposure to a rotating star field is crucial to the development of normal directional preference; exposure to a stationary star field does not support normal development. A point of further interest is that it does not matter whether the star field rotates about the normal pole star (Polaris) or another star (Betelgeuse); birds exposed to a star field rotating about Betelgeuse subsequently take their bearings from that star rather than from Polaris.

These two examples illustrate two important points that were made in the previous discussion. The first is that ecological analyses of learning are based on ecological task descriptions. The role of the task description in Emlen's work has already been described. In Gottlieb's research its importance is shown by the fact that Peking ducklings will only develop a preference for, the species-typical call; exposure to altered calls will not induce a nontypical preference (Gottlieb 1980). Without a task description (i.e. an answer to the question: "What preference normally develops?"), it is clear that the development of auditory preferences in this species would hardly have been susceptible to an experimental analysis.

The second point concerns the use of artificially modified environments in ecologically motivated analyses of development: Both series of studies utilized sophisticated experimental techniques, including surgical manipulations, to elucidate the role of experience in these instances of development. I emphasize the latter point because it is often believed, mistakenly, that the ecological study of behavior is necessarily limited to naturalistic observation and precludes experimental analysis in the laboratory. What is precluded by the ecological approach is the use of ecologically arbitrary experimental designs for such analyses.

The results discussed here come from two illuminating lines of research out of many that might have been selected. Other examples that illustrate the ecological approach to the study of learning would include the studies of bird-song learning by Marler and his colleagues (Marler 1970; Nottebohm 1970; Marler & Mundinger 1971; see Marler 1977, for some general theoretical principles that may be drawn from this work) and the many studies of feeding behavior that have taken ecological data as a starting point (e.g.,
Global principles of adaptation. The discovery of local principles of adaptation is clearly an enterprise of considerable scientific importance in its own right. The search for a general theory of learning, however, demands that we also attempt to discover principles of ontogenetic adaptation that apply to more than a single species or situation. In the past, such global principles have been presumed to be best revealed by isolating the animal from the specific demands of its natural environment. Implicit in this strategy is the assumption that principles of learning apply to the animal alone, hence that ecological considerations are peripheral to an account of learning. By contrast, the ecological approach views learning in terms of adaptation, so that its understanding rests on an analysis of both the animal and its environment. This strategy has been explicit in the preceding discussions of task descriptions and of local principles of adaptation. The search for global principles demands an equally explicit ecological strategy.

The probable importance of an ecological strategy in accounting for learning as a natural phenomenon may be seen by considering the general finding that emerges clearly from many studies of learning that have been conducted by ethologists: In many cases where experience has been shown to play a role in behavioral development, only normally occurring, species-typical experience (that provided by the natural environment) permits the development of adaptive behavior. Indigo buntings must be exposed to orientation cues early in development, but specific natural cues (a rotating starfield) are required for normal development of the orientation skill (Emlen 1970). White-crowned sparrows will not develop song without exposure to a song model, but that model must correspond to the species-typical song; other songs will not be learned (Marler 1970). Red-legged frog tadpoles require early exposure to patterned substrates if they are to acquire a substrate preference, but preferences for a striped (natural) substrate pattern are acquired more readily than preferences for a checkerboard (unnatural) pattern (Wiens 1970).

It is very hard to see how a nonecological theory of learning could ever account for all of the above examples without postulating various ad hoc exclusionary rules to fit the manifest ecological constraints on each species’ learning ability. Whether an ecological theory can give a satisfactory account of these examples remains to be seen, but ecological principles of some kind are clearly needed to reflect the special role that the natural environment plays in each case. Many examples of learning, it appears, are closely tailored to the nature of the specific environments in which the learners live. In the terminology of Bekoff & Fox (1972), development is both environment-dependent and environment-expectant, since it expects the particular environment on which it depends. Understanding learning, therefore, requires description and analysis of the environment that is learned about; it requires an ecological approach to the study of learning as adaptation.

By considering learning as an instance of adaptation, we imply a viewpoint from which learning is seen as a process that ensures a correspondence between an animal’s behavioral skills and the requirements of its natural environment. From the point of view of adaptation, the animal and its environment stand to one another in a complementary relationship, and following the notation of Turvey & Shaw (1979), we may write this relationship as:

\[ \text{Animal} \circ \text{Environment}. \]

The terms “animal” and “environment” in such a relationship are variables that range over a number of species and ecological niches, respectively. To the extent that animals are in fact adapted to their environments, the complementarity relationship holds for natural ecosystems (i.e. animals and their natural environments). It may also hold for some artificial ecosystems, since an animal may well be adapted to environments other than its natural one, but here I shall consider only the natural case.

Typically, we would not attempt to specify all of the aspects of organismic and environmental structure in such a relationship. Rather, we identify some aspect of the animal (such as its learning ability) as being of special interest and describe that aspect in relation to appropriate aspects of the environment. In the ecological study of learning, basing analyses of learning on ecological task descriptions helps to ensure that the appropriate aspect of the environment has in fact been described.

The problem that we face is that of replacing the symbol \( o \) by a principle of learning that remains invariant over all (or at least many) species; from the preceding discussion it can be seen that this might best be achieved by allowing “animal” and “environment” to covary within the constraints imposed by the structure of natural ecosystems. On this view, general principles emerge by virtue of the complementary diversity among animals and their environments, not in spite of the diversity among animals considered alone.

The increased generality that is provided by an ecological approach to the analysis of animal structure and function is well illustrated by Gordon Walls’s classic volume, The Vertebrate Eye and its Adaptive Radiation (1942). Roughly half of Walls’s book is devoted to an ecological analysis of optic structure, in which the problems of vision in different environments (diurnal, nocturnal, aquatic, terrestrial, etc.) are discussed with reference to the eyes of animals that inhabit them. A number of interesting general principles emerge from this undertaking — principles that clearly could not have emerged if the various species had been considered in isolation from the environments to which they have become adapted. Walls does not provide formal expressions of these principles, but an informal example will suffice to make the point.

The shape of the lens shows considerable variation among different species of vertebrates. In some, such as man, it is greatly flattened, with a flatness index (diameter divided by thickness) of about 2.7. In others,
such as most fishes, it is more nearly spherical, with an index of about 1.0. Broadly speaking, the lenses of terrestrial animals are much flatter than are those of aquatic ones, and an explanation of this diversity may be given in ecological terms. In air, light is strongly refracted at the cornea and needs only weak refraction at the lens to reach a focus on the retina — hence a flattened, weakly refracting lens in terrestrial vertebrates. However, in water, light is hardly refracted at all at the cornea and, in consequence, must be refracted more strongly at the lens — hence a spherical, strongly refracting lens in aquatic vertebrates. The general principle implied here holds true in the case of related species with contrasting habits: The spiny anteater (Tachyglossus), a terrestrial marsupial, has a flatness index of 2.75, whereas the duck-billed platypus (Ornithorhynchus), which is largely aquatic, has an index of 1.4 (Walls 1942, p. 669). A particularly interesting test case is the South American four-eyed fish (Anableps). This animal has a remarkable ocular anatomy related to its habit of swimming on the water surface with the top of its head protruding into the air. Each eye has two pupils, one looking up into the air and one down into the water. Light passing through each pupil is focused onto a separate retina by a single lens occupying the middle of the eyeball. The lens is oblate, having a high flatness index when measured in regard to the upward-looking (terrestrial) pupil and a low index in regard to the downward-looking (aquatic) pupil. The peculiar anatomy of the Anableps eye is readily understood in terms of its natural habitat, which lies at the interface of two environments with very different optical requirements (see Walls 1942, frontispiece and p. 434).

The general principle that explains variation in lens shape in terms of the refractive properties of different ecological media is unlikely to provide a full accounting of such variation, but it does illustrate the point that a substantial amount of generality can be extracted from structural diversity by an appeal to ecological considerations. In the ecological study of learning, a search for general principles requires a similar strategy. Rather than being a search for invariant properties of animals (as in the general process approach to learning) it is a search for invariant relationships between animals and their environments. Adopting such an approach, we might find, for example, that the number of encounters (trials) that an animal requires in order to learn to avoid noxious food items is a function (possibly complex) of the harmfulness of noxious items, the relative frequency of noxious items, and the energetic costs associated with the capture of a single food item. The independent variables in such a general principle are, of course, specified as part of the task description, not on the basis of arbitrary laboratory manipulations. Note that any such general principle is quite neutral with respect to the existence of general processes of learning, as was also the case with the thermoregulatory example discussed earlier. It might be that a species whose environment includes very harmful potential food items learns the identity of correct food by “imprinting” food brought to it by its parents (and hence presumably safe), whereas a species for whom may learn more slowly, by means of “association.” Here “imprinting” and “association” are labels identifying local principles of adaptation that reflect different underlying processes of learning. The general principle is not made any less general by virtue of this fact, and, of course, some (or even many) ecological general principles may indeed reflect common processes among the local principles on which they are based. In the ecological approach, the existence of such general processes becomes a matter for demonstration rather than assertion.

The relationships among the three levels of ecological inquiry into learning, task description, local principles of adaptation, and global principles of adaptation, are illustrated in Figure 1. This figure emphasizes that, in contrast to the biological boundaries approach, the ecological approach is inherently ecological; ecological considerations are not simply brought in after the fact to explain data that do not accord with the general process view.

An important point concerns the question of the dimensions along which we should search for global principles among a diversity of local principles of adaptation. It would be premature to attempt to offer a definitive answer to this question, but I shall briefly

![Figure 1. The ecological approach to the study of learning. The four shaded rectangles at the bottom of the figure represent four natural ecosystems (animals and their natural environments). Description and analysis of the phenomena of ontogenetic adaptation within each ecosystem supplies the basis for writing a set of local principles of adaptation (L₁, L₂, etc.) for each species. Ecologically constrained generalization among the sets of local principles, as discussed in the text, produces a single set of global principles of adaptation (G₁, G₂, etc.) that form the basis for a general theory of learning. Note that each set of local principles may contribute to more than one global principle and that every global principle may not apply to all species studied. The numerical relationships between local and global principles (whether one-many, many-one, or both) depends in part on the dimensions along which generalizations are made (see text). In this approach, ecological considerations are intrinsic to the completed theoretical formulation.](https://example.com/figure1.png)
discuss three possible alternatives, which are not meant to be either exhaustive or mutually exclusive.

The first lies closest to the spirit of the ecological approach, as I have outlined it in this paper, and involves searching along common task dimensions, identifying principles of learning relevant to feeding, orientation, habitat selection, social behavior, and so forth. Each such task dimension defines, albeit crudely, an aspect of the adaptive relationship between animal and environment that is common to all those species in which it can be identified. Searching for global principles along task dimensions thus seems a profitable strategy for understanding learning in terms of adaptation, which is a cornerstone of the ecological approach.

The second strategy is more familiar and is associated with comparative psychology as it is traditionally practiced — namely to search within taxonomic groups, to identify mammalian, avian, reptilian, and other principles of learning. The justification for this strategy is well known: Animals that are descended from a common ancestor presumably share characteristics that reflect ancestral constraints on possible evolutionary divergence. However, if a search along taxonomic lines is to contribute to an ecological theory of learning, it is important that the first two elements of an ecological inquiry — namely task descriptions and the elucidation of local principles of adaptation — play a more important role than they do in traditional inquiry (e.g. Bitterman 1975). It is not sufficient merely to compare animals on an arbitrary array of learning tasks. Rather, the tasks used should reflect the real adaptive problems that the various species encounter in their natural environments.

Finally, the third approach involves searching within groups defined by habitat or general life-style — that is, by evolutionary analogy rather than homology. Thus, for example, we might look for general principles peculiar to arboreal animals, carnivores, migratory species, or highly social animals. This again is a relatively familiar comparative strategy, the aim being to discover principles that reflect evolutionary analogies in the abilities (in this case learning abilities) of different animals that adopt similar life-styles. This approach is an especially important source of information on the nature of the selection pressures responsible for the evolution of particular kinds of learning abilities. Once again, it is important that the learning skills among which such general principles of analogy are sought be anchored in ecological task descriptions for the particular species of interest.

I feel that all three of these alternatives will have something to contribute to a final general ecological theory of learning, since they provide insights into three different kinds of generality that hold among animals: adaptive, phylogenetic, and ecological.

Ethology and the ecological study of learning. The study of animal behavior in relation to the natural environment is often viewed as characteristic of the field of ethology, although it is sometimes forgotten that a number of psychologists have also adopted an ecological approach in their studies of behavior (see Miller 1977 for examples). Both by training and by inclination, then, ethologists are well-equipped to make important contributions to an ecological approach to learning, as frequent reference to the work of ethologists in this paper demonstrates. The essential stage of task description is one where ethological research has already provided a substantial body of literature that can serve as the basis for the study of whatever learning may be involved in these forms of behavior. Many instances of learning, such as the development of bird song, habitat selection, orientation, and prey capture, have attracted the attention of ethologists, but such studies lack the conceptual unification that might lead to the formulation of general theoretical principles of broad explanatory power.

The psychological study of learning, while lacking in ecological content, has strongly emphasized the desirability of seeking such general explanatory principles. Perhaps because psychology established its hegemony in the field of learning theory at a time when ethologists were largely concerned with the study of “instinctive” behavior, ethologists have generally drawn heavily on psychological theories in their discussions of learning (e.g. Thorpe 1963; Lorenz 1965; 1969). Finding those theories lacking in various respects, ethologists have offered criticism, but little in the way of alternatives (e.g. Lorenz 1965; Hinde 1973; cf. Marler 1977). It is clear that the ecological approach to learning advocated here will best be advanced by a synthesis between the traditions of psychology and ethology in regard to the study of behavior.

Concluding discussion

The ecological approach to the study of learning that I have outlined in this paper offers a more radical alternative to general process learning theory than does the currently popular biological boundaries approach. The latter has served a most important critical function, but, for the reasons discussed above, it seems to have serious limitations as a true alternative to general process theory. Let me therefore summarize the most important characteristics of the ecological approach, both theoretical and empirical, as contrasted with the general process approach, on the one hand, and with the biological boundaries approach, on the other.

The essence of an ecological approach to the study of learning is the realization that animals learn, under natural circumstances, to perform certain specific kinds of behavior. These instances of learning constitute the natural phenomena that it is the business of learning theory, as a branch of natural science, to explain. Unlike the general process approach, the ecological approach makes no prior assertions as to the existence of general processes underlying these various instances of learning. It is the business of students of learning to discover such processes, if they exist, rather than to assume them as the basis for a program of research. While it differs from the general process approach in reserving judgment on the existence of general processes of learning, the ecological approach differs also from the biological boundaries approach in being specifically concerned with the search for general principles of learning. The ecological approach, while fully endorsing the biological bound-
ties criticism, supplements that criticism with an alternative theoretical framework, quite distinct from that of general process theory.

The ecological analysis of learning is carried out at three different levels. The first anchors the analysis to natural phenomena of learning by providing task descriptions of what it is that animals actually learn in the course of their development. Constructing a task description requires that we study animals under natural or seminatural conditions, rather than merely making reasonable guesses as to what animals actually learn; there are many cases in which such descriptions are already available in the literature. In some instances of learning, constructing the task descriptions may be as difficult, and may require just as much ingenuity, as analyzing the processes whereby learning occurs - it is most important that the significance of this element of the ecological approach be properly appreciated.

Given a task description for a particular instance of learning, the analysis continues with an investigation of the various experiences that contribute to the development of the skill in question, and the ways in which these experiences have their effects. How such investigations are to be carried out depends, of course, on the particular instance of learning being examined. Several exemplary studies are available in the literature; some of these are described above. Developmental analysis of this kind provides the basis for formulating local principles of adaptation that explain how individuals of a particular species learn to cope with the requirements of their particular environment.

The insistence that we formulate local (species-specific) principles of adaptation as a prelude to the search for more general principles is an important difference between the ecological and general process approaches to learning. An equally important difference between the ecological and biological boundaries approaches, both of which see a need for ecological study of particular species, is that the ecological approach advocates a third level of analysis: the search for global principles of adaptation that apply to more than a single species. This difference arises because whereas many biological boundaries theorists despair of finding unity within the wide diversity of animals, the ecological approach seeks such unity in the complementary diversity of animals and their natural environments.

NOTES

1. The points to be discussed do not represent original insights by modern authors. They were well appreciated by Darwin (1859) and by most subsequent evolutionary theorists. However, they are commonly not appreciated in less rigorous discussions of adaptation, and the authors cited must be credited for explicitly stressing their importance.

2. I should point out that the view I am expressing - that the components of an ecological theory of learning will be principles of adaptation - is not to be confused with recent proposals that the mechanisms of learning are analogous to the mechanisms of natural selection, whereby adaptations arise in the course of evolution (Staddon & Simmelhag 1971; Campbell 1974; Staddon 1975; Glassman 1977). Whatever the merits of that view, it imparts no ecological content to the study of learning, and it has no bearing on the arguments at hand.

3. Not all solutions to behavioral problems necessarily involve learning, and a better formulation of the question might be: "How, if at all, does the animal learn to solve these problems?" It behooves the student of learning to select problems for study that are likely, on the basis of collateral evidence, to involve learning of some kind. However, it is also well to recall that many apparently unlearned behavior patterns, such as pecking by gull chicks (Hailman 1967) and the following reaction in young ducklings (Gottlieb 1971), turned out on close inspection to involve significant experiential components.

4. These three kinds of effects are distinguished by Gottlieb (1976). Maintaining experiences are required to support continued development of a pre-existing skill. Facilitative experiences enhance the development of a skill. Inductive experiences are those in the absence of which the skill does not develop at all.

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