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A Synthetic Approach to the Study of Animal Intelligence

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Two Anecdotes

It is 7:00 A.M. The sun has just risen over the botanical gardens, and my research team and I are about to give up our attempt to catch a male Anna's hummingbird with a discrete white spot behind his left eye. "Spot" has been defending a small, flower-rich territory, and we want to put a colored plastic band on his leg as part of our study of nectar-foraging patterns. To catch Spot we had arrived before sunrise and strung a mist net, 5 feet high and 18 feet long, across the middle of his territory. Mist nets, made of very thin black nylon thread, are designed to entangle any bird that flies into them. Unfortunately, a heavy dew at sunrise had collected on the strands of the net, and Spot saw it immediately. He had flown along it and even perched on it. Experience has taught us that once a hummingbird has done this, it will never fly into the net. So we were about to take down the net, but first we were having a cup of coffee. Spot was sitting on his

favorite perch, overlooking the territory from its southwest edge. Suddenly an intruding hummingbird flew into the territory from the northeast and began to feed.

Male Anna's hummingbirds are extraordinarily aggressive animals. Usually they will utter their squeaky territorial song and fly directly at an intruder, chasing it out of the territory. But that is not what Spot does. He silently drops from his perch and flies around the perimeter of the territory, staying close to the ground, until he is behind the other bird. Then he gives his song and chases the intruder—directly into the mist net. Spot pulls up short, hovers over the bird, utters another burst of song, and returns to his perch.

This anecdote raises many questions with interesting implications. For example, did Spot have a "cognitive map" of his territory that allowed him to understand that if he moved to a point behind the other bird he could force the intruder into the net? Since this is only an anecdote, it provides no definitive answer. But many more mundane empirical studies of nectar-feeding birds offer systematic data showing that they do possess considerable knowledge about spatial and temporal patterns of food production on their territories (Gass & Montgomerie, 1981; Gill & Wolf, 1977; Gill, in press; Kamil, 1978).

Consider this observation of chimpanzees reported by Goodall:

> The juvenile female Pooch approaches high-ranking Circe and reaches for one of her bananas. Circe at once hits out at the youngster, whereupon Pooch, screaming very loudly indeed, runs from camp in an easterly direction. Her response to the rather mild threat seems unnecessarily violent. After two minutes, the screams give way to waa-barks, which get progressively louder as Pooch retraces her steps. After a few moments she reappears; stopping about 5 meters from Circe, she gives an arm-raise threat along with another waa-bark. Following behind Pooch, his hair slightly bristling, is the old male Huxley (who had left camp shortly before in an easterly direction). Circe, with a mild threat gesture towards Pooch and a glance at Huxley, gets up and moves away. Pooch has

used Huxley as a "social tool." This little sequence can be understood only because we know of the odd relationship between the juvenile and the old male who served on many occasions as her protector and was seldom far away. (Goodall, 1986, p. 567)

There are many objections to the use of anecdotes such as these. As Thorndike (1898) pointed out, hundreds of dogs get lost every day and nobody pays much attention except the unfortunate dogs' owners. But let one dog find its way from Cambridge to London, or Boston to New Haven, and it becomes a famous anecdote. Anecdotes cannot provide definitive evidence about animal intelligence (or anything else). But it may be a serious mistake to completely ignore their implications, which can provide interesting hypotheses for rigorous test.

Furthermore, the two anecdotes related above are not isolated examples. Most fieldworkers have similar stories from their own experience. Books such as Goodall (1986) and Smuts (1985) are replete with them (see also Kummer, 1982; Kummer & Goodall, 1985). Much more important than the number of these anecdotes, however, is the fact that empirical data are being amassed to support their specific implications. The main point is that these anecdotes and supporting data suggest that the traditional psychological approach to the study of animal learning is too limited.

Psychologists have been studying animal learning for about a century. This century of experimental and theoretical work has produced some remarkable successes, particularly in understanding basic conditioning processes. However, these successes are limited in two major ways. First, they have been confined to a narrow domain. Recent research from a variety of settings has demonstrated that animals have mental abilities far beyond what they were given credit for just a few years ago. We must dramatically expand the range of phenomena addressed by the study of animal learning. Second, there has been an almost complete failure to place animal learning in any kind of comparative, evolutionary framework, primarily because of a failure to develop any detailed understanding of how animals use their ability to learn outside the laboratory. Recent developments in psychology and biology are beginning to suggest how this gap may be filled.

The expansion of the range of phenomena under study is already well under way, with the emergence of the cognitive approach to animal learning (Hulse, Fowler, & Honig, 1978; Roitblat, Bever, & Terrace, 1984) and diverse new techniques for exploring the capacities of animals

(Griffin, 1976, 1978). The development of a meaningful comparative approach is also beginning to emerge, thanks to developments in both psychology and biology.

My purpose in this chapter is to outline the beginnings of a new way to study animal intelligence. I have labeled this the synthetic approach because it represents an attempt to synthesize the approaches of psychology, ethology, and behavioral ecology. I have used the term intelligence, rather than more specific terms such as learning or cognition, to emphasize the breadth of the phenomena to be included. The synthetic approach builds upon previous successes but is much broader and more biological than the predominantly psychological approaches of the past. Its goal is to develop a full understanding of the intellectual abilities of animals, with particular emphasis on psychological mechanisms and functional significance.

What I am proposing is not a new theory. Rather, it is an attempt to outline a new scientific research program (Lakatos, 1974). According to Lakatos, research programs consist of two parts: a central core of laws, principles, and assumptions that are not subject to direct empirical test, and a protective belt of "auxiliary hypotheses" that relate the central core to observations and can be tested and perhaps rejected. The central core and its auxiliary hypotheses function to direct research toward certain problems and away from others. In these terms, I am urging two changes in the central core of the psychological approach to animal learning: a broadening of the discipline's domain and the adaptation of a biological and ecological approach to the study of learning. These changes could redirect attention to important and interesting facets of animal learning that have been ignored by the traditional psychological approach.

The Traditional Approach

The purpose of this section is to identify the central core of the psychological study of animal learning. There are two difficulties. First, the programs Lakatos discusses are from the history of physics, with explicit, usually mathematical, specifications of their central core. In the case of animal learning, the central core is less formalized and more difficult to specify. Another difficulty is that although it is easy to talk and write about "the traditional approach" to animal learning in psychology, in fact there have been a number of different approaches. Nonethe-

less, a few assumptions have been widespread, if not universal. Some of these assumptions formed the central core of the scientific reseach programs that have dominated animal-learning psychology and have directed attention away from important phenomena and issues.

GENERAL PROCESSES

One basic assumption has been that one or a very few general principles can account for all of animal learning. A variety of principles have been proposed, but the two dominant ones have been associationism and reinforcement theory.

Rescorla (1985) provides an extremely coherent overview of the associationist approach that is remarkable in the extent to which it agrees, in form, with Lakatos's description of a research program. The central core is the assumption that virtually all learning can be understood as the formation of an association between two events. The associationist approach then attempts to explain the diversity and richness of an animal's knowledge of its world not by hypothesizing a richness and diversity of learning mechanisms, but by weaving a web of auxiliary hypotheses around the central learning mechanism. Rescorla (1985) identifies three types of auxiliary hypotheses that serve this function: the complexity of the conditions that govern the formation of associations, a wide range of elements that can be associated, and multiple mechanisms by which associations can affect behavior. These auxiliary hypotheses have made associationism a powerful force for understanding some aspects of learning in animals, a force that is often underappreciated by those working in other areas.

The central core of reinforcement theory is that behavior can best be understood in terms of the strengthening or weakening effects of reinforcers and punishers on the responses that have preceded them. This was first clearly formulated by Thorndike (1911) and has been elaborated in many ways by others (Herrnstein, 1970; Skinner, 1938). Like associationism, reinforcement theory attempts to account for the richness and diversity of behavior by using a single principle with a web of auxiliary hypotheses. Among these hypotheses are the complexity of the effects of schedules of reinforcement and alterations in the definition of what constitutes a reinforcer. The study of reinforcement has made many important contributions to our understanding of learning.

Although associationism and reinforcement theory have proved to be powerful concepts, they have often been overemphasized. There are too many phenomena they cannot easily account for, including those studied by many cognitive animal psychologists and those beginning to be revealed by naturalistic studies of intelligence. The learning of associations between events and the effects of reinforcement must be investigated as part of any study of animal learning and intelligence. But these two principles in themselves cannot completely account for how animals adapt their behavior on the basis of experience.

RADICAL BEHAVIORISM

Two kinds of behaviorism need to be distinguished. Methodological behaviorism simply recognizes that behavior is what we must measure in experiments. Its central tenet is that all the mechanisms we may theorize about are known to us only through behavior.

Radical behaviorism goes beyond stating that it is behavior we seek to understand. According to the radical behaviorist, any theoretical constructs, especially about cognitive structures animals may possess, are not just unnecessary, but dangerous (Skinner, 1977); behavior can best be understood in terms of the functions that relate stimulus events to responses.

Radical behaviorism has been unremitting in its concentration on the similarities between species. For example, an often-quoted comment of Skinner's (1959) accompanies the cumulative records from several species: "Pigeon, rat, monkey, which is which? It doesn't matter . . . once you have allowed for differences in the ways in which they make contact with the environment, and in the ways in which they act upon the environment, what remains of their behavior shows astonishingly similar properties" (pp. 374–375).

The interesting aspect of this quotation is that it acknowledges the existence of differences between species but relegates them to the realm of the uninteresting. It provides a clear case of Lakatos's (1974) concept of a negative heuristic, directing research away from certain topics. For the synthetic approach, these differences are of interest. If they had been of more interest to the radical behaviorist, phenomena such as autoshaping and instinctive drift (see below) would have come as less of a surprise.

Another problem with the radical behaviorist position has been that it tends to be radically environmentalistic, regarding the organism as a tabula rasa upon which experience writes. This emphasis ignores the potential importance of the effects of genetics and evolutionary history. The emerging current view, particularly apparent in the cognitive approach to animal learning, is that organisms bring certain processes, such as attention and memory, to bear on problems. This in turn has serious implications for evolutionary analyses of animal intelligence.

COMPARATIVE GENERALITY

Another traditional assumption has been that the basic properties of animal learning are the same in a wide variety of organisms, which has justified the use of relatively few species in animal learning research. The logic underlying this assumption may have been that many of the psychologists studying animal learning were not primarily interested in the species they studied, but were using these species as convenient substitutes for humans. Therefore the only learning processes of real interest were those that could be generalized to our own species. This is a coherent, sensible approach, but it suffers from a basic flaw. The animals under investigation are biological entities, with their own evolutionary history. The way that evolutionary history might influence the outcome of learning experiments was not considered by most psychologists.

As reviewed below, there are special and substantial logical and methodological problems confronting the comparative analysis of learning and intelligence in animals. But to assume the absence of such differences, or at least their relative unimportance, has some major drawbacks because it places the study of learning outside the realm of modern evolutionary theory. Suppose there are, in fact, no important differences in the processes of learning among a wide variety of species—say, all vertebrates. This would imply that learning plays no adaptive role at all for vertebrates. Indeed, a number of ethologists (e.g., Lorenz, 1965) and psychologists (Boice, 1977; Lockard, 1971) have suggested that learning is relatively unimportant to animals in their natural environments. But more recent data have clearly demonstrated that learning and memory do function in crucial ways for foraging animals (Kamil, Krebs, & Pulliam, 1987; Kamil & Sargent, 1981; Shettleworth,

1984) and animals in social situations (Cheney, Seyfarth, & Smuts, 1986; Kummer, 1982). As is explained in more detail below, evidence for the functional significance of learning is evidence that there must be significant variation in intelligence between species.

EMPTY METHODOLOGICAL SOPHISTICATION

Bolles (1985a) suggested that an angry god put a terrible curse on psychology: "You will never discover anything about underlying causal processes, and you will never ever understand the overlying functional significance of anything. You will be forever doomed to be methodologists. You will content yourselves with teaching each other how to do experiments, and you will never know what they mean" (p. 137). According to Bolles, because of this curse psychologists have become more caught up with their procedures than with the animals they study.

Another way to express this problem is to say that psychologists have concentrated disproportionately on internal validity and ignored the issue of external validity. Internal validity refers to the internal logic of the experiment, including factors such as the absence of confounding conditions and the adequacy of controls. External validity refers to the extent to which the results of laboratory studies can be generalized beyond the laboratory situation. When one designs a single experiment, there tends to be a trade-off between internal and external validity. Well-designed and well-controlled experiments are generally carried out under highly artificial or constrained conditions, which limits external validity. But at some point, any area of scientific endeavor must be concerned with the issue of external validity.

For example, consider the study of language acquisition by children. At one time this field was dominated by laboratory research in highly constrained situations and theoretical work on transformational grammars. But at some point researchers began to ask whether the ideas developing from this laboratory work could deal accurately with the actual process of language acquisition as it occurs in normal circumstances. This in turn led to many naturalistic studies of language acquisition, whose results have had a large impact on theoretical ideas and laboratory research (Gardner, 1978).

The only external referent for animal learning research has been ap-

plied research with humans and animals. The applied work with animals immediately suggested problems (Breland & Breland, 1961), but they were largely ignored. The applied work with humans has had some success, but this too has been limited (Schwartz, 1984). What we need are additional external referents against which to judge the generality and importance of the information we have gained about animal learning and intelligence. As we shall see below, the absence of external criteria has caused particularly serious problems for comparative analyses of animal learning.

In summary, then, there are several problems with the traditional approach: a concentration on just a few general processes, with the possible elimination from consideration of many others; a concentration on behavior, ignoring the processes with which animals are endowed; the lack of an evolutionary, comparative framework; and the lack of substantial measures of external validity. These problems with the traditional approach have had particularly serious implications for the comparative analysis of learning and intelligence.

The Comparative Analysis of Intelligence

The traditional psychological approach to animal learning has largely ignored comparative questions, concentrating research on just a few species. This tendency has been documented and criticized many times over the past 35 to 40 years (Beach, 1950; Bitterman, 1960). Despite this, most learning research in psychology is still conducted with just a few species. Why has this criticism had so little effect?

One reason is the commitment to general processes. The assumption has been that just a few general processes can explain most learning in many species. If that were true, there would be no reason not to concentrate on a few available species. And of course the general principles of association and reinforcement have been demonstrated (but not studied in depth) in a wide range of species. One must wonder, however, to what extent the emphasis on general process has restricted the view of the animal learning psychologist.

Another important reason for the lack of comparative work among traditional animal learning psychologists is the substantial methodological and theoretical problems presented by any comparative analysis of

learning. The major methodological problem involves the difficulty of measuring species differences in learning because of the learning/performance distinction. The major theoretical problem is due to the logical status of the so-called mechanisms of learning.

THE LEARNING-PERFORMANCE DISTINCTION

As Bitterman (1960, 1965) has so clearly articulated, the performance of a species in a particular situation is a joint function of its abilities and the particulars of the task presented. Thus the failure of a species (or an individual) to perform well on a particular test does not necessarily mean the species lacks the ability for which it is supposedly being tested. Rather, it may be that the situation is in some way inappropriate. A species may fail to solve a problem, for example, not because it is incapable of solution in a general way, but because the experiment was improperly conducted. In Bitterman's terms, some contextual variable, such as motivational level or response requirement, may have been inappropriate.

Bitterman's (1965) solution to this problem is "control by systematic variation," in which one systematically varies the contextual variables in an attempt to find a situation in which the species will perform well on the task. So, for example, one might vary motivational level, the intensity and nature of the stimuli, the response required, and so on. The problem, of course, is that control by systematic variation can never prove that a species difference exists. It is impossible to prove that there are no circumstances in which a species will learn a particular type of problem. Some untested combination of variables may produce positive results in the future.

This leaves a curious asymmetry in the interpretation of comparative-learning research. The meaning of similar results with different species is supposedly clear: the species do not differ in the learning ability being tested. The meaning of different results with different species is never clear. No matter how many failed attempts there have been, the skeptic can always claim, with impeccable logic, that the apparent difference may be due to something other than a species difference in learning abilities.

"MECHANISMS" OF LEARNING

The second problem that presents substantial challenges to the comparative analysis of intelligence is the logical status of what are commonly called the "mechanisms" of learning. In normal language a mechanism is machinery, like gears in a clock. The machinery is physical and can be observed directly. In comparative anatomy and physiology the mechanisms are also physical; respiration has a physically observable and measurable basis in trachea, lungs, and hemoglobin. In principle, learning mechanisms also have a physical basis in the brain. But that physical basis is as yet unknown in any detail, especially for more complex forms of learning. In any case, the way psychologists define learning (or cognitive) mechanisms is independent of the physical basis of these mechanisms.

The "mechanisms" of learning are known in terms of input-output relationships. That is, models are constructed that accurately predict output, behavior, from the input, previous experience. A successful model is then called a learning mechanism. The things we call learning mechanisms are not really mechanisms at all but hypothetical constructs, models that accurately predict behavior. What does it mean to say that the same hypothetical construct correctly predicts learning in two different species?

It certainly does not mean that the mechanisms of learning, in the physical sense, are identical in the two species. It is instructive, in this context, to look at an example from comparative physiology. There is considerable variety in the physical mechanisms of respiration, even among air-breathing vertebrates. The mechanisms (e.g., the lungs) are not inferred, they are directly observable. It is hard to imagine comparative physiologists arguing much about whether the differences between bird and mammal lungs are quantitative or qualitative, or whether we should use one mathematical model with changeable parameters or two different mathematical models. The differences are there to be directly observed and measured. In other words, some of the arguments about comparative interpretation of possible species differences in learning have their origin in the hypothetical nature of learning "mechanisms," not in the logic of comparative analysis per se.

Given the hypothetical nature of mechanisms of animal learning or intelligence, one of the central arguments of the traditional approach, that of qualitative versus quantitative differences, will often be impos-

sible to resolve, and it misses the point in any case. For example, consider the argument over long-delay taste-aversion learning. Baron, Kaufman, and Fazzini (1969) have shown that as the delay between a bar press and a shock increases from 0 to 60 sec, the extent of suppression of bar pressing decreases. Andrews and Braveman (1975) have shown that as the delay between saccharin consumption and poisoning increases from a few minutes to 25 hours, the suppression of saccharin intake decreases. In describing these results, Mazur (1986) concludes that they "do not require the postulation of a different law to replace the principle of contiguity; they merely require the use of different numbers in describing the relationship between contiguity and learning" (p. 228). Although this statement is literally true—a single model can describe both sets of results with a change in parameter value—what does the word "merely" imply?

Clearly, it implies that the difference is "only" quantitative and therefore not of much interest (to Mazur). But how large does a quantitative difference have to be before it can escape the description "merely"? A difference between seconds and hours is a difference of more than a thousandfold. As Bolles (1985a) points out, a thousandfold difference in a biological system is never just quantitative. One can find

> on the skeletons of some snakes little bumps on certain vertebrae where the legs might be if the snake had legs. They are pelvic bumps, and it is my understanding that these bumps may be 1 or 2 mm in size . . . although a 1- or 2-mm leg is not much of a leg, it is actually about 1/1000th of the length of the legs of a race horse. So the difference in legs between a snake and a race horse is really only a matter of degree. (p. 393)

From a biological point of view, it does not matter whether one chooses to call the differences between taste-aversion learning and bar-press suppression qualitative or quantitative. The difference can be accounted for by postulating a single "mechanism" with a parameter or two whose values can be changed to accommodate the temporal differences. It can also be accounted for by postulating two "mechanisms." What matters is that there are differences, and these raise a large number of issues that need empirical attention. Since these issues are primarily evolutionary and functional in nature, the traditional approach is not likely to pursue them.

An analogy that may be useful in thinking about this problem is to

compare learning mechanisms to computer programs. Suppose one were given two programs that solved arithmetic problems in compiled form, so that the programs could not be listed. How would one go about determining whether these programs were based on the same underlying algorithms? One would have to study the input-output relationships—give each program a set of standard problems and compare the speed and accuracy with which they solved the different problems. If the results for both programs were identical, it would seem highly likely that the programs were the same, although one could not be positive. Perhaps some other arithmetic test would produce results that were different for the two programs.

What would happen if the programs differed in some systematic way? For example, suppose that one program always took longer than the other, but only when division was involved. One would naturally be led to conclude that the programs used different algorithms for division. But wait! A theorist could claim that the difference was only quantitative—perhaps the slower program used the same algorithm but had a pause statement added to its division subroutine.

No analogy should be pushed too far. But my general point is that it would be very hard to know with certainty whether the two programs used the same algorithm. Furthermore, it would probably be impossible to tell the "evolutionary" relationship between the programs—whether they had been independently written or one had led to the other. This, of course, is the problem of homology versus analogy in the evolutionary study of traits.

There is one final point to milk from this analogy. One approach to the problem of comparing the two programs would be to attempt measurement at the molecular level and measure the activities of the microprocessor itself. Thinking about this brings out some interesting implications for the relationship between behavioral mechanisms and the physical processes instantiating them. At one level the mechanism for the two programs would be identical—the same processor, and so on, would be involved, even if the programs were written in different languages. But I am sure suitable measurements could be made that would reveal any difference. This suggests that knowledge of the events in the central nervous system that underlie the intellectual capacities of animals will be useful in understanding these processes. But it will have to be information of a certain type. I suspect it will be a long time before the neuroanatomy and neurophysiology underlying the complex pro-

cesses involved in animal intelligence are understood at all. Behavioral work needs to proceed. The issues are too important to wait on the assumption that the physiological level of analysis will eventually solve these problems. In addition, without good understanding of the way mental processes function at the behavioral level, it is unlikely that physiological work can succeed (Kamil, 1987).

The Null Hypothesis

Many of the problems that the traditional approach encounters in the comparative realm can be seen quite clearly by examining the methods and conclusions of Macphail (1982, 1985), who conducted an extensive critical survey of the literature on the comparative study of learning in vertebrates. His conclusion was that there was no compelling reason to reject the null hypothesis "that there are no differences, either quantitative or qualitative, among the mechanisms of intelligence of non-human vertebrates" (Macphail, 1982, p. 330), and he has reaffirmed this more recently (1985). How does Macphail reach this conclusion?

One approach to this question would be to take each of the phenomena Macphail examined and decide how plausible his conclusions are. However, that would probably take a book as long as his. In any event, I want to raise a more crucial point. Does Macphail's basic approach to the comparative study of vertebrate intelligence have some basic flaw (or flaws) that calls his conclusion into question? One can argue that his logic forced the final conclusion.

The first problem with Macphail's analysis is his definition of intelligence. In his opening chapter, he avoids any explicit definition. In particular, he states that it would be best to leave open the question "whether intelligence is some unitary capacity, or better seen as a complex of capacities, each of which might be independent of the others" (1982, p. 4). Macphail says that a decision about this issue might bias his review. However, his review is in fact biased toward the unitary view. For example, in discussing the results of a comparative research program on reversal learning in birds conducted by Gossette and his associates (Gossette, 1967; Gossette, Gossette, & Inman, 1966), Macphail dismisses their findings. The reason for the dismissal is that different patterns of reversal learning between species were found with spatial and nonspatial cues. Macphail states, "If the ordering of species in serial rever-

sal performance can be changed by altering the relevant dimension, it seems clear that serial reversal in itself cannot give a reliable measure of general intelligence" (Macphail, 1982, p. 223) In the concluding discussion of his last chapter, Macphail talks extensively in terms of general intelligence.

A second contributor to Macphail's conclusion is an extreme willingness to believe in the untested intellectual capacities of animals. If some apparently complex learning ability has been demonstrated in two distantly related species, Macphail is willing to assume it can be found in all species. For example, win-stay, lose-shift learning in object-discrimination learning set is best tested by looking for transfer from object-reversal learning to learning set. This phenomenon has been demonstrated in relatively few species (blue jays—Kamil, Jones, Pietrewicz, & Mauldin, 1977; rhesus monkeys—Warren, 1966; chimpanzees—Schusterman, 1962), and tests for such transfer have failed in at least two cases (cats—Warren, 1966; squirrel monkeys—Ricciardi & Treichler, 1970). The failure with cats is dismissed as apparently due to contextual variables, the failure with squirrel monkeys is not cited. The major implication of the discussion is that though most species have not been tested, they would show the phenomenon.

Another, perhaps more egregious example, is drawn from Macphail's (1985) discussion of languagelike behavior. Such behavior has been demonstrated in some primates using sign language or artificial language (e.g., Gardner & Gardner, 1969; Rumbaugh, 1977). Pepperberg (1981, 1983) has recently demonstrated similar behavior in an African gray parrot using "speech." Although the parrot has not achieved the level of performance shown by the primates (at least not yet), he has demonstrated capacities beyond what anyone (except Pepperberg) might have expected. Macphail (1985) concludes by saying, "As the single avian subject yet exposed to an appropriate training schedule, he [the parrot] gives good support to the view that the parrot's talent for language acquisition may not be significantly different from the ape's" (Macphail, 1985, p. 48). Macphail seems to be implying that the same would be true of every vertebrate species if only suitable testing procedures could be devised. This exceptional willingness to assume that species possess abilities for which they have not even been tested stands in marked contrast to Macphail's extreme unwillingness to accept apparent species differences that have been revealed.

The most important reason for Macphail's conclusion of no species

differences among vertebrates in learning or intelligence is his extensive use of the contextual stimulus argument (Bitterman, 1960, 1965). As discussed above, whenever an explicit comparison of two species in the same learning task turns up differences, one can always argue that they reflect some performance factor (the effects of a contextual variable) rather than a difference in intelligence. Proving that there is no set of circumstances in which an animal can learn a particular task (e.g., that frogs cannot acquire language-like behavior) is impossible.

Thus Macphail's argument leaves us with two competing null hypotheses. One is the null hypothesis of no differences in intelligence among vertebrates. Macphail holds that this null hypothesis should be maintained unless clear, convincing evidence against it is obtained. But clear convincing evidence must prove the second null hypothesis that no contextual variable is responsible for the proposed species differences. This logic essentially makes it impossible ever to demonstrate that there are species differences in intelligence.

Macphail would probably say I have overstated his argument. He does not require absolute proof of the second null hypothesis through systematic variation, only some reasonable attempt at evaluating contextual variables. But who is to determine what constitutes reasonable? In fact, the problem of contextual variables can never be completely dealt with through control by systematic variation.

Macphail has performed a valuable service. His arguments have clearly demonstrated that the traditional approach to the comparative study of learning can never succeed. One can never be certain that a species lacks a particular learning ability. This lesson applies not just to the study of learning, narrowly defined, but to the study of animal intelligence in general. An alternative approach that avoids the problem of contextual variables must be found. As described later in this chapter, there are compelling biological reasons to believe that species differences in intelligence do exist. Given that Macphail's approach can never successfully demonstrate such differences, it is crucial to find an alternative approach that avoids the problem of contextual variables.

The Synthetic Approach to Animal Intelligence

In this section I will outline an alternative approach to the study of the mental capacities of animals. I have labeled this the synthetic approach

because it represents an attempt to synthesize the approaches of psychologists and organismic biologists. The synthetic approach has three major aspects: (1) a broad definition of the phenomena of interest; (2) a comparative, evolutionary orientation; which leads to (3) an emphasis upon the importance of studying learning and its effects both in the laboratory and in the natural environment of the species being studied.

BROAD DEFINITION OF THE PHENOMENA OF INTEREST

Using the term animal intelligence is a calculated gamble. It has the substantial advantages of communicating the general topic of interest to a wide audience in many different fields and of emphasizing the broad range of phenomena to be included. But it also carries a substantial disadvantage. It is a term that has been used and abused in many ways in the past. When technical discussion begins, then, there is a risk of misunderstanding based on people's assuming different definitions of animal intelligence.

I want to be explicit about the definition of animal intelligence I am using. The synthetic approach defines animal intelligence as those processes by which animals obtain and retain information about their environments and use that information to make behavioral decisions. Several characteristics of this definition need to be emphasized.

First of all, this is a broad definition. It includes all processes that are involved in any situation where animals change their behavior on the basis of experience. It encompasses the processes studied with traditional methods such as operant and classical conditioning. It also includes processes such as memory and selective attention, which animal cognitive psychologists study (Roitblat, 1986). It includes processes involved in complex learning of all sorts, including that demonstrated in social situations. It also includes the study of more "specialized" learning, such as song learning and imprinting.

Second, the definition emphasizes the information-processing and decision-making view of animals. This makes it very consistent with the approach of animal cognitive psychologists. It also makes the synthetic approach consistent with behavioral ecology (Krebs & Davies, 1978, 1984), which emphasizes the adaptive significance of the behavioral decisions of animals.

Third, this definition assumes that animal intelligence is multidimensional, not unidimensional, in accordance with recent thinking about human intelligence (Gardner, 1982). It also prohibits any simple ordering of species in terms of general intelligence. Species that are very good at some problems may be bad at others.

Fourth, this definition offers the possibility of conceptually integrating environmental and genetic influences on behavior, thus avoiding the nature/nurture controversy. It is generally recognized that no behavior is determined completely by either genetic or environmental variables alone. However, this realization does not seem to have had much effect on animal learning research in psychology, which still tends to ignore the idea that the learning abilities of animals are part of their biological heritage. The synthetic approach regards learned behavior as the result of experience. But these effects of experience are determined by the intellectual capacities of the organism, which in turn depend upon the expression of genetically and ontogenetically determined abilities.

This focus on processes instantiating behavior obviously entails rejecting most types of behaviorism, but not methodological behaviorism. The primary way to learn about these processes is by studying behavior. There is no desire to throw away the considerable methodological sophistication that has been developed over the past century, only to redirect that sophistication.

COMPARATIVE, EVOLUTIONARY ORIENTATION

There has been considerable disagreement and confusion about the importance, role, and purpose of comparative research on animal learning. Some have viewed animal learning research as primarily a way of understanding basic mechanisms that would, at least in the long run, lead to fuller (or even complete) understanding of our own species. For these scientists, comparative research has been relatively unimportant. Others have viewed comparative research as important but have adopted approaches in conflict with evolutionary theory (Hodos & Campbell, 1969). For example, Yarczower and Hazlett (1977) have argued in favor of anagenesis, the linear ranking of species on a trait. But given the complexity of relationships among existing species, it is hard to see how such linear ranking would be useful, though it is possible.

The synthetic approach adopts a view of comparative research on an-

imal intelligence that is based upon modern evolutionary theory. The essence of the approach is to assume that the various processes composing animal intelligence have adaptive effects and to use this assumption as a starting point for research, particularly comparative work. In this framework the goal of research is to develop a full understanding of animal intelligence at all relevant levels of explanation, including developmental, mechanistic, physiological, phylogenetic, and ecological levels. For comparative work, this sets the goal of understanding patterns of similarities and differences among species. The evolutionary framework offers several new research strategies for the study of animal intelligence, discussed in the last section of this chapter.

One important implication of the synthetic approach is that both qualitative and quantitative differences between species are of interest. This is important for two reasons. First, the distinction between qualitative and quantitative differences is often a matter of individual judgment. Second, examining the comparative study of morphological traits clearly shows that the distinction between qualitative and quantitative differences is blurred. Understanding qualitative differences, particularly the relationship between qualitative differences and the ecology of the species in question, is a crucial part of developing a full understanding of the phenomena of interest.

For example, consider once more the comparative physiology of respiration. Those writing about the comparative study of learning often use respiration, or some other physiological system, as an analogy that may offer some guidance (e.g., Bolles, 1985a; Revusky, 1985). At some levels the respiratory system is the same in a wide variety of animals. For example, fish, amphibians, reptiles, birds, and mammals all use various hemoglobins to bind oxygen and transport it through the circulatory system. But at other levels respiratory systems differ dramatically. Many amphibians utilize a positive-pressure ventilation system to move air through the lungs. Mammals utilize negative-pressure ventilation in which pressure in the thoracic cavity is slightly lower than atmospheric pressure. Birds, in contrast, have a flow-through lung ventilation system that requires two respiratory cycles for the complete passage of a breath of air. These differences are related to various ecological correlates of the different niches of these organisms (Hainsworth, 1981). Revusky (1985) uses the analogy between learning and respiration to argue for the existence of a general learning process. But the substantial variation in the respiratory systems of different animals

can be used to reach another conclusion: that full understanding requires the analysis of differences among species as well as similarities.

THE EMPHASIS ON BOTH LABORATORY AND FIELD

Because the synthetic approach is evolutionary in orientation, it necessarily views events in the field, under natural conditions, as crucial. That is, it is assumed that the intellectual capacities of animals serve important biological, adaptive functions. Therefore studies of learning, memory, and so on, under natural conditions can throw considerable light upon animal intelligence. In most cases coordinated laboratory and naturalistic research will be the most informative.

This coordinated approach to laboratory and field research on animal intelligence is important for two reasons. First, it addresses the problem of external validity raised earlier. If the principles of animal intelligence derived from laboratory research prove useful in the field, this will increase our confidence that important mechanisms of animal behavior have been successfully identified. Second, it is important for theoretical reasons. Since the synthetic approach depends heavily on identifying the specific ways animal intelligence affects biological success, field research will be necessary. These issues will permeate the rest of this chapter.

THE PLACE OF GENERAL PROCESSES IN THE SYNTHETIC APPROACH

The emphasis on general learning processes has been so pervasive that explicit discussion of their place in the synthetic approach could be valuable. Two extreme views about general processes can be identified (Bitterman, 1975). The extreme general process view is that a single general process is responsible for all learning. The extreme antigeneral process view, perhaps best exemplified by Lockard (1971), holds that there is no generality, that learning in each species is unique.

The synthetic approach views both these positions as too extreme. On the one hand the available evidence, especially the research of Bitterman and his colleagues with honeybees (e.g., Abramson & Bitterman, 1986; Bitterman, Menzel, Fietz, & Schafer, 1983; Couvillon & Bit-

terman, 1984) clearly demonstrates impressive similarity in basic associative learning among diverse species. On the other hand, the demonstration of a general learning process present in many species does not rule out the possibility of important, significant species differences, both qualitative and quantitative.

Assume that animals use a host of processes to obtain environmental information and that some of these are quite general across species, others widespread but less general, and others very limited in distribution. A research program based upon the assumption of general processes would appear successful—general processes would be found. However, the less general processes would remain undiscovered. Furthermore, and more important for any comparative, evolutionary study of animal intelligence, differences among species and the adaptive role of cognitive processes outside the laboratory would remain unknown.

Arguments for Increased Breadth

The synthetic approach calls for two broad changes in the traditional psychological approach to animal learning: increasing the breadth of phenomena being studied, and placing these phenomena in an evolutionary, ecological framework. In this section I will present the arguments for increased breadth.

COGNITIVE PROCESSES IN ANIMALS

Perhaps the greatest challenge to the traditional approach from within psychology has been the emergence of the cognitive approach to animal learning. This development has been thoroughly documented in a number of publications (Hulse et al., 1978; Riley, Brown, & Yoerg, 1986; Roitblat, 1986; Roitblat et al., 1984). The cognitive approach emphasizes the internal states and processes of animals.

Organisms are assumed to have internal cognitive structures that depend on their individual development as well as their evolution. External objects cannot enter directly into an organism's cognitive system, and so they must be internally encoded—that is, "represented." Accordingly, much cognitive research involves techniques for studying the representations used by an organism, the processes that produce,

maintain, and operate on them, and the environmental and situational factors that affect them (Roitblat et al., 1984, p. 2).

One important area of cognitive research focuses upon the "memory codes" animals use. For example, in a symbolic matching-to-sample task, the animal is first presented briefly with a single stimulus, the sample. Then it is presented with an array of test stimuli. Choice of one of the test stimuli will be reinforced. Which stimulus is correct depends upon which sample stimulus was previously presented. There are at least two ways the animal could code the sample information: retrospectively, by remembering the sample itself, or prospectively, by remembering which test stimulus would be correct. Roitblat (1980) found that errors tended to be directed toward test stimuli resembling the to-be-correct test stimulus, implying a prospective code. Cook, Brown, and Riley (1985) have obtained data in the radial maze implying that rats use both retrospective and prospective memory in this spatial task.

Another cognitive issue that has received a great deal of attention is animals' ability to time the duration of events. One procedure that has been used to study timing is the "peak procedure" of Roberts (1981). On most trials, rats receive food for bar pressing after a signal has been present for a fixed duration. On occasional probe trials, the signal remains on for a much longer period. When the rate of bar pressing on these probe trials is analyzed as a function of time into the trial, the response rate is highest at that point in time when food is usually presented on non-probe trials. The process underlying this ability to gauge time appears to have many of the properties of a stopwatch. For example, the clock can be stopped or reset (Roberts, 1983).

Another cognitive ability that has been extensively studied is counting. The major methodological problem facing research on counting, or sensitivity to numerosity, is how to demonstrate that behavior can be brought under the discriminative control of number and not any of the many other attributes that may correlate with number. Although not every study has addressed this problem, it has long been recognized (Koehler, 1950; Thorpe, 1956). Fernandes and Church (1982) presented rats with sequences of either two or four short sounds. If there were two sounds, the rat was reinforced for pressing a lever on the right. If there were four sounds, the rat was reinforced for pressing the lever on the left. Not only did the rats perform accurately, but they maintained this accuracy when nonnumerical aspects of the sequences, such as stimulus duration and interstimulus intervals, were varied.

Davis and Memmott (1983) demonstrated sensitivity to sequentially presented stimuli with a much different procedure. Rats were trained to respond on a variable-interval food reinforcement schedule until they were responding steadily. They were then exposed to three unsignaled shocks during each session. Responding was initially suppressed, but after some time responding accelerated after the third shock, even though there was considerable variation in when during the session the shocks could occur. For example, in control sessions in which there were only two shocks, one early and one late, there was no acceleration of responding after the second shock, which came near the end of the session.

The existence of cognitive abilities such as counting, timing, and memory coding clearly challenge the traditional approach, especially radical behaviorism. The nature and implications of this challenge have been discussed in many places in the literature (e.g., Roitblat, 1982, and replies; Riley et al., 1986). The cognitive approach is an alternative research program to radical behaviorism and also can be claimed to include associationism, since modern theories of association are very cognitive in nature. Furthermore, as I will discuss below, the various aspects of the cognitive approach fit very well with the synthetic approach, particularly when it comes to comparative, evolutionary issues.

COMPLEX LEARNING IN ANIMALS

The cognitive approach has begun to emphasize more complex forms of animal learning, but many examples of research on complex learning remain to be integrated within the cognitive approach. In some cases these areas of research predate the emergence of the cognitive approach by many years.

One clear example of this is provided by the literature on object-discrimination learning set (Bessemer & Stollnitz, 1971). In an object-discrimination learning set (ODLS) experiment, animals are given a series of discrimination problems to solve. Each problem is defined by the introduction of a new pair of stimuli, one arbitrarily designated as correct. Of main interest is an improvement in the speed of learning new problems, especially above chance choice on the second trial of new problems. Many primate species (Bessemer & Stollnitz, 1971), as well as several avian species (Hunter & Kamil, 1971; Kamil & Hunter, 1969), have

been shown to reach high levels of performance on the second trial of new problems.

The model that best accounts for ODLS performance in primates is a cognitive model. The basic idea is that the animals learn a pattern of choices descriptively labeled "win-stay, lose-shift." That is, on Trial 2 of a new problem, they remember two aspects of what happened on Trial 1: which stimulus was chosen and whether they received reinforcement. Then if they remember reinforcement (win) on Trial 1, they choose the same stimulus on Trial 2. If they remember nonreinforcement (lose) on Trial 1, they shift their choice on Trial 2. The results of many experiments on long-term and short-term memory, on the effects of switching stimuli between Trials 1 and 2, of positive transfer from reversal learning to ODLS, and of stimulus preferences on Trial 1 are all consistent with this model.

Despite this impressive literature, the ODLS phenomenon has been largely ignored by those working on animal learning. It apparently lies outside the realm of phenomena traditional workers are willing to consider. Given the apparent involvement of long- and short-term memory, and strategy learning, it is particularly surprising that animal cognitive psychologists have ignored ODLS.

There are many other examples of complex learning in animals that are generally ignored, in the sense that no consistent attempt has been made to integrate these phenomena into a systematic cognitive-based scheme. These include evidence for categorical learning by pigeons (Herrnstein, 1985), detailed spatial representational systems in a variety of organisms (bees—Gould, 1987; primates—Menzel & Juno, 1982, 1985), and various forms of reasoning in chimpanzees (Gillan, Premack, & Woodruff, 1981).

These phenomena suggest that the cognitive approach needs to be expanded. At least to an outsider like me, it appears that many of the issues of central concern for animal cognitive psychologists originate in procedures used in the past. A good example of this point is provided by research on selective attention in animals. Some psychological work on selective attention has attempted to determine whether attention could account for certain phenomena such as reversal learning (Bitterman, 1969; Mackintosh, 1969). Other research has attempted to demonstrate attention to abstract dimensions, such as color or line orientation in matching to sample tasks (e.g., Zentall, Hogan, & Edwards, 1984). These types of research are very different and perhaps in the long run

less informative than direct attempts to study selective attention and its characteristics. One area in which selective attention and its effects have been examined is research focused upon the detection of cryptic, hard-to-see prey. Selective attention appears to play a substantial role in prey detection (Bond, 1983; Dawkins, 1971a, 1971b; Pietrewicz & Kamil, 1981). Animal cognitive psychology needs to broaden its scope and focus more directly on the information-handling processes of animals, with less focus on the particular issues generated by methodological developments of the past. The broad definition of intelligence offered by the synthetic approach would hasten this process.

EVIDENCE FROM THE FIELD: SOCIAL KNOWLEDGE

The emergence of behavioral ecology in the past 20 years has led to a dramatic increase in our knowledge of the behavior of individual animals in the field (see Krebs & Davies, 1978, 1984). This literature contains many examples of data demonstrating that animals know a great deal about their environments, especially in two contexts—foraging and social behavior. In this section I discuss some of the data on social relationships. Data on foraging behavior will be reviewed later.

As I indicated at the very beginning of this chapter, many anecdotes based on observations in the field suggest that animals possess considerable knowledge about their world, particularly social interactions. Because anecdotes have generally been regarded as scientifically unacceptable, they are most often unreported. As Kummer (1982) has observed, this is unfortunate. It has left each fieldworker aware only of his or her own observations.

My own experience confirms this. After observing the behavior of "Spot" described at the beginning of this chapter, I filed the incident away and for a long time never discussed it with anyone. One night, with some hesitation, I told the story to a group of fieldworkers. It turned out that another hummingbird researcher had seen a similar incident in another territorial species. Every fieldworker present that evening had stories that suggested animals possess more knowledge of their environment than typically considered by the laboratory researcher.

Although these are only anecdotes and their scientific validity is limited, it is time to take their implications seriously and begin to design experiments to test the implications. For example, Goodall (1986) re-

ports many observations of the chimpanzees at Gombe that indicate these animals are acutely aware of the social relationships of their group. In Goodall's terminology, animals manipulate others and assess others' interactions. Are there any more systematic data to support these implications?

Kummer and his associates have tested some of these ideas in their research program with hamadryas baboons. Hamadryas baboons have a single-male, multiple-female social system in which males "appropriate" females. Kummer, Gotz, and Angst (1974) found that if a male was allowed to watch another male with a female, this inhibited the tendency of the observing male to attempt to take over the female, even if the observing male was dominant to the other male. Something analogous to a concept of "ownership" appears to be present.

Even more intriguing, Bachmann and Kummer (1980) found that male hamadryas baboons assess the relation between another male and a female. They tested twelve baboons, six of each sex. In the first stage they tested all possible different-sex pairs for grooming preference. This allowed the experimenters to construct a hierarchy of preference of each animal for each of the opposite-sexed animals. They then allowed males to watch another pair for 15 minutes. At the end of the 15 minute observation period, they gave the observer a graded set of opportunities to attempt to appropriate the female. They found that the observer assessed the relationship between the male and female he had been observing. The probability of the observer's attempting to appropriate the female depended on the female's preference for the original male. If that preference was weak, appropriation was more likely.

The research program of Cheney and Seyfarth is generating similar kinds of data for vervet monkeys. Cheney and Seyfarth (1980) conducted playback experiments in the field during which the scream of a juvenile was played through a hidden loudspeaker to groups of females that included the juvenile's mother. Mothers responded more strongly to these calls than the other females did. More surprisingly, the other females often responded by looking at the mother before the mother herself had reacted. This indicates that the females recognized the relationships of other females and young.

More recent data indicate that vervets have knowledge about other social relationships. Cheney and Seyfarth (1986) recorded the probability of agonistic encounters between members of a vervet group as a function of recent social interactions. There were two main findings. First, they found that individuals were more likely to behave aggres-

sively toward other group members who had recently fought with their own kin, indicating that they know their own kin. Kin recognition is well known in many species. Second, Cheney and Seyfarth found that individuals were more likely to interact aggressively with others whose close kin had recently fought with their own kin. This indicates that vervet monkeys know about the relationships of other monkeys in their group. This appears to be learned, since monkeys under three years of age did not show the effect. How the relationships are learned is unknown.

Cheney and Seyfarth (1985) have argued that primate intelligence may have evolved primarily to deal with social relationships. Monkeys and apes clearly recognize social relationships and remember recent affiliative and aggressive interactions. But when tested for similar nonsocial knowledge, the monkeys appear surprisingly unresponsive. In various field experiments, vervets failed to respond to signs of predators. Cheney and Seyfarth's (1985) argument seems premature because these experiments on nonsocial knowledge may have failed to produce positive results for many reasons other than the monkeys' lack of knowledge. Nonetheless, their more general point about the importance of cognition in social settings deserves careful attention, not only in primates but in many group-living animals.

CONCLUSIONS

It is clear that a trend toward studying more complex forms of animal learning is well under way. It is important that this trend continue. Many unanticipated intellectual abilities have been revealed, and this implies that there are more waiting to be discovered.

Griffin (1976, 1978) has argued that interspecies communication offers an important tool for investigating the knowledge animals possess about their world. This is certainly true, and it is encouraging to see the technique being used with more species, including not only apes (Savage-Rumbaugh, this volume) but birds (Pepperberg, 1981, 1983), dolphins (Herman, Wolz, & Richards, 1984), and sea lions (Schusterman & Krieger, 1986).

There are two general suggestions about how this search for complex processes in animals should proceed that I would like to make at this point. First, some research should concentrate primarily on what animals know, without worrying too much, for the time being, about how

they acquire the knowledge. For example, the research of Premack and his associates with Sarah, a chimpanzee trained to use plastic symbols as a medium for communication, indicates that Sarah understands many relationships among stimuli. Although this research tells us little about how Sarah acquired this knowledge, it begins to tell us some of the things any complete theory of animal intelligence will have to be able to explain.

Second, it is important to continue to test animals in relatively unconstrained situations. It is quite possible that by restricting attention to experimental situations in which animals had few response alternatives and had to deal only with a few simple stimuli, psychologists have underestimated the abilities of their subjects. For example, the research of Menzel and Juno (1982, 1985) has demonstrated one-trial discrimination learning and extensive long-term memory for the spatial location of many objects in group-living marmosets, in marked contrast to the relatively poor performance of marmosets in more traditional experimental settings (e.g., Miles & Meyer, 1956). The distinguishing features of the procedures of Menzel and Juno (1982, 1985) were probably the lack of constraints on the behavior of the marmosets and the use of knowledge about the natural foraging environment of these marmosets in designing the problems. These two characteristics were probably crucial to making it possible for the animals to demonstrate what they knew about their environment.

Arguments for a More Biological Approach

In this section I will review three areas of research—biological constraints on learning, "specialized" learning, and learning under natural conditions. The results of research in these three areas, considered together, provide convincing evidence that learning must be considered in a biological, evolutionary framework.

BIOLOGICAL CONSTRAINTS ON LEARNING

The phenomena that are usually called biological constraints on learning indicate the intrusion of biological factors into standard, traditional conditioning situations. Breland and Breland (1961) were the first to rec-

ognize the importance of constraints in operant-conditioning situations. They observed what they called instinctive drift, a tendency for "natural behaviors" of animals undergoing operant conditioning to intrude upon and interfere with the emission of the response being reinforced. The Brelands clearly recognized the fundamental importance of their observations, which they viewed as a "demonstration that there are definite weaknesses in the philosophy underlying these [conditioning] techniques" (Breland & Breland, 1961, p. 684). However, their findings had little effect at the time. The later discoveries of taste-aversion learning, autoshaping, and species-specific defense reactions had more impact.

Taste-aversion learning was first reported by Garcia and Koelling (1966). In essence, taste-aversion learning suggests that some stimuli are more associable than others, challenging the often implicit assumption of associationists that stimuli are generally equipotential (Seligman, 1970). These studies show that many animals are more likely to associate intestinal illness with gustatory (or olfactory) stimuli than with external stimuli. Garcia and Koelling (1966) proposed that these results demonstrate that rats may have a genetically coded hypothesis: "The hypothesis of the sick rat, as for many of us under similar circumstances, would be, 'it must have been something I ate.'" (Garcia & Koelling, 1966, p. 124).

The phenomenon of autoshaping was first reported by Brown and Jenkins (1968). Brown and Jenkins found that if they simply illuminated a light behind a pecking key for a few seconds, then presented food, the pigeons began to peck the key even though these pecks had no effect on the presentation of the reinforcer. Although they felt that an appeal to some species-specific disposition was necessary, and though Breland and Breland reported many similar findings in less constrained situations, Brown and Jenkins do not cite the Brelands. The implication that species-specific predispositions affect the key peck has been confirmed. Jenkins and Moore (1973) showed that the topography of the pigeon's key peck depends on the reinforcer used. Mauldin (1981; Kamil & Mauldin, 1987) found that three different passerine species each used species-specific response topologies in an autoshaping situation.

The concept of species-specific defense reactions originated in a seminal paper by Bolles (1970). Bolles argued that many of the results of avoidance-conditioning experiments could best be understood in terms of the innate species-specific responses of the species being tested, such

as fighting and fleeing. The opening sentence of his abstract was, "The prevailing theories of avoidance learning and the procedures that are usually used to study it seem to be totally out of touch with what is known about how animals defend themselves in nature" (Bolles, 1970, p. 32).

I have been brief in describing these developments because there are already so many extensive reviews of biological constraints available in the literature (e.g., Seligman & Hager, 1972; Hinde & Stevenson-Hinde, 1973). And there is still considerable controversy about the extent to which these phenomena require abandoning any of the central assumptions of the traditional approach. For example, Revusky (1985) argues against radical behaviorism but also contends that taste-aversion learning can be encompassed in a general associationist approach (see below).

There can be no doubt that these "biological constraints" on learning demonstrate that the evolutionary history of the species being studied can affect the outcome of a conditioning experiment. Whether the differences between taste-aversion learning and other aversive conditioning are considered qualitative or quantitative, differences that seem most explicable on functional grounds do exist. The form of the response in a Skinner box depends on the natural repertoire of the animal, as do the results of avoidance-learning experiments. However, the impact of these findings on the psychological study of animal learning has been limited.

The very label given to these phenomena, biological constraints on learning, reveals this limited impact. The label implies that there is some general process, learning, that is occasionally constrained by the biology of the organism (Kamil & Yoerg, 1982). Surely a broader view is justified. The animal comes to the learning situation with a set of abilities that determine what behavioral changes will occur. These abilities are part of the animal's biological endowment. (I do not imply that they are completely genetically determined—clearly ontogenetic factors play an important role.) In that case a functional, evolutionary approach is necessary.

"SPECIALIZED" LEARNING

The value of a functional approach to the study of learning can be seen clearly in the literature on specialized learning. Specialized learning ap-

pears in specific biological contexts and plays very specific roles. Examples include song learning, imprinting, and homing/migration. In each of these cases, available data demonstrate that the phenomena in question meet any reasonable definition of learning—changes in behavior based on experience. The data also show important species differences in learning, which can often be related to differences in the natural history of species.

Naturalistic studies of nest and egg recognition by gulls and terns suggest the existence of important differences in learning among closely related species that correlate meaningfully with natural history (Shettleworth, 1984). Royal terns nest in dense colonies where it is difficult to discriminate among nest sites. Their eggs are highly variable in appearance, and they learn to recognize their own eggs. Herring gulls build elaborate nests that are spaced farther apart, and they learn to recognize their nests but not their eggs. By the time the chicks are old enough to wander from the nest, the parents have learned to recognize them (Tinbergen, 1953). Yet another pattern is shown by kittiwakes. These birds nest on cliff ledges, and their chicks do not (cannot) wander from the nest site. Parent kittiwakes recognize only their nest sites and do not discriminate their own eggs or young from those of others (Cullen, 1957).

As Shettleworth (1984) has pointed out, these kinds of differences do not necessarily result from differences in learning *ability*. It may be that all the species have the same ability to learn to recognize their eggs, young, and nest sites, but natural circumstances of the species vary so as to favor one type of learning. For example, kittiwakes might learn to recognize their eggs if their eggs varied as much in appearance as do those of royal terns. The necessary experiments, such as placing eggs that vary in appearance in kittiwake nests, have not been carried out. However, this consideration does not apply to all examples of specialized learning.

In the case of song learning, at least some of the necessary experiments exploring differences in learning abilities have been done. Many male passerine birds sing songs that function both to attract a mate and to defend a territory against other males (Kroodsma, 1982). In many species these songs are acquired through experience. Chaffinches, marsh wrens, white-crowned sparrows, and many other species must hear adult song when young to sing appropriately when mature. In many cases there are "dialects" of birdsong—different versions are observed

in the same species in different geographical areas. The dialect an adult male sings often depends upon which dialect he heard during development.

The findings of Kroodsma and his associates on differences in song learning between eastern and western marsh wrens (currently classified as two subspecies) provide particularly clear evidence on differences in song learning between these two populations of marsh wrens. Kroodsma and Verner (1987) found that the normal repertoire size—the number of different songs sung by a single individual—varied considerably between the two populations. Eastern birds had repertoire sizes of about 30–60 songs while western birds had repertoire sizes of 120–220. While this could represent a difference in learning ability, it could also be the result of differences in early experience. It seems likely that the eastern wrens hear fewer songs when young than do western birds.

Kroodsma and Canady (1985) have performed the experiment necessary to distinguish between these possibilities. They raised eastern and western marsh wrens in identical laboratory environments. All subjects heard 200 tutor songs during development. Eastern birds learned 34–64 different songs, while the western wrens learned 90–113 songs under identical conditions. Furthermore, Kroodsma and Canady (1985) found significant differences in the size of the song-control nuclei in the brains of the two groups. Eastern birds had smaller song-control areas. The differences in song learning ability and neuroanatomy appear to be associated with several ecological differences between the populations, including year-round residency and high population densities in the western population.

Thus the evidence on song learning among passerine birds clearly demonstrates that species differences in ability exist. Many such differences are known, and they appear to correlate with natural history and ecology (Kroodsma, 1983; West & King, 1985). The finding that two subspecies of wrens learn different things from the same experience is particularly noteworthy. There can be important differences in specialized learning among extremely closely related animals. The question is whether such differences can be expected in more general types of learning.

The discussion of general and specific adaptations by Bolles (1985a) provides a good framework for this discussion. He points out that some adaptations are

common, but unrelated, evolutionary adjustments to common circumstances. The phenomenon is called convergence, and color vision is an illustration of it. Full spectrum color vision pops up here and there in the evolutionary tree . . . it appears in some mammals, in most birds, in some fish, and in some of the arthropods. Animals in between are more or less color-blind . . . One way to think of color vision is that it has been discovered or invented several times independently. (p. 394)

Bolles (1985a) contrasts these reversible adaptations with others that apparently are not reversible, such as feathers:

Only birds have feathers. But the feather idea was apparently stupendously successful, because there are no birds without feathers. Once feathers came upon the scene, that was it, all descendants were stuck with feathers. Some birds (e.g., penguins) have funny feathers. . . . [Feathers] may change shape and size and color and waxiness and so on, but evidently if you have feathers you can depend upon all your descendants having feathers. . . . Is associative learning like feathers? Is the ability to learn such a stupendous advantage that once in possession of it, there is no way back? (pp. 394–395)

There can be little doubt that some specialized forms of learning are like color vision. Song learning appears scattered, albeit fairly widely, among passerines, varying significantly in its characteristics. The same may be said of imprinting. But are there forms of learning that are like feathers?

Bolles suggests that associative learning may be like feathers. The similarity in basic conditioning processes among widely different species suggests that this is so. The same argument can be made about the law of effect. The effects of reinforcement have also been demonstrated in many species. However, several points must be made about the analogy between feathers and learning.

First of all, even if some kinds of learning are like feathers, this does not mean there are not important differences between species in the learning. Although all feathers have certain features in common, they also vary. They are different at different stages of a bird's life and on different parts of a bird's body. And there are substantial variations be-

tween avian species. A large part of understanding feathers is under-
standing this variation. We need to examine even the most general kinds
of learning for significant variation. To do so will require knowledge of
the function of learning. I will return to this point later.

Second, even if there are general kinds of learning, this does not nec-
essarily settle the question of homology and analogy. These concepts are
labels for two very different possible evolutionary reasons for similarity
between species. Homology is similarity through common evolutionary
origin or descent. Its counterpart is analogy—similarity despite sepa-
rate evolutionary origin because of similar adaptive pressure (see Atz,
1970, for a discussion of the difficulties of applying these concepts to be-
havior). General forms of learning, unlike feathers, may have arisen two
or more times during evolutionary history. For example, the similarities
Bitterman and his co-workers have found between associative learning
in honeybees and mammals may be the result of analogy, or conver-
gence (Abramson & Bitterman, 1986). It can be argued that the world is
structured in such a way that any learning mechanism that accurately
and efficiently predicted events would have to have certain character-
istics, namely those that associative learning shows. (Dennett, 1975, has
argued that the law of effect must be part of any adequate and complete
psychological theory. This philosophical argument implies that evolu-
tion may have invented the law of effect any number of times.)

Third, it would be premature at this time to attempt to decide wheth-
er any particular kind of learning is general. Biological variation, wheth-
er in general adaptations like feathers or in more specialized adapta-
tions like color vision, requires some understanding of the function of
the trait in question. Variation in feathers and in color vision relates to
adaptive functioning. For example, in the case of color vision one can
hypothesize that honeybees have color vision because they feed from
colorful flowers (and this is exactly what made von Frisch, 1954, so sure
that honeybees did have color vision).

The problem is that in the case of possibly general processes of learn-
ing, we have little idea of their specific functions. One can reasonably
speculate that association learning is useful for an animal because it al-
lows accurate prediction of future events. One can reasonably argue that
the law of effect is useful because it allows the animal to obtain resources
like food or water. But these are very general arguments and do not eas-
ily lead to the selection of particular species for study on ecological
grounds. What is needed is some more definitive and specific idea of

how learning and cognitive processes actually function under natural conditions. Fortunately, for the first time recent developments in behavioral ecology are making data relevant to this problem available in a substantial way.

LEARNING IN THE FIELD

Certain kinds of learning have long been known to occur in the natural world of animals: song learning and imprinting are the outstanding examples. But these are specialized forms of learning. Is there any evidence that the types of learning psychologists have typically been interested in occur outside the laboratory?

Many have maintained that learning in a more general sense is not important to animals under natural conditions (Boice, 1977; Lockard, 1971). This presented a problem to anyone attempting an evolutionary, adaptive approach to learning. If learning is unimportant in the field, why is it so evident in the laboratory? Do animals carry around what Boice called surplusage—unneeded and unnecessary abilities?

The problem appears to have been methodological, at least in part. Learning is much more difficult to observe than is learned behavior. Imagine a bird eating a monarch butterfly and subsequently throwing up. After that experience, it will simply avoid eating monarchs (Brower, 1969). The scientist watching birds would have to see the brief first encounter to understand that later avoidance of monarchs was learned. This raises the second problem. The identification of learning requires documenting changes in the behavior of individuals over time. Until relatively recently, there were very few extended field studies of known or marked individuals. In the past 20 to 30 years such studies have become much more common, thanks in part to the emergence of behavioral ecology. These studies have revealed that animals in their natural environments face many problems that they appear to solve through learning and cognition (see Krebs & Davies, 1978, 1984, for reviews of behavioral ecology; Shettleworth, 1984, for an explicit discussion of the behavioral ecology of learning). For example, bumblebees learn how to handle different flower species and which flowers are most profitable (Heinrich, 1979); nectar-feeding birds remember which flowers they have emptied (Gass & Montgomerie, 1981; Kamil, 1978); food-caching birds remember the locations of their stored food (Kamil & Balda, 1985; Shet-

tleworth & Krebs, 1982) as well as the contents of the caches (Sherry, 1984); and young vervet monkeys learn the social relationships among members of their groups (Cheney & Seyfarth, 1986). In light of the accumulating evidence, it is difficult to conceive of anyone's believing that learning is not important in the natural world of animals outside the laboratory.

In addition to these empirical developments, important theoretical developments in behavioral ecology have emphasized the potential biological importance of learning. A variety of models have shown that if animals are sensitive to many of the features of their environment, they can increase the efficiency of their behavior. For example, the original "diet" selection model of MacArthur and Pianka (1966) assumes that predators know the nutritional value and density of their prey and the time required to handle it. Given that they possess this information and that they can rank prey types in terms of the ratio of nutritional value to handling time, a relatively simple rule can determine which prey types should be eaten whenever encountered and which ones should never be eaten in any given set of circumstances. Although this model has not been completely successful in predicting selection among prey types, it has had considerable success (for recent reviews see Krebs, Stephens, & Sutherland, 1983; Schoener, 1987). Studies stimulated by this model have shown that animals respond adaptively to changes in the density of their prey (e.g., Goss-Custard, 1981; Krebs, Erichsen, Webber, & Charnov, 1977) and learn to rank different prey types as the model predicts (Pulliam, 1980). Other models have similarly predicted learning effects that have been confirmed by subsequent experiments (see Kamil & Roitblat, 1985, for review; see Stephens & Krebs, 1986, for detailed presentation of foraging theory, especially chap. 4).

There can be no doubt that animals use learning to modify their behavior under natural conditions and that such learning can have very important adaptive implications. This is good news for the student of animal learning: the phenomena we have been interested in are biologically significant. However, we must also recognize the implications of this conclusion, the most central being that the study of learning must be placed in a biological context, and we must deal with the thorny problems this outlook raises.

In summary, then, three types of research indicate the need for a biological approach to learning: (1) biological constraints, which clearly

show that the evolutionary history of the species can affect the outcome of conditioning experiments in a variety of ways; (2) studies of specialized learning, which indicate that there can be significant variation in learning mechanisms that correlate with the ecologies of the species being studied; and (3) evidence from behavioral ecology, which shows that general forms of learning are of adaptive significance and may also, therefore, vary in ways that correlate with ecology.

The Implications of an Adaptive Approach to Intelligence

In earlier sections of this chapter, I argued that learning is adaptive and proposed that the synthetic approach should operate under that assumption. This assumption has important comparative implications, primarily that there *must be* significant variation in intelligence among species. Why is this a necessary implication?

Let us return to the feather analogy used by Bolles (1985a). He pointed out that learning might be like feathers—such a stupendously successful adaptation that, once developed, it could not be lost. Some might be tempted to use this analogy to argue that some adaptations are so successful that they simply do not vary significantly among species that possess them. This conclusion is not supported by available evidence on successful adaptations.

Feathers represent an extremely successful adaptation. But not all feathers are the same. Different types of feathers serve different functions and have different structures. Some feathers, such as down, serve as insulation. Other feathers function primarily in flight. Still others, the filoplumes, apparently serve as sensory organs, sensitive to the position of other feathers. Furthermore, within a feather type there can be considerable between species variation in structure between species that is related to special adaptations. For example, the underside of an owl's wings has a velvety pile produced by special processes of the barbules, which reduces the sound of the wings when the owl swoops down on prey. Birds of the open sky have long primary flight feathers best suited to fast, straight flight, whereas woodland birds have shorter primaries that increase maneuverability. Diving birds have overlapping feathers that reduce drag (Lucas & Stettenheim, 1972; Spearman & Hardy, 1985).

The list of functional variations of feathers is extremely long, even without mentioning perhaps the biggest source of variation, the evolution of brightly colored feathers for interspecific display.

The point of this discussion of more than you (or I) ever wanted to know about feathers is that traits with adaptive functions vary between species, in ways that make sense in terms of the ecology and adaptations of the organisms they serve. If animal intelligence is adaptive—and as I have already stated, ample evidence of this is emerging—then intelligence must vary between species. The variation may be qualitative or quantitative; intelligence may consist of a complex of processes. But differences there must be. I cannot think of a single adaptive trait that does not vary in some way between species, often closely related species—the structure of the eye, the forelimb or hind limb, the stomach, the lungs. Why should animal intelligence be any different?

One reason animal intelligence could be different has been proposed by Shettleworth (1982, 1984)—the distinction between function and mechanism. Shettleworth argues that because natural selection selects only among outcomes, not among the processes that produce them, any of a number of different mechanisms may be selected in any given situation. While this is true in global terms, it may well be false when examined in detail. Different mechanisms are unlikely to produce exactly the same outputs. In fact, as long as we are limited to input-output studies of the mechanisms of intelligence, we will classify two mechanisms producing the same results as the same mechanism (as would evolution).

However, as in the computer program example explored earlier, different mechanisms are likely to have different input-output relationships. If the input-output relationships differ, detailed analysis may prove that one mechanism is more functional than the other for problems the species faces. In that case natural selection will favor the more functional mechanism.

Returning to the main argument, my analysis of Macphail's approach to the evolution of intelligence among vertebrates suggests that his analysis is based upon prevailing but unproductive assumptions and definitions. Macphail recognized this possibility when he pointed out that "even the tentative advocacy of [the null] hypothesis is in effect a *reductio ad absurdum* which merely indicates that comparative psychology has followed a systematically incorrect route" (Macphail, 1982, p. 334). That is exactly my contention. The challenge is to devise an alter-

native approach that can be used to investigate the evolution of animal intelligence while avoiding the snares that entangled Macphail and others.

Another potential problem with the literature upon which Macphail's analysis is based must also be noted. It is quite conceivable, perhaps even likely, that some mechanisms of intelligence are widespread throughout broad segments of the animal kingdom while others are not. Indeed, one could argue that the literature on classical conditioning demonstrates that the associationistic mechanisms involved are widespread whereas the literature on song learning, for example, demonstrates narrow distribution of song-learning mechanisms. It may be that the psychological study of animal learning has concentrated upon general mechanisms, ignoring those with more limited distribution. But some of these mechanisms of limited distribution may be more general, across tasks, than very specific forms of learning like song learning. In particular, some more complex forms of learning—so far little studied outside a few primate or avian species—deserve comparative attention (Humphrey, 1976).

Research Strategies

The purpose of this section is to propose a set of research strategies to further our knowledge of animal intelligence. In outlining these strategies I have been guided by the two criticisms of the traditional approach developed earlier: that we know relatively little about the intellectual capacities of animals and that we understand very little about how these capacities function or evolved. I have also sought to develop a set of strategies that will avoid the problems revealed by analysis of Macphail's review of the comparative literature on animal learning.

There are two components to any strategy for studying animal intelligence: selecting the procedures to be used and selecting the species to be studied. These are not unrelated problems. Research will proceed most readily if there is a good match between the task employed and the species under study.

These suggested research strategies originate from several considerations: (1) the characteristics of research that has produced good evidence for complex intelligent processes in animals; (2) the decision-making processes that are being revealed by laboratory and field re-

search in behavioral ecology; and (3) an examination of the biological approach to comparative research.

DEVELOPING A NATURAL HISTORY
OF ANIMAL INTELLIGENCE

One important step to developing a new approach to the comparative study of animal intelligence will be to develop a natural history of animal intelligence. This would consist of a detailed study of intelligence under natural conditions. The focus would be upon the problems animals are faced with in the field and how they use their mental capacities to solve them. In many cases field experiments or laboratory work closely coupled to natural history would be necessary.

I have already referred to many examples of field data that demonstrate or suggest how intelligence is used to solve the problems nature presents to animals. These include timing in hummingbirds, spatial memory in food-storing animals, and knowledge of social relationships in primates. The two major arenas for the operation of animal intelligence are foraging and social behavior. These areas need to be examined much more closely, and in a wider variety of species, from the point of view of the functional significance of animal intelligence.

USING NATURAL HISTORY TO CHOOSE
SPECIES AND DESIGN PROCEDURES

Once the study of natural history has revealed a particular problem that is (or might be) solved by learning in the field, this knowledge can be used to select species for study and to design experimental procedures for testing. This is a strategy ethologists have used with considerable success in studying "specialized" learning such as song learning, imprinting, and migration. There are also a number of examples of this approach dealing with processes that may be more general. These include the detection of cryptic prey (Bond, 1983; Pietrewicz & Kamil, 1981); spatial memory in food-caching parids (Sherry, 1984; Sherry, Krebs, & Cowie, 1981; Shettleworth & Krebs, 1982) and nutcrackers (Balda, 1980; Kamil & Balda, 1985); and pitch perception in starlings (Hulse, Cynx, & Humpal, 1984).

Another approach has been to design experimental situations to test models of natural behavior, particularly optimal foraging models. For example, there have been tests of patch selection (Smith & Sweatman, 1974), within-patch persistence (Cowie, 1977; Kamil & Yoerg, 1985; Kamil, Yoerg & Clements, in press), and collecting food to be brought to a central place (Kacelnik, 1984; Kacelnik & Cuthill, 1987). One problem with some of these studies is that researchers sometimes fail to consider whether the species they choose to study are appropriate for the model they wish to test.

This raises the general point of evaluating ecological validity. It is relatively easy to argue that laboratory tasks should reflect the problems animals normally face in nature. But it is not so easy to judge how well any particular task meets that requirement. The best way to address this issue is to collect laboratory data that can be compared with effects known to occur in the field. For example, when Pietrewicz and I were first developing our procedure for studying cryptic prey detection by training jays to detect cryptic moths in slides, we collected data that could be checked against phenomena known to occur in the field. We found that the moths in the slides were least detectable by the jays when shown in their species-typical body orientation (Pietrewicz & Kamil, 1977). The jays slow their search immediately after finding a moth (unpublished data), a result identical to the "area-restricted search" often observed in the field (Croze, 1970). They also search more slowly when the prey are more cryptic (Getty, Kamil, & Real, 1987; Kamil & Olson, in preparation), an effect also analogous to data collected in the field (Fitzpatrick, 1981). These isomorphisms between laboratory and field mean that when we investigate parameters that cannot be studied under natural conditions, there is some reason to believe the results are applicable to the field.

We hope that adopting this research strategy based upon natural history will have two effects: first, that it will lead to a clearer and fuller understanding of animal intelligence; second, that it will change the focus of research on animal learning and cognition, making it more animal oriented and less process oriented. This will allow greater integration with organismic biology. It will also focus more attention on a crucial evolutionary issue, the adaptive significance of animal intelligence. But it will not solve the problem of contextual stimuli and the difficulty of establishing that species differences in learning or cognition even exist. However, the synthetic approach does suggest some ways around this problem.

USING EXTERNAL CRITERIA TO MAKE
COMPARATIVE PREDICTIONS

One way to minimize the problem of using contextual stimuli as an al-
ternative explanation for species differences is to have some external cri-
terion that predicts differences among a number of species. For exam-
ple, Rumbaugh and Pate (1984) have used an index of encephalization
to predict species differences among seven nonhuman primate species
on a complex learning task. The encephalization index accurately pre-
dicts the performance of the species. Since there are many predictions,
supported in detail by the comparative data, contextual stimuli do not
provide a likely alternative explanation. The probability that contextual
stimuli will produce a ranking of nine species by chance is exceedingly
small. Thus the use of an external criterion to make a priori specific pre-
dictions provides an explicit alternative to the null hypothesis of no spe-
cies differences. If this alternative makes many predictions and these are
supported, then contextual stimuli cannot be taken seriously as an ex-
planation.

Indexes of brain size or encephalization provide one source of exter-
nal predictions. These indexes may be particularly useful for comparing
closely related species, as in Rumbaugh's research program. Natural
history and ecological considerations can provide another source of a
priori predictions of species differences in animal intelligence. If some
animals face specific foraging or social problems that others do not face,
and if learning is used to solve these problems, then a comparative pre-
diction is at least implicit. For example, do food-storing birds have a
greater ability to remember spatial locations than other birds? Are ani-
mals that utilize food resources that are renewed on a strong temporal
schedule, like trap-lining hummingbirds, better at timing? Are animals
that live in stable, long-lasting social groups better able to learn about
social relationships either between themselves and others or among
others?

The key to overcoming the problem posed by contextual variables is
generating multiple predictions about species differences. The ecolog-
ical approach leads to such multiple predictions because of the process-
es of convergence and divergence. Divergence refers to differences be-
tween closely related species owing to differences in their ecologies. The
differences in the beaks of the Galápagos finches are the classic case.

Convergence refers to similarities between distantly related species because of similar ecological pressures and adaptations. For example, nectar feeding has evolved independently among many groups of birds, including the hummingbirds of North and South America, the honey creepers of Hawaii, and the sunbirds of Africa and Asia. Many of these birds have decurved beaks that are well suited to extracting nectar from flowers.

The ways convergence and divergence can be used to generate multiple predictions can be seen by considering a specific example. Suppose one hypothesized that nectar feeders should have particularly good spatial memory (Kamil, 1978) or timing ability (Gill, in press). This hypothesis could be tested by comparing closely related animals, only some of which feed on nectar, such as the Hawaiian honey creepers, which vary enormously in foraging specializations. Any supporting evidence could then be tested with other groups of nectar-feeding birds. It could also be tested by doing comparative research with other groups that include nectar feeders, such as bats.

The strategy of selecting species for study based upon convergence and divergence can be applied to many aspects of animal intelligence. For example, if the social context has been crucial for the evolution of learning, as Cheney and Seyfarth (1985) suggest, then at least some of the phenomena observed in group-living primates should be found in some avian species. Many birds have long life spans spent in stable groups with established genealogies (e.g., Florida scrub jays—Woolfenden & Fitzpatrick, 1984; bee eaters—Emlen, 1981). Some of these groups have been studied for as long as 20 years. The findings reported suggest that these birds may be making judgments of the sort described for primates, but the appropriate data have not been collected. It would be important to collect them.

USING SPECIFIC PROCESSES TO GENERATE MULTIPLE PREDICTIONS

Another way to minimize the interpretive problems posed by contextual variables is to design several experimental procedures, each measuring the same intellectual ability, and test two or more species with all the procedures. The species tested should be chosen with some external

criterion so that specific predictions are made in advance. Then if the results of each of the procedures indicate the same ordering of the species, contextual variables are unlikely to be responsible.

One example of this strategy can be found in ongoing research on spatial memory in Clark's nutcrackers. These birds are known to use spatial memory in recovering their caches (Balda, 1980; Balda, Kamil, & Grim, 1986; Kamil & Balda, 1985). This memory is remarkable in at least two ways: it is long lasting and of large capacity. We have found that nutcrackers perform better than pigeons in an open field analogue of the radial maze (Balda & Kamil, in press). Data collected by Olson (in preparation) indicate that the nutcrackers also perform better than pigeons in a spatial operant task. As data from different settings accumulate and are consistent in showing that nutcrackers remember spatial locations better than pigeons, our confidence that there is a species difference in cognitive ability increases.

Conclusions

In this chapter I have argued for a new, broader approach to studying the evolution of the cognitive capacities of animals. This synthetic approach is based upon several arguments. (1) Data from the natural world of animals as well as from the laboratory clearly show that the intellectual capacities of animals are greater than previously thought. This means that we need to use a broad definition of animal intelligence. (2) The traditional psychological approach to the study of animal learning has been defined too narrowly, and its logic has prevented meaningful comparative, evolutionary analysis. (3) The literature on several phenomena, including constraints on learning and "specialized" learning, indicates that an approach based on research strategies drawn from biology and behavioral ecology can be useful in analyzing the evolution of animal intelligence. (4) As a prerequisite to engaging in a meaning comparative analysis of animal cognition, we must develop hypotheses that make multiple and detailed predictions about species differences in intelligence. Natural history and behavioral ecology are important sources of such hypotheses.

We have a great deal yet to learn about the cognitive abilities of animals. If we adopt a broad approach, using the best of what psychology and biology have to offer, we are most likely to succeed in our efforts to

understand these abilities and their evolution. The next twenty years of research on these problems should be very exciting.

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