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A Comparative-Ecological Approach to the Study of Learning

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The purpose of this chapter is to discuss the effects of a parameter which is present in every learning experiment, but about which we know relatively little—the species being tested. The effects of the species variable have been studied relatively infrequently by animal learning psychologists for at least three reasons. (1) Psychologists have tended to assume that a few general processes will account entirely for most, if not all, of the important phenomena of animal learning in a broad range of species. This assumption has been criticized frequently in recent years (e.g., Seligman, 1970; Seligman & Hager, 1972), but still dominates the field of animal learning. (2) There are serious conceptual problems in attempting to interpret species differences in performance in a learning experiment (Bitterman, 1960, 1965). The basic problem is that if one species performs better than another on a learning task, this does not necessarily represent a species difference in learning ability. It may represent an inadequacy in the design of the experiment for one(or both) species. (3) Psychologists have been without a systematic, biologically sensible method of selecting species for comparative study. As Hodos and Campbell (1969) have pointed out, the psychological view of species has been dominated by the "scala naturae" concept.

The scala naturae concept holds that there is a continuous and linear sequence of species, beginning with the most primitive and culminating in the most complex, man. As Mayr (1982) has discussed, this idea became increasingly untenable as biologists became increasingly familiar with the tremendous diversity of life. Mayr (1982) claims that the scala naturae concept was dealt its final death blow in 1812, when Cuvier "asserted emphatically that there are four distinct phyla of animals . . . and that there was absolutely no connection among them" (pp. 201–202). In any event, there can be no doubt that in clinging to the scala

naturae, psychologists were adapting a wholly incorrect and untenable view of species, and the nature of the differences between species. The major problems associated with the scala naturae are: (1) its failure to recognize the tremendous diversity of life, and (2) its assumption that differences between species can be thought of as unidimensional.

Hodos and Campbell (1969) suggested a sophisticated strategy for attempting to discern the phylogenetic history of a behavioral trait. This strategy is not based on the scala naturae, but on the judicious choice of species for comparisons based on modern ideas of phylogenetic relationship. But this strategy still faces the problems outlined by Bitterman (1960, 1965). It also is not well suited to the investigation of aspects of species differences other than phylogenetic history.

Another important perspective from which to approach the species variable is provided by the concept of adaptation. From this point of view, animals can learn because the ability to learn confers selective advantage upon those animals which possess it. This implies that the characteristics of learning processes have been shaped by the evolutionary process, and that species differences in learning are to be expected. By definition, each species has a unique evolutionary history. To the extent that this history affects learning, species will differ in their response to a learning experiment. Furthermore, inasmuch as learning is seen as an adaptation, the effects of a learning procedure upon a species will depend on how the learning paradigm makes contact with the adaptations and response repertoire of the animal (Johnston, 1981; Kamil, Peters, & Lindstrom, 1982; Kamil & Yoerg, 1982). In this chapter we offer two examples of research which suggest how this facet of learning can be analyzed: the comparison of closely related species and the analysis of the problems animals are required to learn in nature.

AUTOSHAPING IN THREE PASSERINE SPECIES

In the typical autoshaping experiment with avian subjects, a key light is reliably followed by food reinforcement, regardless of the behavior of the bird. Despite the absence of any contingency, the lit key comes to elicit key pecking responses. It has been suggested that during autoshaping the lit key, or trial stimulus, comes to release the same species-specific fixed action patterns as those released by the reinforcer. This view is supported by several experimental results, particularly those of Jenkins and Moore (1973). They found that the topography of the autoshaped key peck response of a pigeon depended upon the reinforcer used. If food was the reinforcer, a *food-type* open-beak peck was used, while if water was the reinforcer, a *water-type* closed beak peck was used.

Another way to test the hypothesis that autoshaped key peck responses are fixed-action patterns would be to autoshape several different avian species whose species-specific pecking responses differed in topography. If autoshaped responses are species-specific, the response topographies of autoshaped key peck

responses of these species would be expected to differ. Mauldin (1981) conducted an extensive autoshaping experiment with three passerine species, blue jays (Cynanocitta cristata), starlings (Sturnus vulgaris) and robins (Turdus migratorius), which provides data to test this hypothesis. These three species were chosen because they vary considerably in the topography of their natural feeding responses (see below), and because each species breeds in the Amherst, MA, area, and was therefore readily available for hand-raising in the laboratory.

Mauldin tested members of each species under two different experimental conditions, positive autoshaping and negative automaintenance. In positive autoshaping, a neutral stimulus is paired with food delivery, as in standard Pavlovian conditioning, but the neutral stimulus is associated with a manipulandum (Brown & Jenkins, 1968). For example, in most autoshaping experiments with birds, the netural stimulus has been a lit pecking key. Even though no response is required for food to be delivered, the birds soon come to peck the key. Even more impressive are the results of negative automaintenance. During negative automaintenance, conditions are exactly the same as those during positive autoshaping, except that if the bird pecks the key, no reinforcement is delivered. The only contingency operating is one that should act against pecking, yet pigeons continue to peck on many trials (Williams & Williams, 1969).

Mauldin also tested each species in three control conditions: trial stimulus only, reinforcement only, and a random control in which both trial stimulus and reinforcement were presented, but the occurrence of each was random with respect to the occurrence of the other. After initial testing under these conditions, each group was transferred to either negative automaintenance (the positive autoshaping group) or to positive autoshaping (all other groups). In general terms, Mauldin found that all three species key pecked during positive autoshaping, that none of the three species showed much key pecking during any of the control conditions, and that all three species showed only low levels of key pecking during negative automaintenance, especially the blue jays. For the purposes of this chapter, we concentrate upon the results of positive autoshaping.

The birds were all taken from the nest at 8–10 days-of-age and hand-raised in the laboratory on a standard diet of Purina turkey starter and myna bird pellets. The birds were 14–26 months-old at the time of the experiment, and had no previous key pecking experience. They were maintained at 80% of their free-feeding weight throughout the experiment.

The apparatus was a modified Lehigh Valley Electronics operant chamber, containing a 33 x 30.5 x 35.5 cm high subject cubicle. All mounting screws in the cubicle were countersunk and puttied, and the cubicle was painted a uniform white. The cubicle was illuminated brightly and evenly by three 120 v. bulbs mounted about a light-diffusing false ceiling. A translucent Lehigh Valley Electronics pecking key was centrally mounted on the intelligence panel, and could be illuminated by a relatively dim 12 v. bulb. The reinforcement magazine was located to the right of the key, and was also illuminated by a 12 v. bulb. A

UF-100 Davis feeder was mounted on top of the chamber, and white noise was provided through a small speaker. A Lehigh Valley Electronics INTERACT computer system controlled all stimulus events and response contingencies, and recorded the data. A Sony video camera and video tape recorder were used to monitor all sessions, and a Beaulieu high speed Super-8 movie camera was used to record selected trials, particularly at asymptote, for each bird.

The birds were habituated to the apparatus, then magazine trained until they met a criterion of retrieving reinforcement (*Tenebrio* larvae) within 4 seconds of delivery on 5 consecutive trials. Once this criterion had been met, each bird received another 30 minutes of testing without reinforcement. Autoshaping began in the next session. Daily autoshaping sessions consisted of 50 trials. Each trial began with illumination of the pecking key with a dim, white light. After 10 seconds, the key went dark and a reinforcement was delivered to the magazine, which was illuminated for 1 second. The intertrial interval averaged 60 seconds, using the schedule values suggested by Fleshler and Hoffman (1962). This training continued until stable levels of responding had been obtained, which required 18–23 sessions.

As shown in Fig. 7.1, all birds acquired the pecking response during autoshaping, but there were species differences in this acquisition. The blue jays began to peck sooner than the other species, but their asymptotic rates were relatively low. The robins pecked at an intermediate level at asymptote. The starlings began pecking relatively late in training, but had the highest asymptotic rates. These differences are interesting, but difficult to interpret. Mauldin (1981) has suggested that they may reflect species differences in foraging behavior and the developmental cycle of the three species. The results correlate with the length of time the young are dependent upon adults for food. Blue jays remain dependent for a month or more, robins for several weeks, and starlings for only 2 to 3 weeks.

The high speed photography revealed that, as expected, there were marked and consistent differences between the species in key peck topography at asymptote (see Fig. 7.2). The blue jays pecked in distinct bouts of several pecks each. Between bouts, the jays moved around the cubicle, maintaining orientation towards the key and magazine area. They pecked the key with two different topographies. Sometimes they pecked upward at the center of the key with a closed beak. At other times, they used a hammering type of peck in which the head and body moved together in a powerful thrust at the key, with the beak wide open and snapped shut at, or just before, contact. This hammering, forceful type of key peck is very similar to that described by Hardy (1961), who observed blue jays using it in the field to open acorns. We have also observed this response when lab-raised blue jays are given items like unhusked sunflower seeds to eat.

In contrast, the robins pecked the key fairly continuously during each trial, with only occasional pauses during which they oriented towards the magazine. Their key peck topography was quite dramatic. Pecks were intiated by a rapid

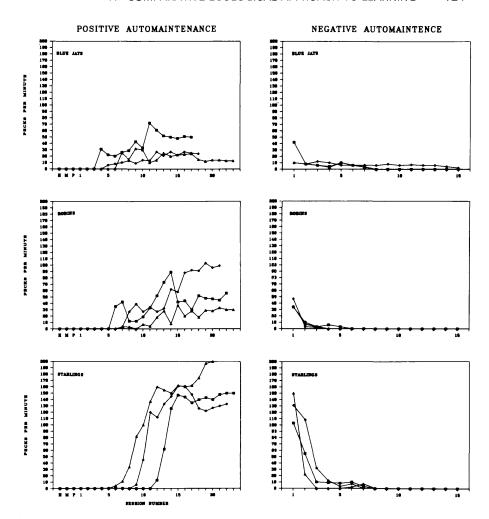


FIGURE 7.1. Rates of key pecking during habituation (H), magazine training (M), postmagazine training (P), and each session of positive automaintenance (FT+) for each of the blue jays (top), robins (middle), and starlings (bottom) tested.

lunge, often accompanied by a wing flap, beginning from a position 5–8 cm away from the key. During this lunge, one or both feet often left the ground. The head was thrust forward with the beak snapped shut. This behavior strongly resembles the behavior of robins grabbing worms on a lawn.

The key peck topography of the starlings was quite different from those of the other two species. The starlings remained very close to the key when it was illuminated, and pecked constantly with a rhythmic motion of the body. In

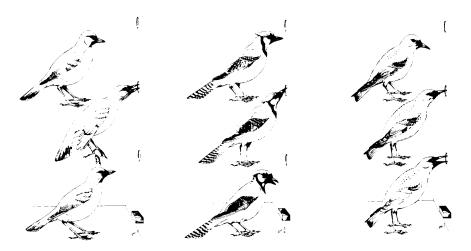


FIGURE 7.2. Typical response topographies of robins (left), blue jays (center), and starlings (right) observed after positive automaintenance. Prepared from high speed movie frames.

essence, they repeatedly leaned towards the key, with minimal body movement. The starlings contacted the key with a closed beak, opened the beak after contact, paused briefly, then leaned back and closed the beak. This topography is very similar to the ''gaping' response pattern which Dunnett (1955) described as typical of this species during virtually all feeding activities in the field.

How should these species differences be interpreted? From one point of view, there is little need to be concerned with them. After all, each species learned to peck the key, and the topographical variations are relatively trivial from a learning theory viewpoint. This argument ignores the differences in the rates of acquisition and of asymptotic pecking. But it still has considerable force, primarily because there is a basic similarity among the species. In spite of these similarities, however, there are differences. How might the topographical differences between species be explained?

A model for the explanation of these differences can be found by looking at how conceptually similar morphological differences are understood by evolutionary biologists. Within many families of birds, particularly insular families that have evolved in geographic isolation, considerable variation in the beak shapes of different species is often observed. One of the most dramatic cases of such variation is found in the family *Drepanididae*, the Hawaiian honey creepers (Berger, 1972). Figure 7.3 shows the beak shapes of three species within this family. This morphological variation is understood in terms of the ecological efficiency of the different beak shapes. As in the case of the Galapagos finches, the beak of each species is well suited to the feeding specializations of each species. The honeycreepers with long, thin, decurved beaks like the liwi (*Ves*-



FIGURE 7.3. The beaks of three Hawaiian honeycreepers, the palila (left), iiwi (center) and akiapolaau (right).

tiaria coccinea) are nectar feeders, and their beaks are well adapted for probing flowers. The honeycreepers with large, stout beaks, such as the palila (*Psittirostra bailleui*) are seed eaters. The unusual beak shape of the akiapolaau (*Hemignathus wilsoni*) is well suited to its woodpecker-like habits. It uses the short, strong lower beak to pound at bark and rotten wood, the long, thinner more flexible upper beak to probe and pry holes for insects (see Berger, 1972).

The variation in beak shapes among the Hawaiian honeycreepers are thus understood, at least in part, as adaptations which function efficiently for the animals. The same type of reasoning can be applied to the variation in key peck topographies observed by Mauldin (1981). In each case, the topography of the key peck observed in the autoshaping paradigm may have been shaped by natural selection so that it is particularly efficient for the feeding strategies of the species. The hammering blow of the blue jay for opening acorns, the leap of the robin for capturing worms, the probing response of the starling for finding insects in loose earth. It can be argued that the outcome of the autoshaping acquisition experiment was determined, at least in part, by the adaptations of the animals being tested.

STAY AND SHIFT LEARNING IN HUMMINGBIRDS

Although the topographical differences observed by Mauldin (1981) are interesting, they may not reflect basic differences in what is learned, and how it is learned. However, several phenomena in the biological constraints literature suggest that the adaptations of the organism may affect learning in other ways. The classic case, of course, is taste-aversion learning (Garcia & Koelling, 1966). However there is a basic problem with much of this literature. In most cases, virtually no hard data are available on the natural behavior patterns of the subject species in nature. This makes the link between laboratory behavior and adaptation highly speculative. In order to study the connections between learning and adaptation, it is necessary to work with species that have been studied intensively under natural conditions. One such group of animals is the nectar feeding birds. In the last 15 years, ecologists have conducted a great deal of field research with

these animals, especially on their foraging behavior (see Pyke, 1981, for review). As a result, the characteristics of the spatiotemporal distribution of their food are well known. If these birds use learning to deal efficiently with these problems, then this information gives us insight into the adaptive function of learning for these animals.

Nectar feeding birds often feed from small flowers which contain very small amounts of nectar, which is quickly depleted and very slowly renewed. Under these conditions, the birds can be most efficient if they avoid revisiting flowers that they have already emptied. Several field studies with individually color marked, territorial birds have found that these birds do, in fact, avoid such revisits not only within foraging bouts, but over longer periods of time (Gass & Montgomerie, 1981; Gill & Wolf, 1977; Kamil, 1978). Some of these data strongly suggest that memory is involved in this avoidance (Kamil, 1978). These findings allow the formulation of several hypotheses about the learning abilities of nectar feeding birds. For example, suppose these birds were given a conditional spatial discrimination problem, in which the conditional cue was a location in which they had recently fed. They would be expected to be able to learn to avoid this location more easily than they could learn to return to it.

This prediction has been tested in a recent experiment by Cole, Hainsworth, Kamil, Mercier, and Wolf (1982). Hummingbirds were placed in a case with two feeding sites at which artificial flowers could be placed. Each trial consisted of two stages, an information stage followed by a choice stage. During the information stage, the hummingbird was presented with a single flower containing a small amount of nectar, and allowed to empty the flower. The position of this single flower varied randomly from trial to trial. The choice stage began 10–12 seconds after the information stage was completed. The bird was presented with two flowers, one at each feeding site. One of these flowers contained nectar, the other did not. If the bird was being trained on stay learning, then the flower containing nectar in the choice stage was in the same position as the single flower presented during the information stage. If the bird was being trained on shift learning, the flower containing nectar was in the other position, and the flower in the same position as that used during the information stage was empty. During the choice stage the bird was allowed to visit (insert its beak into) only one of the flowers. Eight hummingbirds were tested, each receiving both stay and shift training to a criterion of 3 consecutive sessions above 80% correct. Half of the birds received the stay training first, half the shift training first.

The results were very clear (see Table 7.1). In every case, regardless of the order of training, shift learning was much more rapid than stay learning. The slowest shift learning shown by any bird (200 trials, 96 errors) was much quicker than the fastest stay learning (282 trials, 130 errors). Even when shift and stay learning came second, and constituted a reversal, this relationship held. Although the birds in the two conditions began reversal training at almost exactly

TABLE 7.1 Trials and Errors to Criterion of Each Hummingbird during Shift and Stay Learning

Trials to Errors to Criterion Criterion 160 82 180 96 96 42 144 43 (145±17.9) (65.7±13.7)

*Did not reach criterion; this represents a minimum estimate.

the same low levels of percentage correct, shift learning took place much more rapidly than stay learning.

There are several possible explanations for these results. The superiority of shift learning may reflect an acquired bias toward shifting, learned before the birds were captured, although it would have to be a bias maintained through the course of extensive stay training. This superiority may also represent some more basic difference in the manner in which the birds solve the two problems, such as an associative predisposition. Either alternative would be consistent with an adaptive approach. Natural selection acts on the phenotype, affecting the gene pool only indirectly. Any phenotype which resulted in rapid shift learning among specific flower locations would be favored by natural selection, whether based on a response bias, associative predisposition, or some other mechanism. Regardless of the mechanism responsible, it is quite clear that the results of the learning experiment are congruent with naturalistic observations describing the problem these animals actually face in nature.

A recent set of experiments by Wunderle & Martinez (personal communication) indicate that the results of Cole et al. (1982) may have been due to learning by the hummingbirds in the field, before they were captured. Wunderle & Martinez worked with bananaquits (*Coereba flaveola*), small nectarivarous birds of the Caribbean. When they tested bananaquits that had been wild-caught as adults, they replicated the findings of Cole et al. However, when Wunderle & Martinez tested birds that were captured quite young and hand-raised in the laboratory, there were no differences between shift and stay learning. It is possible that hand-raised hummingbirds might show superior shift learning, especially since hummingbirds are more specialized for nectar foraging than bananaquits. But these results clearly show that the implications of the Cole et al. (1982) findings must be interpreted cautiously.

There is an interesting paradox here. If the hummingbird results are due to earlier learning in the field, this would imply no specialization for shift over stay learning at birth. On the other hand, the maintenance of shift learning through prolonged laboratory conditions in which stay responses were regularly rewarded, and shift responses were not rewarded, would provide evidence for the importance of learning under field conditions. If learning is important, why isn't it specialized? The shift learning that may have taken place in the field, before the hummingbirds were captured, may have been unusually resistant to extinction. This raises some interesting developmental questions.

Given the dramatic similarities in learning across species demonstrated in many studies (e.g. Couvillon & Bitterman, 1980), the possibility exists that a major evolutionary question is why learning so often appears to have high phylogenetic inertia? That is, although psychologists have often taken the generality of relatively few learning processes for granted, if learning is relatively insensitive to selective pressures, this needs to be understood. Perhaps an answer can

be found in a detailed analysis of the advantages learning provides an animal in its natural environment.

RESEARCH TACTICS

An adaptation is any morphological or behavioral characteristic that increases the biological fitness of those animals which possess it. The fact that the ability to learn is so widespread in the animal kingdom implies that it must be adaptive. But we have had relatively little specific evidence that demonstrated how learning could contribute to biological fitness. Recent evidence from behavioral ecology, particularly studies of foraging behavior (see Kamil & Yoerg, 1982, for review) and of social behavior (e.g., Mason, 1982), have shown learning at work in specific natural settings. The results of the two experiments described in this paper indicate that adaptations of the subjects in a learning experiment can affect the outcome of that experiment. The time has come to begin the systematic study of learning as an adaptation.

Unfortunately, psychologists are mostly unaware of the research strategies that have been developed to investigate behavior as adaptation. The fields of animal behavior, behavioral ecology, and ethology offer several useful examples of such strategies. A central theme of these overlapping disciplines, particularly behavioral ecology, is the adaptive significance of behavior. These strategies easily could be applied to research on learning. As several recent articles have discussed this approach (e.g., Johnston, 1981; Kamil & Yoerg, 1982; Shettleworth, 1982) the presentation here is brief.

The essence of the adaptive approach is to examine the relationship between the demands of the natural environment of the animal and the characteristics of the animal. Thus, the first step in analyzing a behavioral trait as an adaptation is to obtain detailed information about the ecology of the species under investigation. In the case of learning, it is necessary to know the types of problems animals may solve through learning in their natural environments (the task descriptions of Johnston, 1981). One relevant type of information would be descriptions of how food is systematically distributed in nature, and how individual animals respond to these distributions. Fortunately, field studies of foraging behavior are beginning to provide this kind of information (see Kamil & Yoerg, 1982, for review; Kamil & Sargent, 1981, for many examples). This literature has provided the basis for some psychological learning experiments (e.g., Baum, 1982; Lea, 1979; Pietrewicz & Kamil, 1977, 1979, 1981), and could be utilized much more extensively.

The importance of the expected fit between the organism and its environment cannot be overemphasized. It is central to any ecological, adaptive approach, but is usually ignored by psychologists. The difference between the ecological and

psychological approaches can be seen quite clearly in the different manner in which each field has used the concept of optimization. Within behavioral ecology, optimization theory, such as models of optimal foraging has its roots in the analysis of naturally occurring, well-documented problems. Examples include the patchy distribution of prey (Charnov, 1976), diet selection (MacArthur & Pianka, 1966) or prey crypticity (Hughes, 1979). Mathematical or graphical models of these situations are constructed and solved for their optimum, usually in terms of maximizing net rates of energy intake. These solutions are then used as predictions of behavior. But the models are considered appropriate only for species which actually face these problems in nature.

In contrast, the optimization approach in the operant conditioning literature has viewed the maximization of the rate of reinforcement as a general property of operant behavior (e.g., Shimp, 1969; Rachlin, 1978), which could apply generally across species and situations. For example, consider the recent experiments of Mazur (1981) and Vaughan, Kardish, and Wilson (1981). These two experiments investigated the operant behavior of pigeons on complex schedules in which responses on one alternative increased the probability of reinforcement on the other alternative. Under these conditions, the performance of the pigeons was clearly suboptimal. They obtained many less reinforcements than were available. Most important, perhaps, was the finding that the performance of the pigeons deteriorated with experience on these schedules. As training proceeded, the pigeons obtained fewer and fewer reinforcements.

These experiments are relevant to the operant conditioning version of the optimization theory. Clearly, the maximization of reinforcement rate is not a general principle which governs behavior under all conditions. The fact that the pigeons got worse as training proceeded suggests that even in the face of declining reinforcement rates, the pigeons *could not help themselves*. The rule governing their behavior led to reductions in reinforcement.

But these experiments are irrelevant to ecological optimization theories. The schedules of reinforcement used almost certainly are completely unlike any foraging problem that pigeons, and perhaps any animals, face in nature. To put it baldly, from an ecological perspective, these experiments demonstrate that it is possible for clever human experimenters to fool less clever pigeon subjects. Of course, the cleverness of the experimenters had its origins in knowledge of some of the rules governing choice behavior. The matching law (Herrnstein, 1961) predicted the obtained results.

More substantively, the ecological view of these results might be clearer if they are considered in relation to other learning experiments in which animals performed poorly. Perhaps they are most analogous to observations such as those reported by Breland and Breland (1961) on the "misbehavior of organisms." The Brelands described several operant conditioning situations in which animals achieved very suboptimal rates of reinforcement because of inappropriate behavior patterns. These behavior patterns, which appeared to be species-specific

behaviors elicited by various features of the environment, interfered with the behavior patterns which were being reinforced. The experiments of Mazur (1981) and Vaughan et al. (1982) may reflect the same sort of effect. The schedules used elicited inappropriate behaviors which reduced rates of reinforcement, but in a more subtle manner than in the Breland experiments.

Mazur (1981) concludes that his results "suggest that choice behavior is controlled by *a process* that produces a matching of behavioral outputs to reinforcement inputs, not a process of reinforcement maximization" (p. 825; italics added). This is a reasonable conclusion, at least for the conditions tested in these experiments. But it is not very satisfying without some better knowledge of the nature of the underlying process. Our basic point is that in the case of this research, as in the case of the Breland's work, the source of the nonoptimal behavior resides in the structure of the organism. And the structure of biological organisms must be understood, at least in part, in terms of the adaptations and natural response repertoires of the subjects.

As the hummingbird experiment (Cole et al., 1982) demonstrated, it is possible to use the ecological approach to make a priori predictions about within species differences by beginning from a consideration of adaptation. This approach provides a method for alleviating a major problem with concepts such as preparedness (Seligman, 1970). Seligman proposed that different laws of learning might apply to problems for which animals are well prepared by their biological heritage, as opposed to problems for which they are nonprepared or contraprepared. However, Seligman gave no method for determining a priori what problems would be prepared, nonprepared, or contraprepared. The ecological approach provides such a method, based on a careful, empirical analysis of the natural world of the animal.

Within-species experiments will be more valuable when the different tasks which are compared are similar in structure. This was the case with the hummingbird spatial learning experiment. The stay and shift tasks were virtually identical, with the same discriminative stimulus, and very similar response requirements. This similarity in task structure makes it particularly plain that the differences in the rate of acquisition of the two problems tells us something about the structure of the subjects, due to either genetic or learned predispositions. This advantage can be increased considerably by combining this method of predicting within-species effects with an ecologically based method of selecting species for comparative study. From this perspective, the major weakness of the Cole et al. (1982) experiment was the failure to include a second, nonnectar feeding species for comparative purposes (primarily because there are no species closely related to hummingbirds which do not feed on nectar).

The comparative strategy that follows most directly from an ecological perspective is one based on divergence and convergence. Divergence is the evolution of differences among closely related species due to differences in adaptive pressures. The differences in the beak shapes of the Hawaiian honeycreepers

provide an excellent example. Convergence is the evolution of similarities among unrelated species due to similar adaptive pressures. For example, nectar feeding birds of several different families have very similar beak shapes, even though the nectar feeding specialization evolved independently in each family. When used in conjunction, divergence and convergence provide a method of species selection which allow repeated, independent tests of hypotheses which relate specific characteristics of learning to particular ecological factors.

For example, consider the ecological view of shift and stay learning. In making predictions about how a particular species will perform on these two tasks, we look to the type of food distribution the species faces in nature. The critical dimensions are the ratio of meals to food patch size, the depletability of the patch, and the rate of renewal of the patch. Animals which feed on small, depletable, slowly renewing patches should show fast shift learning. Those who feed on large, nondepletable or very rapidly renewing patches should show fast stay learning. This hypothesis could be evaluated by selecting closely related species which are divergent along these dimensions, and testing each species on both stay and shift learning. The results of this set of experiments could be extended by identifying distantly related species which are convergent on these dimensions and testing them on stay and shift learning. Thus the hypothesis could be tested several times through careful species selection based upon ecological considerations.

This approach to the comparative study of learning will be a difficult one to carry out. It will require research with a broad range of species and the acquisition of detailed information about the ecology of these species. But it offers an excellent chance to escape many of the difficulties of interpreting comparative learning research pointed out by Bitterman (1960, 1965). Two of the specific advantages to this ecologically based approach are: (1) the use of closely related divergent species will minimize the effects of gross differences in morphology and perceptual abilities. Differences between closely related species could be easier to interpret and attribute to specific causes than differences between unrelated species which differ in many ways. (2) Testing each species under two or more conditions, and focusing upon between species differences in the within species effects can avoid many interpretational problems which center around the suitability of the experimental environment for the species being tested. For example, if we had only tested hummingbirds on stay learning and demonstrated slow stay learning, many interpretations would be possible. It could have been argued that some detail of the experimental procedure—motivational level, intertrial interval, response requirements, etc.—was inappropriate for these animals. But the demonstration of rapid shift learning under identical conditions eliminates these arguments (see Kamil & Yoerg, 1982, for further discussion).

Although an ecological approach has distinct advantages, it also faces problems and challenges. One major challenge will be to learn how to put together different levels of explanation into a single, integrated system. Learning psychologists have been interested primarily in mechanism, while the adaptive approach focuses upon function. Natural selection operates on the phenotype; any mechanism which produces an efficient result can be favored. Thus, knowledge of the function of learning in a given situation does not specify the mechanism (Shettleworth, 1982). But the effort to understand the mechanisms of learning will be more successful if it is carried out in the context of knowledge of the adaptive functions of the ability to modify behavior as a result of experience.

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