

Behavior Analysis and Behavioral Ecology: A Synergistic Coupling

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Recent trends in behavioral ecology and behavior analysis suggest that the two disciplines complement one another, underscoring the desirability of an integrated approach to behavior. Three examples from the foraging literature illustrate the potential value of an interdisciplinary approach. For example, a model of natural selection for foraging efficiency—optimal foraging theory—makes several predictions consistent with an hypothesis of a more proximate phenomenon, the reduction in delay to primary reinforcement. Not only are the ecological and behavior analytic approaches to behavior complementary, but each may provide insights into the operation of controlling variables in situations usually thought of as being the other's domain.

The relation of operant conditioning to evolutionary phenomena has received considerable attention (e.g., Fantino & Logan, 1979; Skinner, 1966, 1975, 1984; Staddon, 1983). The present paper will focus on potential advantages to be gained by both behavior analysts and ethologists of incorporating principles and research strategies from one another's domains. It does this in the context of research in foraging which has seen sustained and profitable interactions between biologists and psychologists over the past seven years (e.g., Kamil & Sargent, 1981). I begin by discussing some general points, following which I give three examples from the foraging literature that illustrate the value of an interdisciplinary approach.

Much has been written in recent years about situations in which learning has been shown to be closely tied to biological constraints. Two resultant criticisms of traditional reinforcement theory are (1) that traditional reinforcement theorists assume incorrectly that stimuli, responses, and reinforcers must be associated with one another with equal facility (or "equipotentiality") and (2) that lab-

oratory work on reinforcement theory is "artificial," resulting in behavior principles that lack generality for any natural setting (the problem of "external validity," discussed below; see also Schwartz, 1974). The first criticism is at best only partially valid, as Fantino and Logan (1979) and Logue (1979) have argued. In fact, rather than espouse the principle of equipotentiality, Thorndike, Tolman, and Skinner explicitly disavowed it.

The second criticism, however, is central to efforts extending behavior principles from the operant conditioning laboratory to the domain of organisms foraging in the wild. Consider schedules of reinforcement. These have been shown to be powerful determinants of behavior for many species. They mimic a vital aspect of any organism's environment: accessibility to vital resources. As Fantino and Logan (1979, p. 495) have noted: "The analysis of schedules of reinforcement would seem to have general validity for any organism exhibiting behavioral plasticity, because any natural environment requires the partitioning of both responses and time." Although different patterns of responding may emerge depending on the particular species being studied and on how stimuli, responses, and reinforcers are selected, schedules first need to be studied in arbitrary situations in order to understand how schedules of reinforcement operate in the absence of biological constraints. For instance, if we are interested in the isolated effects of

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timing on responding, we should employ interval schedules in situations as arbitrary as possible. Otherwise, the effects of temporal partitioning may be obscured by demonstrably powerful biological factors. The principles generated by such an analysis must, however, at some point take into account the biological constraints operating more evidently in less arbitrary situations. From this viewpoint, the empirical analysis of schedules of reinforcement is crucial because it may reveal fundamental means by which behavior can be changed by limiting access to essential resources. Moreover, the effects of limiting access to resources may be most clearly assessed under conditions in which the effects of biological factors are minimized.

Recently, the study of reinforcement schedules has been expanded to assess the correspondence of principles generated by behavior analysts with those generated by behavioral ecologists. The correspondence is being addressed in the arena of foraging. Much theoretical work in foraging has focused on the premise that natural selection favors the most economic of alternative foraging patterns (e.g., MacArthur & Pianka, 1966). Optimal foraging theory has been applied to a number of foraging decisions which a predator may make, such as how and where to feed (Pyke, Pulliam, & Charnov, 1977; see Kamil & Sargent, 1981, for a discussion of other theoretical approaches). Although most of the foraging studies have been carried out in the natural environment or in laboratory studies that simulate the field situation, several simulations of foraging have been conducted in the operant laboratory (e.g., Abarca & Fantino, 1982; Collier & Rovee-Collier, 1981; Killeen, Smith, & Hanson, 1981; Lea, 1979). Such studies permit rigorous control of variables in practical, accessible settings and the application of a laboratory technology developed over several decades (e.g., Ferster & Skinner, 1957). Moreover, the experimental analysis of foraging appears to be a ripe area in which to combine the methodologies and assumptions of the

field and the laboratory. It has been hoped that this approach may successfully encourage an interdisciplinary or "integrated" approach to behavior.

The analysis of foraging in the operant laboratory mimics foraging in the field with procedures that have been studied exhaustively. The technology and data base developed in the operant laboratory over the past several decades (e.g., Ferster & Skinner, 1957; Honig, 1966; Honig & Staddon, 1977; Skinner, 1938) may help assess the effects of variables believed to influence foraging in the field. In moving an experiment on foraging from the field into the laboratory, one is using manipulative research in the hope of increasing the internal validity of the conclusions drawn. Altmann (1974) has assessed the relative merits of manipulative versus nonmanipulative research (corresponding very roughly to experimental versus field research). As Fantino and Logan (1979) have noted, this newer usage conveys the understanding that although control is present in the nonmanipulative (observational) situation, naturally occurring controlling variables, rather than artificially manipulated ones, determine behavior. Control is inherent in either situation; manipulative procedures simplify the task of pinpointing the controlling variables. Altmann's comparison of the relative merits of manipulative and nonmanipulative research emphasizes the degree of internal versus external validity associated with each. *Internal validity* refers to the validity of conclusions inferred about changes in the behavior of the sample of organisms on which the research was carried out. *External validity* refers to the validity of generalizations from these internally valid conclusions to some other situation or population. Both internal and external validity are critical to the overall validity of any conclusion. First, if the researcher cannot eliminate alternative explanations of the behavior displayed by the sample under study (low internal validity), generalization to other situations will be irrelevant. Second, a result with high internal validity that does not apply to

the behavior of individuals beyond the immediate sample (low external validity) will not aid in the explanation of naturally occurring behavior.

In other words, while the rigorous control exercised in manipulative research can generate conclusions high in internal validity, when this is done at the cost of overly simplifying a very complex phenomenon, a substantial degree of external validity may be sacrificed. However, while nonmanipulative research, conducted in natural settings, may yield conclusions potentially high in external validity, the frequent inability to eliminate alternative hypotheses may unacceptably lower the internal validity of field research. Clearly, both research strategies have strong and weak points. In each case the methods' weaknesses tend to be imposed by their strengths.

Two caveats are in order. On the one hand, I emphasize that field research often uses experimental manipulation (e.g., Werner, Mittelbach, & Hall, 1981). On the other hand, the results of manipulative laboratory research "are not lacking in external validity when they account for outcomes discovered through nonmanipulative field research" (Mellgren, 1985). Moreover, I emphasize that behavior in the experimental chamber, however unlike behavior in more "natural" settings, is still behavior and, as behavior, is worthy of study. A complete understanding of behavior must surely span the spectrum from the somewhat arbitrary behaviors examined in rigorously controlled settings to the somewhat idiosyncratic species-specific behaviors found in more "natural" settings.

As should be evident, I have some misgivings about "natural" settings. In particular, I am not always sure about what is "natural" and what is not. Some psychologists, for example, have suggested that closed economies provide more natural settings than open economies. On a closed economy (as defined by Hursh, 1980, and studied by many, including Collier & Rovee-Collier, 1981; Rachlin, Battalio, Kagel, & Green, 1981; Rashotte, O'Connell, & Beidler, 1982), sub-

jects earn all of their food in the experimental chamber. On an open economy, however, food is also provided outside the experimental chamber in order to maintain subjects at a particular deprivation level. Open economies have been used for decades in literally hundreds, probably thousands, of conditioning studies. Collier (1982) has pointed out, however, that these studies assess behavioral principles while subjects are pursuing an "emergency strategy" of feeding brought on by the unnatural degree of deprivation. Collier's points are well taken and the reader unfamiliar with them would do well to consult his and Rovee-Collier's recent papers (e.g., Collier & Rovee-Collier, 1981, 1983). It is not always clear, however, that a particular closed economy is necessarily more appropriate than a particular open economy. As Fantino and Abarca (1985) have put it: "Are pigeons in the wild truly in a closed economy allowing unlimited food . . . ? The subject at 100% free-feeding body weight with access to food 24 hours per day may be more of a laboratory creation than a natural one. In any event, the problem of economic context is an important one . . . which underscores the difficulties in arriving at satisfactory analogues between laboratory and wild."

INTERDISCIPLINARY ADVANCES: THREE EXAMPLES

Fantino and Logan (1979) ended their book with a call for more interdisciplinary research by ethologists, behavioral ecologists, and operant psychologists, noting that foraging was a natural area in which interests, theories, and methodologies of these diverse disciplines might complement one another profitably. In the subsequent six years, the degrees of interdisciplinary activity and interest in foraging have exceeded what could have been anticipated. Several foraging conferences, with strong interdisciplinary representation have taken place (e.g., Commons, Kacelnik, & Shettleworth, in press; Kamil, Krebs, & Pulliam, in press; Kamil & Sargent, 1981), and scores of

productive research programs have greatly enhanced our appreciation of foraging. In the section to follow, I discuss briefly but three of these contributions.

Prey Detection

Research by Kamil and his colleagues has utilized operant techniques in a fascinating exploration of how blue jays detect their prey. For example, Pietrewicz and Kamil (1981) used the concept formation technology developed by Herrnstein and Loveland (1964) and by Herrnstein, Loveland, and Cable (1976) to assess how blue jays detect a cryptic prey, the *Catocala* moth. On each trial the experimenters projected a slide onto a large pecking key. On trials in which the slide included a moth, a peck at the slide produced a meal worm for the food-deprived jay. If no moth were included in the projected slide, the jay could peck a smaller key to advance to the next trial. If the jay made either a false alarm (pecking the large key when no moth was projected) or a "miss" (pecking the smaller key when a moth was projected), a long delay occurred prior to the subsequent trial. As Pietrewicz and Kamil (1981) noted:

This technique is particularly well suited to the study of prey detection. It allows exact control over the appearance of the prey and the order in which prey types occur and eliminates possible preferences for particular prey types on the basis of factors such as taste and capture or handling time. (p. 312)

Using this procedure, Pietrewicz and Kamil were able to show how naive and experienced predators detected cryptic prey and that repeated encounters with rare prey types increase their detectability. The study shed light on how predators deal with crypticity and how crypticity functions to reduce predation.

Optimization Approaches

Whereas the work on crypticity illustrates how operant technology may be put to good use in helping the researcher pose and answer questions about foraging, Pulliam (1981) has stressed a theo-

retical, rather than a methodological correspondence. In particular, he argues that the optimization approaches of some ecologists and psychologists have important conceptual parallels. He notes:

I suspect that psychologists are better equipped to test many of the predictions of optimal foraging theory than are ecologists. The attempts of ecologists to test their own foraging theories have, for the most part, been less than elegant. This is largely because ecologists are less laboratory oriented than are psychologists. Still, why should psychologists want to test ecological theories?

I have argued that optimization approaches of ecologists and psychologists are in some ways very similar. When an animal can change the relative frequency of its encounters with identical food reinforcers, maximization of the rate of reinforcement is the same as maximization of energy intake. (pp. 387-388)

In other words, Pulliam argues that subjects that maximize rate of reinforcement—as some behavior analysts maintain they do—are, incidentally, also maximizing energy intake. Because maximization of energy intake may lead to maximization of fitness, Pulliam is also suggesting that maximization of reinforcement rate, in the short run, may lead to maximization of fitness in the long run.

The Delay-Reduction Hypothesis

Pulliam's article suggests a complementary relationship between optimal foraging theory and reinforcement theory. Research on the delay-reduction hypothesis suggests a similar, though perhaps more precise, complementarity between optimal foraging theory and principles that have evolved in the operant conditioning laboratory. This work which serves as a final example of interdisciplinary research, addresses aspects of foraging within the framework of the delay-reduction hypothesis (DRH) developed over the past sixteen years (e.g., Fantino, 1969, 1977). According to the DRH, the strength of a stimulus as a conditioned reinforcer is determined by the correlation between the stimulus and food. Specifically, a stimulus correlated with a greater reduction in time to food will be a stronger reinforcer (as measured in a choice test) than one correlated with

a lesser reduction in time to food. Stimuli uncorrelated with reductions in time to food should not serve as reinforcers at all. As Fantino and Abarca (1985) have shown, optimal foraging theory (OFT) and the DRH appear to complement one another. A model of natural selection for foraging efficiency makes several predictions consistent with an hypothesis of a more proximate phenomenon, that is, reduction in time to primary reinforcement. Specifically, it may be shown mathematically that, under a wide range of conditions and assumptions, OFT and the DRH make identical predictions about the acceptance or rejection of food items (see Fantino & Abarca, 1985).

The DRH states that the effectiveness of a stimulus as a conditioned reinforcer may be predicted most accurately by calculating the reduction in the length of time to primary reinforcement, correlated with the onset of the stimulus in question, relative to the length of time to primary reinforcement measured from the onset of the preceding stimulus. Expressed differently, the greater the improvement in terms of temporal proximity or waiting time to reinforcement, correlated with the onset of a stimulus, the more effective that stimulus will be as a conditioned reinforcer. The hypothesis, first developed to account for choice for two variable-interval (VI) schedules of reinforcement in concurrent-chains schedules, has been extended to such areas as observing in both pigeons and human subjects (Case & Fantino, 1981; Fantino, Case, & Altus, 1983), self-control (Ito & Asaki, 1982; Navarick & Fantino, 1976), elicited responding (Fantino, 1982), and three-alternative choice (Fantino & Dunn, 1983).

A fuller exposition of this hypothesis is found in Fantino (1969, 1977); its relation to OFT is discussed in Fantino and Abarca (1985), Fantino, Abarca, & Ito (in press), and in Fantino (in press). Here I present five of the major conclusions of this work on operant analogs to foraging, conclusions that support the basic contention of this paper: theory and research in behavior analysis can profit from and

in turn assist theory and research in behavioral ecology.¹

1. When the time spent searching for two or more prey types is increased, acceptance of the less preferred prey type should increase according to OFT and the DRH. Using operant methodology first developed by Lea (1979), both Abarca and Fantino (1982) and Fantino et al. (in press) have supported this prediction more strongly than earlier experiments from behavioral ecology laboratories.

2. When the time spent handling two or more prey types is increased, acceptance of the less preferred prey type should *decrease*, a prediction derivable from both OFT and the DRH. Again, Fantino et al. (in press) have supported this prediction.

3. When the accessibility (i.e., availability) of the more and less preferred outcomes is varied independently, variation in accessibility of the more preferred outcome has a greater effect on choice, consistent with the DRH (Fantino & Abarca, 1985).

4. Variations in "percentage reinforcement," specifically in the probability that the preferred outcome terminates in food (as opposed to time out), are also consistent with optimality analyses such as the DRH (Abarca, Fantino, & Ito, 1985).

5. Because OFT and the DRH are equivalent under many conditions, implications drawn from one theory may also be relevant for the other. For example, an analysis of OFT has led to a counter-intuitive implication of the DRH that had not been uncovered in the sixteen years since introduction of the DRH. Specifically, under certain conditions the more accessible the less profitable outcome, the *less* acceptable it should be. This prediction is currently being assessed, as is a parallel prediction concerning the distribution of choice responses in the concurrent-chains

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