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The Effects of Prey Vulnerability, Density, and Patch Replenishment in an Operant Analogue of Foraging

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THE EFFECTS OF PREY VULNERABILITY, DENSITY, AND PATCH REPLENISHMENT IN AN OPERANT ANALOGUE OF FORAGING

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

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Michael James DeWulf

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ABSTRACT

The Effects of Prey Vulnerability, Density, and Patch Replenishment in an Operant Analogue of Foraging

by

Michael James DeWulf, Doctor of Philosophy
Utah State University, 1988

Major Professor: Dr. Carl D. Cheney
Department: Psychology

Foraging behavior has recently become a popular area of research with which ethologists, behavioral ecologists, and experimental psychologists converge their traditionally separate disciplines into a more multidisciplinary framework. Ethologists and behavioral ecologists usually study foraging as it occurs in the natural environment or the "field," while experimental psychologists contrive laboratory simulations of foraging and make the assumption, sometimes incorrectly, that generalization occurs across settings, situations, and species. Scientific advances are now beginning to occur in the ability of laboratory researchers to better simulate foraging as it occurs in the field. Field researchers are also becoming more willing to accept these findings as important. The purpose of this dissertation was to use a laboratory analogue of foraging behavior to examine the effects of prey vulnerability, density, and prey-patch replenishment on the number of prey rejections and switches between patches. This analogue may have more biological validity than previous simulations in the operant laboratory by simulating conditions of replenishing and depleting patches under adjusting (progressive and regressive) random-ratio schedules of reinforcement.

Three experiments were conducted. The first examined the effects of response-cost on acceptability of prey items offered. Results indicated that as the cost of obtaining one prey item increased while the cost of another was held constant, subjects consistently pursued the lower-cost prey and rejected higher-cost prey at increasing probability ratios of 1:3, 1:10, and 1:15. The second experiment covaried response cost (vulnerability) with the probability of encounter (density) for two prey types and evaluated their effects on the acceptability of prey. This experiment showed that when the density of the low-cost prey increased ($p = .66$), the subjects were more selective. Subjects were less selective when the density of the low-cost prey decreased ($p = .33$). In the third experiment, prey-patches were replenished at reinforcer-determined (regressive random ratio) baseline rates and compared to several fixed-time schedules of patch replenishment. Results of Experiment III indicated no major differences in patch use behaviors (number of switches between patches). The validity and utility of this simulation was discussed as a useful model for the experimental analysis of foraging behavior.

(128 pages)

CHAPTER I

INTRODUCTION AND STATEMENT OF THE PROBLEM

One definition of foraging is "to wander or rove in search of food or other provisions" (Menzel & Wyers, 1981). Not only does this definition imply random movement (which is not supported by current research), but it fails to account for the foraging behavior of the caddisfly (Macronema transversum) or the black widow spider (Lactrodecus mactans), which are "sit and wait" predators (Type I; Schoener, 1969). The above definition would be more appropriate for an active (Type II) forager, such as a coyote (Canis latrans), which moves widely throughout a home range in search of food and other resources. Perhaps the definition would be applicable to a wider variety of species if it read to actively search or passively await (in a patch) food and other provisions (such as shelter). Foraging behavior has been broken into a chain of discrete behavioral links, typically consisting of search, detection, pursuit, capture, killing, and consuming prey (Cheney, 1979). Each of these stages can be behaviorally defined, depending on the organism in question, and viewed for analysis as a heterogeneous chain of operant behaviors. Figure 1 displays the natural foraging episode described by Cheney (1979). This flow chart suggests that one component of foraging (e.g., search) is reinforced by another component (e.g., detection), which sets the occasion (is a discriminative stimulus) for a third (e.g., pursuit), and so on. The cycle then repeats when the animal begins searching again (for unknown reasons, food deprivation probably being a major factor). Several authors have used similar

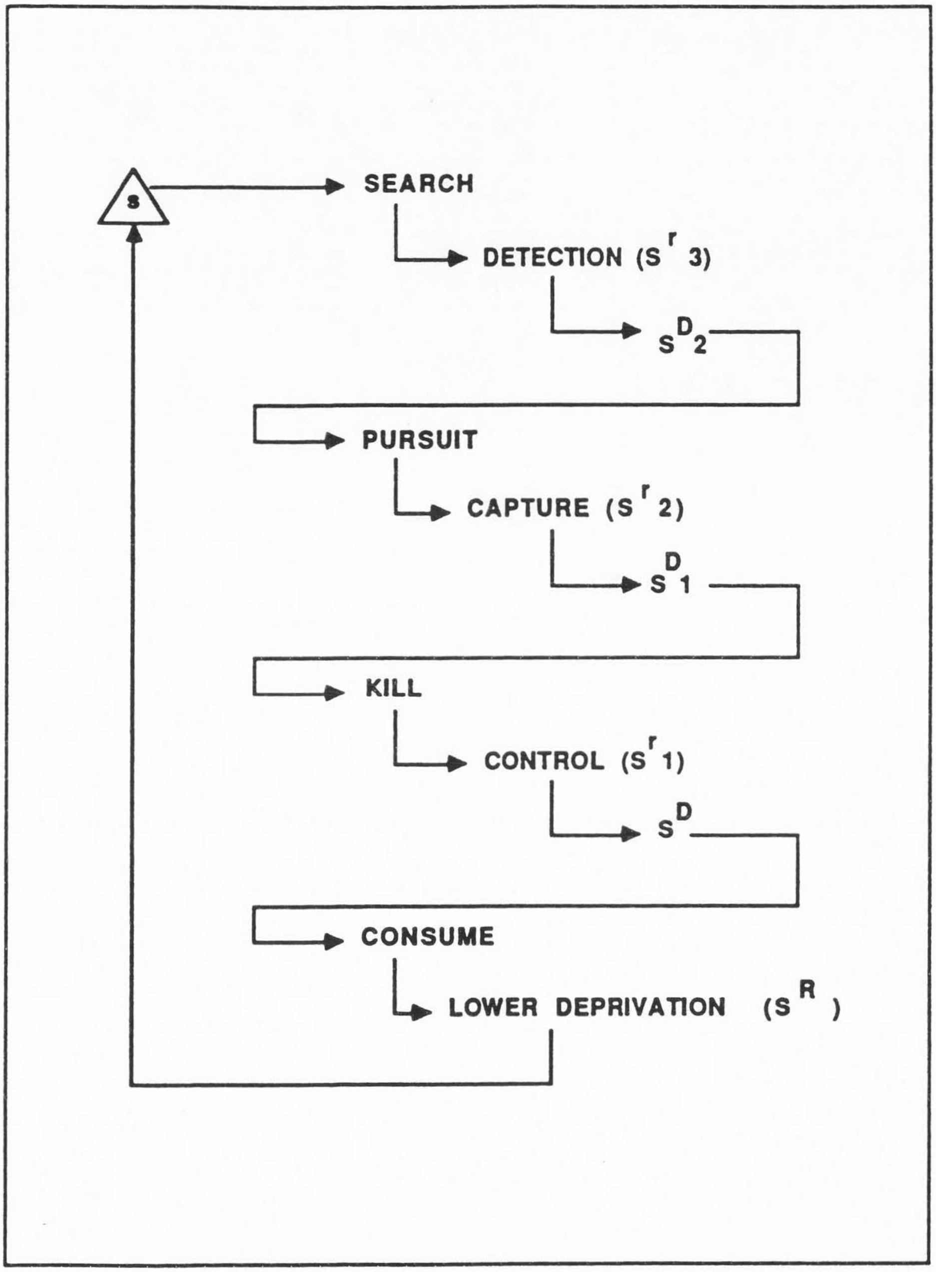


Figure 1. The natural foraging episode in terms of setting events, discriminative stimuli (S^D), and reinforcers (S^R; from Cheney, 1979, with permission).

classification systems to describe foraging behavior (e.g., Abarca, Fantino, & Ito, 1985; Collier, 1977, 1983; Collier & Rovee-Collier, 1981; Krebs, 1973). The advantage to breaking this foraging episode into separate three-term contingencies is that each can be individually manipulated for analysis.

Because there is such variety in the methods used to study foraging, it is no surprise that foraging behavior has become a multidisciplinary endeavor among behavioral ecologists, ethologists, socio biologists, evolutionary biologists, and more recently, experimental psychologists (Lea, 1987). Foraging is also an excellent area for field and laboratory researchers to combine their assumptions, methods, and predictions to create a more integrated and inclusive approach to understanding behavior occurring in these environments. Collaboration among these traditionally separate disciplines should advance the study of foraging, as studies in the field will lend validity to laboratory studies and vice versa (Lea, 1981).

The validity of laboratory analogues of foraging and the outcomes they produce can only be measured in terms of how a particular analogue relates to observations in the field and other models developed both in the field and the laboratory. Analogue research on foraging requires the investigator to have (a) some basic knowledge of the subject's natural foraging behavior (e.g., how and what the forager eats), and (b) internally and externally valid experiments (e.g., appropriate schedules of reinforcement used to simulate prey and patch dynamics, such as variable-ratio (VR) or random-ratio (RR) versus variable-interval (VI) schedules). Although any type of laboratory analogue research has unavoidable limitations in generalizing to "real life" situations (in foraging, lack of interspecies competition, risk of predation, etc.), most experts agree that many of the contingencies faced by food-deprived laboratory animals share important characteristics with animals foraging in the wild (Baum, 1982a, 1982b, 1983; Collier & Rovee-Collier, 1981; Epstein, 1984b; Fantino & Abarca, 1985; Lea, 1981; Pulliam, 1981; Skinner, 1953, 1961). Considering the earlier definition, the environment in which an animal forages is not always of major importance--it is the relationship between the environment and food gathering behavior that behaviorists or "praxists" (defined as "the study of behavior;" Epstein, 1984a, p. 101; Skinner, 1938) consider their subject matter. As a result, additional laboratory analogues of foraging have been called for by field and laboratory researchers alike (Baum, 1983; Fantino, 1985; Kamil, 1983; Krebs, 1978; Lea, 1981; Shettleworth, 1984, 1987; Staddon, 1980). As a result of this interest in laboratory research related to foraging, it is fast becoming one of the most widely studied areas in behavioral ecology and experimental psychology. The 1980s have seen the development of texts dealing specifically with foraging behavior (Commons, Kacelnick, & Shettleworth, 1987; Kamil, Krebs, & Pulliam, 1987; Kamil & Sergeant, 1981; Stephens & Krebs, 1986).

The central issue in current research is whether behaviors exhibited by animals in the wild are controlled by the same mechanisms (principles of behavior, such as positive reinforcement, extinction, etc.) as those in the operant laboratory (Lea, 1981, 1982; Schoener, 1987). If such principles occur in the natural environment, then operant conditioning research may reveal some variables which control foraging in the field, while field research will help validate the behavioral principles observed in the laboratory. Most important, the analysis of such behavior can, and will, progress if researchers in the field and in the laboratory are willing to collaborate on methods of conducting research, posing questions of interest, and further developing experimentally and biologically valid simulation procedures. A great deal of interdisciplinary progress has been made in recent years, but more research is needed to extend this progress.

Experimental psychologists have had difficulty simulating a dynamic foraging episode (i.e., one with a changing environment) in the laboratory, but have developed sophisticated quantitative procedures for predicting choice behavior of animals working for food under a given set of constraints (e.g., schedules of reinforcement). Unfortunately, some of the constraints imposed by laboratory research have lacked external validity. For example, the delay-reduction hypothesis (e.g., Fantino & Abarca, 1985) and the ubiquitous matching law (Herrnstein, 1970, 1974) are powerful principles for predicting choice behavior under variable-interval (VI) schedules of reinforcement. However, VI schedules are not commonly observed in the natural environment, so field investigators view research using such schedules as somewhat limited. Models of choice have been developed with an extensive literature base in psychology, but the models themselves have been the focus of study, rather than foraging, per se.

More work needs to be done in expanding such models to account for relevant foraging behavior in the wild. For example, schedules simulating search need to account for features of replenishment and depletion in the wild. Additionally, patches would be better simulated by spatially separated operanda, each with its own food source.

In summary, the problems with current foraging research center around (a) the lack of methodological integration among researchers in different disciplines and between those working in the field and the operant laboratory; (b) much research has been conducted with regard to specific theories or models in behavioral ecology and psychology, but have failed to conduct a basic experimental analysis of foraging (Sidman, 1960); and (c) many operant analogues of foraging have used schedule-dependent models of choice, and thus have limited generality to foraging in the natural environment.

Most studies of foraging have manipulated some aspect of a forager's prey or patch distribution and observed the resulting behavioral changes (e.g., Kamil & Sergeant, 1981). The experiments reported in this dissertation are of that sort. The objectives of the present research were to determine (a) how cost (i.e., prey vulnerability) affects the forager's decision to pursue or reject two prey types, (b) how the density of high- or lost-cost prey types covary with vulnerability, and (c) whether simulating prey replenishment based on the number of prey (reinforcers) taken per patch approximates prey replenishment based only on time. Three experiments were conducted to fulfill these objectives and determine how prey vulnerability, density, and patch replenishment affect the forager's choice.

A procedure is described for studying foraging behavior in the operant laboratory that has been refined at Utah State University over the past 10 years (Bonem & Cheney, 1985; Cheney, 1979; Cheney, Bonem, & Bonem, 1985; Cheney, Bonem, & Nittrouer, 1982; Cheney, DeWulf, & Bonem, 1986; Cheney & Shamaly, 1983; DeWulf, Bonem, & Cheney, 1986). This procedure simulates independent variables such as prey vulnerability (cost), prey density (probability of encounter), and replenishment and depletion of patches under adjusting random ratio (RR) schedules of reinforcement. For some foragers, these schedules are similar to one which replenishes and depletes patches in the wild. Baum (1983) has stated:

> Search provides food neither on a variable-interval nor a variable-ratio schedule, but some combination of the two. Search is like a variable-ratio schedule that increases as a function of amount eaten (i.e., depletes) and decreases as a function of time (i.e., replenishes)... To my knowledge, no one has studied such adjusting variable-ratio schedules. (p. 268)

By studying foraging behavior as a heterogeneous chain of operant behaviors and examining interactions (there is not always perfect agreement about the specific components which constitute the foraging chain or where the divisions of it lie), we will learn more about the variables which control an animal's choice to pursue or reject prey items encountered, as well as the decision rules used by foragers in a patchy environment (one in which prey are found in clumps rather than randomly distributed). The study of foraging as an example of choice behavior has also been discussed in terms of economics (Hursh, 1980, 1984; Rachlin, Battalio, Kagel, & Green, 1981; Rapport, 1981; Tullock, 1971), self-control (Fantino, 1981; Rachlin & Green, 1972; Snyderman, 1983, 1987), welfare (Timberlake, 1984), and cultural anthropology (see Schoener, 1987 for a brief discussion).

Optimal Foraging Ecology

Optimal foraging theory is an ecological theory that explains foraging as an evolutionary phenomena facilitated by natural selection that tends to make animals efficient foragers (Charnov, 1976a, 1976b; Emlen, 1966; Houston, 1987; Krebs, Houston, & Charnov, 1981; Krebs, Stephens, & Sutherland, 1983; MacArthur & Pianka, 1966; Pulliam, 1976; Pyke, Pulliam, & Charnov, 1977; Pyke, 1978b, 1978c, 1981a; Stephens & Krebs, 1986). The popularity of optimal foraging theory over the past 20 years is partly a result of its ability to predict and it's apparent relationship to behavioral economics, evolutionary theory, and psychological models of choice.

Optimal foraging theory began with two papers published in the same issue of the American Naturalist, one dealing with diet theory (Emlen, 1966) and the other dealing with both diet theory and use of a patchy environment (MacArthur & Pianka, 1966). These authors were not the first theorists in the area of foraging, but it is nonetheless doubtful that either realized how their theoretical models would expand the field of behavioral ecology, an effect that Schoener (1987) suggests is only now beginning to be fully realized (but cf. Gray, 1987).

MacArthur and Pianka (1966) were the first foraging theorists to suggest a distinction between foraging for prey (prey choice strategies) and foraging for patches (patch use strategies), although they also pointed out that prey and patch choice strategies were quite similar as well. Specific quantitative models developed to account for the optimal number and types of prey to include in the diet are known as "optimal diet models" (e.g., Emlen, 1966; Emlen & Emlen, 1975; Goss-Custard, 1977a, 1977b; Krebs, Erichsen, Webber, & Charnov, 1977; Krebs, 1978; Werner & Hall, 1974). Models related to the use of a patchy environment are commonly known as "patch use models" (e.g., Charnov, 1976b; Krebs, 1978; Krebs, Ryan, & Charnov, 1974; MacArthur & Pianka, 1966). Each of these models quantitatively specifies the optimal foraging strategy in terms of some currency, such as energy gain (E) relative to some cost, such as time required to handle the prey (h), yielding the ratio E/h (commonly known as the "profitability" of a prey item). The models differ in the decisions that are analyzed--what to include in the diet or how long to forage in a patch before leaving.

There has been a great deal of interest in testing optimal foraging models, largely because if one can meet the assumptions of the model, it can be tested from a variety of approaches (e.g., Hanson, 1987; Mellgren, Misasi, & Brown, 1984). The predictions of optimal foraging models are tested by comparing the actual behavior of the forager to the quantitatively optimal behavior calculated under similar, but hypothetical circumstances; hence its relation to microeconomic theory and the concepts of utility, income, price, and elasticity and substitutability of demand (Crawford, 1986; Hursh, 1980, 1984).

The early optimal foraging models assumed variables such as energy gain, handling time, and travel time held constant values. Early models also assumed energy gain was a continuous event. Optimal foraging models which were developed later ("second generation models") were stochastic (they had random variation, which accounted for changing environments), rather than deterministic, and they assumed energy intake to be a discrete, rather than continuous, event (Iwasa, Higashi, & Yammamura, 1981; Schoener, 1987).

In the current foraging literature, there is general disagreement as to whether optimal foraging models can be scientifically tested. Kacelnick (1987) suggests that those who are opposed to optimality theory argue that (a) it is untestable and therefore unsuitable as a scientific endeavor (Gray, 1987; Ollason, 1980), or (b) it is testable but unsupported (Herrnstein, 1982; Mazur, 1981; Vaughan, 1982). Those in support of optimal foraging theory suggest that (a) it is testable and generally supported by the data (Pyke et al., 1977; Rachlin, 1978), or (b) that it is not testable, but nevertheless an important tool to use in posing and answering research questions (Krebs, 1978; Pyke et al., 1977). The question is still widely debated, but it is interesting that experts in the field agree about practically nothing concerning optimal foraging theory (see Skinner, 1987 for a similar discussion concerning recent developments in psychology).

Operant Laboratory Investigations of Choice and Foraging

Psychologists studying foraging consider it in terms of setting events, behavioral consequences, and how foraging places constraints on reinforcement (Baum, 1982b, 1983; discussions on the relationship between operant behavior and evolution can be found in Fantino & Logan, 1979; Lea, 1982; Shettleworth, 1974; Skinner, 1966, 1975, 1984; Staddon, 1983, 1987). Choice has been studied extensively in the operant laboratory in T-mazes, shuttle boxes, and operant chambers requiring various response topographies, such as running down an alley, pressing a lever or treadle, and pecking a key. Such investigations often study generic choice between two alternatives, each under a different schedule of reinforcement (e.g., Bhatt & Wasserman, 1987; Davison & Temple, 1974; MacEwen, 1972). These schedules of reinforcement are viewed as being analogous to the components within the foraging chain (Cheney, 1979; Lea, 1979; Zeiler, 1987).

Behavioral ecologists may be better suited to study foraging in the field, while operant psychologists further develop laboratory techniques for studying foraging in the laboratory (Fantino & Logan, 1979; Ferster & Skinner, 1957; Honig, 1966; Honig & Staddon, 1977; Killeen, Smith, & Hanson, 1981; Lea, 1979; Skinner, 1938). For example, operant technology demonstrating concept formation in the pigeon (Herrnstein & Loveland, 1964) has been used as a referent by which behavioral ecologists have studied cryptic (camouflaged) prey detection (e.g., Krebs, Stephens, & Sutherland, 1983; Pietrewicz & Kamil, 1981).

The schedule used most often to study choice in the operant laboratory has been the concurrent-chains procedure (e.g., Autor, 1960; Baum, 1974b; Fantino, 1969; Fantino & Abarca, 1985; Fantino &

Logan, 1979; Findley, 1958; Herrnstein, 1964; Rachlin, 1967; Reynolds, 1963; Squires & Fantino, 1971). In this procedure, a subject is provided access to two spatially separated, simultaneously available (concurrent) response alternatives (these are viewed most commonly as two distinct patches or "places to work"). The program on each alternative is a two-component chain.

In a chain schedule, a response in the presence of one discriminative stimulus produces a second (different) stimulus. When the response requirement for the second stimulus has been completed (again on the same or different schedules), it results in unconditioned reinforcement. Generally speaking, the chain is similar to that of foraging behavior in the wild, although potentially slower. Traditionally, only two operanda have been used to study choice behavior in the operant laboratory. However, some studies have been expanded to include three-alternative choice procedures (Fantino, Abarca, & Dunn, 1987).

In a typical foraging simulation, the concurrently available response alternatives serve as prey patches, while the two components of the chain schedule represent search and handling time, respectively. Completion of the initial link (search) schedule requirement produces the terminal link stimulus (the animal "detects" a prey item), which, once completed, results in a simulated kill and assumed consumption. Once the terminal link has been completed, the concurrent initial links are once again available. Most simulations of foraging have required some type of response cost for the animal to move from one alternative to the other (travel-cost), such as a third key under a different schedule of reinforcement (e.g., DeWulf et al., 1986) or a hurdle the animal must cross (e.g., Baum, 1981).

The concurrent chains procedure allows the subject to engage in one of two simultaneously available response alternatives programmed under identical or different schedules in the initial and/or terminal links of the chain. This has important parallels with naturally occurring foraging when viewed as a heterogeneous chain of operant behaviors. For example, each component of the chain has a discrete discriminative stimulus, response requirement, and behavioral outcome. The naturally occurring foraging episode can be reduced to a number of such three-term contingencies, as depicted in Figure 1.

Quantitative descriptions of choice such as the delay reduction hypothesis (Fantino, 1977) and the ubiquitous matching law (Herrnstein, 1970, 1974) have been developed to predict and explain choice behavior. The delay reduction hypothesis states that "the strength of a conditioned reinforcer is a function of the reduction in time to primary reinforcement, correlated with the onset of that stimulus" (Fantino, 1981, p. 169). Presented in its most simple quantitative form, the delay reduction hypothesis quantitatively predicts the following:

$$\text{Reinforcing strength of Stimulus A} = f\,\frac{T - t\,(a)}{T}$$

Where t(a) is the temporal interval between the onset of Stimulus A and primary reinforcement, T is the total time between reinforcer presentations, and the function, f, is assumed to be monotonically increasing and continuous (Fantino & Abarca, 1985). The delay reduction hypothesis predicts that the animal will consistently choose the alternative associated with a greater reduction in time to primary reinforcement. Therefore, the animal should always pursue prey items that are quickly captured and consumed, regardless of their E/h ratio or density. This hypothesis has somewhat limited generality when applied to specialized aspects of foraging, such as central place foraging.

Support for the delay reduction hypothesis has come from numerous studies conducted in the operant laboratory (e.g., Abarca & Fantino, 1982; Fantino, 1969; Fantino & Abarca, 1985; Fantino, Abarca, & Ito, 1987). For example, Abarca and Fantino (1982) studied pigeons responding under concurrent chain schedules of reinforcement with fixed-interval (FI) initial links and variable-interval (VI) terminal links (such schedules are rare in nature). The size of the intervals in each of the schedules was varied, and subjects consistently chose the schedule with the greatest reduction in time to primary reinforcement, also providing support for optimal foraging theory (although predictions diverge in other choice tests, such as those where the delay reduction hypothesis predicts choice of the alternative associated with a greater reduction of time to primary reinforcement and optimal foraging theory predicts choice of the alternative yielding the greatest gain in terms of E/h).

The delay reduction hypothesis provides a model of conditioned reinforcement that can be tested from a variety of approaches (e.g., studies of reinforcement schedules, foraging, and self-control), although it has some potential limitations to naturally occurring foraging behavior (for a comprehensive review see Fantino, 1981).

Data from studies supporting the delay reduction hypothesis generally also support the matching law, which suggests that responses are distributed in proportion to the density of reinforcement available in each of the choice alternatives. Herrnstein (1974) conducted a study where pigeons responded under concurrent variable-interval (VI) schedules of reinforcement. The interval following 4-second access to grain was then varied. Results indicated that the subjects closely matched their responses to the reinforcement density in each of the choice alternatives. This general result has been supported in a number of subsequent studies (Baum, 1974a; Herrnstein & Loveland, 1964; Houston, 1986; Ito & Fantino, 1986; Rachlin, 1978, 1982).

The matching law states that the relative frequency of responses to a choice alternative is proportional to the relative density of reinforcement on that alternative (not to be confused with maximizing predicted by optimal foraging theory). The matching equation can be stated quantitatively as follows:

$$\frac{P1}{P1 + P2 + \dots Pn} = \frac{R1}{R1 + R2 + \dots Rn}$$

Where P is the number of responses, R is the number of reinforcers, and numeric variables refer to the respective choice possibilities (Herrnstein, 1974). No formal quantitative tests of the optimal diet model, delay reduction hypothesis, or matching law were conducted. The primary purpose of this investigation was to further examine an operant model of choice as it specifically relates to activities in the pursuit component of the foraging episode. Furthermore, the present investigation expands the scope of earlier models developed in the operant laboratory by testing a specific method of simulating prey patch replenishment and depletion.

CHAPTER II

REVIEW OF THE LITERATURE

Theories of Prey Choice

The classic question in optimal foraging theory is what the forager should include in the diet. MacArthur and Pianka (1966) and Emlen (1966) developed the first published quantitative accounts of what have come to be known as "optimal diet models." Several similar models were quick to follow (Emlen, 1968; Rapport, 1971; Schoener, 1969; Tullock, 1971). MacArthur and Pianka (1966) developed a graphic model pertaining to both choice of prey and choice of patches (it has been called the "fundamental theorem of optimal foraging theory," by Charnov (see Schoener, 1987, p. 10). The optimality theory promulgated by these early authors suggests that while foraging, an activity should be engaged in as long as the momentary gain in E/h exceeds that of competing activities. The model specifically addresses the variables that lead to greater specialization in the diet. Variables examined include (a) increased overall prey density, (b) increased search cost, (c) specialization of predator handling behavior, and (d) prey which are difficult to capture. The model predicts that prey should be ranked according to their E/h ratios, such that as overall prey density increases, the diet should become more specialized (it should shrink).

Optimal foraging theory in general, and optimal diet models in particular, make certain assumptions about the animals' foraging ecology. The three major assumptions outlined by Stephens and Krebs (1986) are:

1. Decision Assumptions. These depend on what is being analyzed. For example, one can study prey choice by offering (a) identical prey with unequal handling times or (b) prey of different sizes. Two common decision variables analyzed in the study of patch choice are: (a) residence time and (b) giving-up time. Residence time (RT) is the interval which elapses between entering and leaving a patch, while giving-up time (GUT) refers to the interval between the last prey capture and leaving the patch.

2. Currency Assumptions. These variables include average long-term rate maximization, short-term maximization of E/h, energy maximization, handling time reduction, nutrients obtained, or any other currency the forager may maximize.

3. Constraint Assumptions. These are typically events which limit a forager's ability to obtain food, such as information about the environment, mating, sleeping, prey densities, day-night cycles, and independent search and handling times. If these and certain other assumptions are satisfied, then the optimal diet model predicts the following with regard to maximizing the diet:

A. The predator will rank all potential items according to their E/h ratios (from highest to lowest) such that increasing density of a higher ranked prey item will lead to greater specialization in the diet.

B. Prey choice is independent of the density of lower ranked prey items and depends only on the density of more profitable types.

C. The animal should either always pursue or always reject a prey item regardless of the relative density of that prey type (commonly known as the zero-one rule, all or none selection, or partial preferences).

Several studies have sought to test optimality models. Many authors have developed models that relax certain assumptions of traditional optimal diet models. Most of these stochastic models were developed to account for optimality predictions based on changed decision, currency, and/or constraint assumptions, and hence, make different predictions concerning optimal foraging behavior (Green, 1987; Kacelnick, Krebs, & Ens, 1987; Stephens & Krebs, 1986).

For example, Pulliam (1974) developed a stochastic optimization model (one which has random variation) that predicted the diet for active foragers feeding on stationary prey. This particular model makes different assumptions about prey density, specifically that the density of prey is variable rather than constant. Thus, it makes different predictions about what the forager should include in the diet. The model assumes that the predator knows the density, energy yield, and distribution of prey (complete information) and predicts the optimal diet, search time, and optimal time to capture a prey item in a changing environment. The conclusions of the model are similar to the traditional optimal diet models in predicting the diet of the forager with clumped (patchy) and randomly distributed prey.

Some theorists have developed optimal diet models to account for the changed assumption of nutritional intake rather than maximization of E/h as the currency to be maximized (Pulliam, 1975; Rapport, 1971).

These models, unlike traditional optimal diet models, predict partial preferences. When the currency to be maximized is not E/h, the predictions of the model change. In a review by Schoener (1987), none of the 44 studies testing the prediction of partial preferences supported it. Foragers do display partial preferences, and sampling of prey may be one of several possible explanations (Lima, 1984; Shettleworth, Krebs, Stephens, & Gibbon, 1988). The second generation models have thus adjusted the model to account for the data, but seem to be moving in the right direction by formulating models to account for different assumptions, such as changed foraging constraints (e.g., Lucas, 1983, 1987).

McNair (1979) presents a generalized version of the optimal diet model that relaxes some of the traditional assumptions. First, he relaxes the prediction that prey choice depends only on the density of the more profitable type. He presents a model which suggests that the last prey type encountered influences whether or not that prey type will be included in the diet. McNair's model takes into account the "training effects" of prey detectability, probability of capture, and experience in handling prey. The model also relaxes the assumption of prey density remaining constant as did Pulliam (1974) and Rapport (1971) in their stochastic models of optimal diet. This particular model suggests that prey are not necessarily ranked according to their E/h ratios, and that training effects alter the probability of pursuing prey upon the next encounter. Gray (1987) suggests that second generation models are a great improvement over traditional models, but still make obvious predictions about the diet.

Additionally, he argues that if such models are constantly refined to account for the data, they can never be disproved and are thus inappropriate as a scientific source of endeavor.

Another variation of the optimal diet model has been developed to account for changed time constraints. This model also allows for partial selection of prey because of the relaxed assumption of time spent in a foraging bout. The model put forth by Lucas (1987) suggests that as time dedicated to a foraging bout decreases, the diet should expand to include even low-ranking prey, thus violating prediction that foragers should ignore unprofitable prey regardless of their density. Lucas (1987) also discusses the model as it relates to the principle of lost opportunity (the effort of pursuing a low-ranking prey also results in a decreased chance to detect potentially more profitable types).

Charnov (1976a) presents yet another model of diet choice based on size selection of prey. Unlike the traditional decision assumption of energetic efficiency, Charnov's model predicts the diet of the mantid (Hierodula crassa) taking into account variables related to risk of predation (pursuit distance), rate of food moving through the gut, and prey density (the data analyzed come from a study by Holling, 1959, cited by Charnov, 1976a). The mantid's viewed large and small mealworms in random order moving along a conveyor belt. Results indicated that mantid's consistently chose large over small worms, suggesting that large worms were possibly more salient (detectable) than small worms. Predictions of the model were compared to Holling's data and fit reasonably well. Charnov wisely concludes that maximization of E/h is only one of many potential variables that may play a role in prey choice.

Empirical Studies of Prey Choice

Field studies. The studies reviewed in this section are semi-naturalist field studies, most of which were conducted outdoors under surprisingly well-controlled conditions. Field studies of prey choice are much less common than comparable simulations in the operant laboratory. This may partially be a result of the inherent difficulties involved with constant observing, monitoring, and control of several aspects of prey and patch dynamics in the natural environment.

Goss-Custard (1977a) conducted a study in estuaries of 300-500 meters to determine if the wading bird redshank (Tringa totanus) would select polychaete worms (Neiris diversicolor or Nephthys homberg) that maximized E/h. The density of large and small worms was varied at several ranges to determine whether prey density affects diet choice. Results of this study suggest (a) that large worms were preferred to small ones, (b) smaller worms were taken more quickly if their density was greater, and (c) the combination of prey items that provided the greatest E/h were chosen most frequently. The results support predictions of the optimal diet model in terms of (a) selection of prey by their energy yield and (b) the diet becoming more specialized as the density of large, but not small, prey was increased. The results failed to support the prediction that foragers should not display partial selection. Probably the most significant finding of this study was that prey choice was independent of the density of small (less preferred) worms, but depended only on the density of large worms.

In a similar study, Goss-Custard (1977b) studied the choice of prey distributed over four patches: small prey (too small to be identified through the observation telescope, but consisting of Corophium volutator, Cyathura carinata, Hydrobia ulvae, and smaller-sized other types), polychaete worms (Nereis diversicolor), crabs (Carcinus maenas), and bivalve moluscs (Macoma balthica and Scrobicularia plana). This study differed from Goss-Custard (1977a) in that choice among prey of various types was examined, rather than choice among sizes of prey belonging to the same taxonomy. The results suggest that the redshank preferred the unidentifiable small prey, thus not maximizing E/h. The results are also inconsistent with Goss-Custard (1977a) where the redshank preferred large to small worms. In at least two of the patches where the temperature was lower, the redshank selected the polychaete worms (possibly because they were easier to detect), suggesting that detectability may be important in determining prey choice, or they may have selected the worms because of nutrient requirements.

Davies (1977a) studied the choice of insects by 12 (six pair) flycatchers (Muscicapa striata) in a large garden and yard. The exact type of prey items consumed by the flycatcher was unknown, but the droppings of each subject were analyzed to determine their contents (by examining undigested whole wings of various distinct types of (insects). Size of prey was determined by correlating the wing size with the probable body size. Results suggested that at least five factors affected the choice of prey by the flycatchers: (1) prey density and type of prey eaten by adults versus nestlings, (2) selection of large prey based on size and type, (3) distance of prey from the central place and prey activity, (4) nutrient constraints, and (5) selection of prey by male flycatchers for both adult birds during mating season when the females remained in the nest to incubate the eggs.

The results support the prediction that the birds maximize E/h in foraging both for patches and prey within the patches. Support for this prediction originates from data suggesting that: (a) the flycatchers foraged for larger prey near the ground when it was more profitable to do so; (b) the birds decreased the size of their diet when the density of large prey increased; (c) the adult flycatchers selected different prey for nestlings to eat relative to their own (adult) diet; and (d) when foraging near the ground, the birds switched patches when it was generally more profitable to do so.

Additional results suggested that energy is not always the currency to be maximized, as the second generation models suggest. First, the flycatchers selected prey that were rich in calcium during the mating season (ostensibly to increase the strength of the eggshell). Secondly, the strategy for maximizing short-term gain is different than that of long-term gain (e.g., fending off predators). Finally, the animal must engage in alternative behaviors such as minimizing risk of predation, as well as maximizing E/h and assuring continuation of the species.

Davies (1977b) tested a more specific version of the optimal diet model by studying the behavior of pied wagtails (Motacilla alba yarelli) and yellow wagtails (M. flava flavissima) feeding on insects in groups over water pools, and individually over dung pats in a meadow. The study specifically examined how risk of predation and number of wagtails present affected the wagtail's decision as to what to eat and where to forage. Examination of the wagtails' droppings provided information about the diet. Results suggested that the diet changed only when the density of the higher ranking prey was varied, and that as the density of higher ranking prey decreased, the wagtails consumed more of the lower ranking prey, presumably to maintain a constant rate of energy intake.

Additional results suggest that wagtails forage both in flocks and individually, switching many times between the two alternatives. In some cases, persistent switching resulted in maximizing E/h, but in others, it did not. This may have been due to compensation between other competing behaviors such as mating and risk. Switching between dung pats and water pools was qualitatively consistent with predictions from the optimal diet model, but no quantitative test of the model was provided. Results were generally consistent with those confirmed by Goss-Custard (1977a), but again failed to support the prediction of no partial preferences.

Another study lending support to the prediction that animals maximize E/h was Sutherland (1982). The study examined oystercatchers (Haematopus ostralegus) feeding on various sizes of cockles (Cerastoderma edule). Eleven large patches (100 meters square) and one smaller patch were sampled for an estimate of density between five cockle size types. Shells were collected to determine if the cockles foraged on the larger cockles so as to maximize E/h. The results suggest that maximizing E/h is not the only behavior important in maximizing foraging efficiency. A large cockle was taken whenever it was encountered, but a disproportionate number of smaller sized cockles were also taken. This result is consistent with a number of others that examined optimal diets (e.g., Goss-Custard, 1977a; Davies, 1977a) and suggests, as others do, that partial preferences may be due to sampling of prey or incorrectly assuming that the forager possesses complete information about the environment.

Campbell (1987) conducted a field investigation on the diet of small, medium, and large sea stars (Asterias forbesi) feeding on three sizes of blue mussels (Mytilus edulis). The experiments were designed to test whether the sea stars selected prey that were larger than the mean energy yield for the patch (maximized E/h). Results indicated that the mean size of the mussels selected by the sea stars was 35.98 mm, compared to a patch mean of 31.86. Small sea stars selected prey with an average size of 33.11, medium = 39.82, and large = 42.08, suggesting that prey size selection was correlated with predator size, but predators did not maximize E/h in all size classes. The study also suggested that in lieu of E/h, developmental stages of the predator may have been a contributing factor.

Laboratory studies. As stated at the outset, laboratory studies of prey choice are much more common in the literature than field studies of prey or patch choice. Several studies provide tests of the optimal diet model (e.g., Mellgren et al., 1984), while others are strictly laboratory studies on reinforcement schedules, relating to optimal foraging theory in a more or less indirect way (e.g., Fantino & Abarca, 1985).

Erichsen, Krebs, and Houston (1980) provided a test of the optimal diet model in a laboratory study with captive great tits. Subjects were presented with two types of prey (cryptic or camouflaged and noncryptic) passing along on a conveyor belt in front of the home cage. Prey items were two different sizes of mealworms, with the larger and more profitable being the cryptic (less salient) prey. The results supported the prediction that the animals would choose the prey yielding the greatest energy gain, but failed to support the prediction that a forager should never specialize on lower ranking prey types. This specific study, however, states that the animal should specialize on lower ranking prey at certain values, as the data suggest (also supported by Lucas, 1983, 1987). This study, like others, failed to support the prediction that there should be no partial selection.

A classic laboratory test of the optimal diet model was conducted by Werner and Hall (1974). These investigators presented bluegill sunfish (Lepomis macrochirus) with four size classes of Daphnia magna in small wading pools (aquaria) and examined the stomach contents of the fish after a foraging bout. The study quantitatively tested a version of the optimal diet model that predicts that the forager should include a greater variety of prey types in the diet when absolute prey density is low (generalist), and to be selective among prey when absolute density is high (specialist). The results were compared to predictions of the model, but no quantitative agreement was obtained. The study supports the notion of selecting energy-rich prey, and that diet choice depends on the density of large, but not small, prey. The results again failed to support predictions related to partial preferences.

Zach and Falls (1978) examined prey choice in captive ovenbirds (Seiurus aurocappillus) foraging for various sizes and types of prey. Prey consisted of 12 various types of insects including beetles, ants, and spiders. Results indicated that the ovenbirds chose large, novel prey types, fed almost entirely on one specific type, and exhibited partial preference. Although no quantitative test was performed, the study qualitatively supported predictions related to choice of the most profitable prey specialization on more profitable prey when absolute density increased, and partial preferences when absolute density of prey was low.

Krebs et al. (1977) presented five captive great tits sitting on a perch with profitable (large) and unprofitable (small) mealworms along a moving conveyor belt under a fixed-time (FT) schedule. In conditions where density of both prey types was low, the tits were not selective between them (i.e., they were generalists). When density was high for both prey types, the tits became more selective, choosing to ignore the less profitable prey and to pursue only more profitable items. This choice, however, was not due to the density of the less profitable type, but depended only on the density of the more profitable type (i.e., if the density of the more profitable prey was decreased, the model predicts that the birds would be less selective, and as the density increased, more selective). This study, like others (e.g., Sutherland, 1982), found that animals do not exclude less profitable prey as abruptly as the optimal diet would predict, but the model suggests that perhaps periodic sampling of prey may be responsible for the gradual exclusion of less profitable prey observed.

Some of the most challenging data to the optimal diet model to date was conducted by Emlen and Emlen (1975). This study tested predictions of the optimal diet model in 40 male laboratory mice (four experimental groups). Subjects were presented with natural and treated sorghum seeds (the treatment substantially reduces size and the caloric value of the seed). Each of the mice was offered one of the two seeds while data was collected on the amount and type of seed eaten per unit time. Results in terms of the optimal diet model failed to account for the data without modification. The authors suggest that deviations from optimality predictions could be an artifact of (a) the constraint that the mice could not choose specific items or discriminate among different types of seeds, (b) there is error in calculating the optimal diet under such circumstances, or (c) the mice are not foraging optimally.

Peden and Rohe (1984) provided a study of prey choice in the operant laboratory with pigeons (Columba livia) to determine if subjects would choose prey types so as to minimize the number of key pecks (handling time) per food item delivered. Pigeons were maintained at either 80% or 100% free-feed weight and worked under chained schedules of reinforcement that simulated search, procurement, and handling. During baseline conditions, pecks on the left and center key had no consequence, while each peck (FR 1) to the right key resulted in food delivery. In contingency sessions, the birds responded under a three-component chain simulating a search component where 3, 9, or 15 pecks on the left key (initial link) led to the illumination of the center key (detection or encounter). The terminal link schedule was either low cost (3 pecks) or a high cost (21 pecks), with a probability of .05 for either terminal link occurring. The procurement component required the bird to peck the left key once to reject prey items offered or to complete the response requirement on the center key, leading to illumination of the right key whereby one peck would produce food (handling). Results suggested that the birds consistently procured low cost prey and consistently rejected high cost prey when the search cost was low, but not high (the birds became generalist only as absolute density of prey decreased; see Collier, 1977, for similar results).

Lea (1979) conducted an operant investigation of foraging using pigeons responding under chained fixed-interval (FI) schedules of reinforcement. Completion of the initial link was consequated with access to the terminal choice state. In the terminal link, either a red or green key signalled prey detection. The bird could then
(a) reject prey offered by pecking the white key (three times),
(b) stop responding altogether (this also constituted rejection), or
(c) continue pecking the colored key on the FI terminal link schedule.
Completion of the terminal link led to primary reinforcement. The FI

schedule requirement was manipulated in both links of the chained schedule, as well as the duration of feeding time and post-reward detention.

Results suggested that the pigeons behaved "optimally" in some instances and suboptimally in others. Results consistent with the optimal diet model related to maximizing E/h and foraging more selectively as prey density increased, but failed to support the prediction of partial preferences. Results further suggest that these subjects failed to reject schedules when the initial link cost was greater than the handling cost for the less preferred prey types. This does not support predictions of the optimal diet model or the delay reduction hypothesis. Lea (1979) suggests that the failures of optimality may reflect that animals may be efficient but not always optimal foragers.

A study by Shettleworth (1985) was designed to determine if pigeons in a shuttlebox would choose food items with the greatest E/h. The birds were presented with several small or one large prey simultaneously. Optimal foraging theory would predict that the bird should select the prey which maximizes E/h, but the birds consistently chose to pursue several smaller prey rather than one large one, even when such a choice did not maximize E/h. The results are inconsistent with optimal foraging theory, but support the delay reduction hypothesis, which suggests that the animal will choose the food type associated with the smallest delay in time to primary reinforcement. Moreover, it could also be that pursuing several smaller prey (leading to additional conditioned reinforcement) may be preferable under certain circumstances (such as increased time in a foraging bout).

Theories of Patch Choice

A second question to which optimal foraging theory and other psychological theories have been applied is that of patch choice. Early studies were generally restricted to predicting patch RT, but more recent theoretical and empirical work has expanded on the question of patch choice to include GUTs, which are the intervals of time that elapse between the last prey capture and leaving a patch (Cheney et al., 1985; Krebs et al., 1974; Smith & Dawkins, 1971 provide examples of empirical work; and Iwasa et al., 1981 or McNair, 1982, 1983 give theoretical explanations).

Optimal foraging theory predicts that an animal will abandon one food patch (switch) in search of another when the average rate of capture falls to a level equal to or below the average rate of energy intake in alternative patches. This is not to be confused with switching used to refer to a change from one prey species to another as it is used in behavioral ecology. This prediction is commonly known as the Marginal Value Theorem (MVT; see Charnov, 1976b; Krebs et al., 1974), the "moving-on threshold" (Stephens & Krebs, 1986), or the "marginal capture rate" (Cowie, 1977), and has been supported in a number of studies examining patch RT (e.g., Krebs, 1978; Krebs et al., 1974) and extended to predict optimal GUTs in others (McNair, 1982, 1983). The GUT concept is actually older than the MVT, although much research has focused on the MVT and used to make predictions about GUT, for which it is ill-suited (McNair, 1982, 1983).

The MVT suggests that animals change (or switch) patches because of depression (Charnov, Orians, & Hyatt, 1976). As foraging time increases in one patch, the more depressed it becomes of food, and the forager must eventually move on to more successful hunting grounds so as to maintain a steady rate of energy intake. In other words, energy intake decreases as a function of time spent in any given patch. Patch depression differs from depletion in that the latter implies a decrease in the instantaneous rate of energy intake from a patch (Charnov, 1976b). That is, patches can deplete without becoming void of prey altogether; see the "sudden death" situation described by Dow and Lea (1987).

The general patch model outlined by Stephens and Krebs (1986) assumes that:

1. The decision variable to be analyzed is patch residence time rather than GUTs.

2. The currency assumption is long-term average rate maximization.

3. Constraint assumptions are that (a) search and handling time are independent events, (b) patch encounter is sequential rather than simultaneous, (c) prey density decreases as a function of time spent in a patch, and (d) the forager has complete information concerning prey and patches.

Some important general points about the patch model are also summarized by Stephens and Krebs (1986). One concerns the fact that the model solves for the encounter-contingent policy (the predator decides beforehand whether to accept or reject prey and patches upon encounter) but does not solve for foragers that acquire and use information about patches while foraging in them. Also, the model applies only to patches which depress, and the MVT only to patch RTs, not GUTs. Charnov's (1976b) model assumes that (a) the animal spends time in patches and traveling between them, (b) prey is distributed randomly in patches, and (c) the forager controls where it forages and when to leave any given patch.

Another possible explanation for patch switching is that the animals come to "expect" a fixed number of prey from a patch and move on to a new patch once that amount has been obtained (Gibb, 1958). This notion has been called "hunting by expectation," (HBE) but recent studies suggest that this possibility has not been widely supported. Some authors point out, however, that the major study refuting the HBE hypothesis (Krebs et al., 1974) did not actually test which strategy the animal used to switch food patches (see Gray, 1987, or Pulliam, 1981, for an extensive discussion). It appears that there is not wide agreement concerning scientific tests between the MVT and GUTs or between the MVT and HBE hypothesis.

Iwasa et al. (1981) compared several alternative explanations ("decision rules") for optimal patch switching and concluded that such behavior may be determined by the spatial distribution of prey within a patch. They suggest that there may be as many as three strategies a forager uses when choosing to switch patches: (1) A fixed amount of time has elapsed, (2) a fixed number of prey have been captured, or (3) the interval between successive food captures has exceeded a fixed amount of time. These predictions combine the aspects of patch RT, GUTs, the MVT, and HBE hypothesis.

Other variables that have been shown to affect patch switching include increased travel cost (Baum, 1981, 1982b; Cheney et al., 1982; Cowie, 1977; Mellgren et al., 1984) and increased risk of predation (Caraco & Lima, 1987; Cerri & Fraser, 1983; Charnov, 1976a) and distance from the central place (see Ford, 1983, or Kacelnick & Cuthill, 1987).

Empirical Studies of Patch Choice

Field studies. Most field studies of patch choice have studied avian predators foraging on small prey. Krebs et al. (1974) published one of the first empirical studies of patch choice in the field. This study examined optimal patch RT in black-capped chickadees (Parus atricappillus) foraging for hidden mealworms in artificial pinecones. Their results supported predictions of the MVT, but results were less clear-cut regarding Gibb's (1958) HBE hypothesis. The chickadees failed to respond as though they had learned to expect a fixed amount of mealworms from each of the pinecones, but allocated a variable amount of time to each pinecone and abandoned a patch after a relatively fixed GUT (said to be inversely related to the average rate of capture in the patch).

Similarly, Cowie (1977) conducted a study with great tits (Parus major) foraging in a 4.6m x 3.7m aviary for mealworms hidden in sawdust that contained five artificial trees with patches made of drainpipes (6.5 cm in diameter). The purpose of the study was to examine optimal foraging predictions in regard to patch choice as it specifically related to manipulations in travel time. One major problem for this study is that the author treated travel time as the time required to pry a cardboard lid off of the drainpipes (patches). Although the results suggested that the tits foraged in accord with optimal foraging predictions, one must be cautious in assuming that this was an adequate test of the optimal diet model.

In another field study, Pyke (1978a) conducted a study of patch use in broad-tailed Hummingbirds (Selasphorus platycercus) and Rufous Hummingbirds (S. rufus) foraging on nectar producing plants. Hummingbirds were studied in areas 50m x 30m, while data was collected on the number of flowers visited, time spent at each, total number of flowers available, and travel time between flowers. Results indicated that there was good agreement between predictions of a stochastic version of the MVT and the data (i.e., the birds did abandon a patch when the feeding rate fell to a level equal to or less than that of alternative patches in the forager's habitat).

Using a different approach, Pyke (1981b) studied the foraging mode of a single male Eastern spinebill (Acanthorhynchus tenvirostris) presented with four different patches of floral arrangements. The purpose of the study was to examine the foraging mode of hovering or perching as it relates to optimal foraging theory. The results were applied to a hoverer (the American hummingbird) and a percher (the Australian honeyeater). While hovering results in a greater variety of patches to choose from, it also requires far more cost in terms of energy expenditure than a comparable amount of perching. Results suggested that each of the modes result in greater maximization of E/h for each of the two foraging modes.

Smith and Dawkins (1971) studied great tits foraging in an indoor aviary with an experimental area measuring 4.6 x 3.7 x 2.0 meters. The patches consisted of food pots of different prey densities covered with aluminum foil lids. Observers used automated keyboards to record data pertaining to patch entry, patch exit time, searches (removes lid from pot), and detection of prey (mealworms hidden in the pots). The results indicated that the birds did not forage in accord with optimal foraging theory. That is, they did not spend the short amount of time available for foraging strictly in patches with the greatest densities, but foraged first in the patches with the most prey, and allocated the remaining time to patches with moderate prey densities.

A similar approach was used by Smith and Sweatman (1974) in a laboratory investigation of patch choice using titmice as subjects. The titmice were given access to several patches of different prey densities, as did the tits studied by Smith and Dawkins (1971). The subjects were allowed to forage only for a short time, so the optimal strategy would be to forage only in patches of greatest density. Results indicated that the birds did not forage only in patches of greatest density, but they allocated more time to the richest patch and a smaller amount of time to patches of lesser quality. When the patch with the greatest density of prey was changed, the birds found it relatively quickly if the patch was previously rich, and slower if they were placed in patches with a previous history of low density. They argue that the results may suggest that the titmice may have been optimizing long-term average rate maximization by foraging in a manner consistent with a changing environment. The authors further suggest patch sampling and the spatial distribution of food must be examined more closely in future work dealing with foraging behavior in changing environments.

Laboratory studies. Operant laboratory investigations of patch choice have focused on patch RT and GUT as a function of travel cost and the size of the schedules during search and handling components. Studies in this literature suggest that GUT (as defined by behavioral ecologists) corresponds to operant investigations of switching (or changing over) between two choice alternatives. Patch choice has thus been studied using independent variables related to travel cost. Semi-naturalistic studies of patch choice in the laboratory have also been conducted to better simulate patch choice in natural environments, but are not as numerous as comparable operant investigations of choice.

Csaszar, Johnson, White, and Collier (1986) required rats to work for food on four separate levers in an operant chamber (one bar for search, two for procurement, and one for rejecting prey). The size of the schedule on each of the levers was not varied; rather a changeover delay (COD) was imposed contingent upon a prey rejection. The interval of time for the COD was varied. The authors predicted that an increase in the time until the next search component would function similar to an increase in travel cost. In other words, as the interval of time between prey capture and allowing the animal to engage in search (COD) increased, the breadth of diet would increase, as it would if the cost of obtaining the same prey item had been increased. Results suggested that the birds responded to the COD as if it were a cost, and increases in the COD resulted in fewer switches between patches. As the COD decreased, more switches were evident.

Mellgren (1982) allowed rats to forage for food in a large room containing nine patches. Each patch consisted of a large sand-filled box containing buried food pellets. The study provided a test of optimal foraging predictions by noting the contents of each food patch and allowing only one subject to forage at a time. The amount of food available in each of the patches (density) served as the primary independent measure, and the food percent taken from each patch was then compared to "optimal" behavior under similar conditions.

Subjects proceeded through four phases. Phase I consisted of nine 12-hour sessions with a constant number of food pellets available in each patch. The second phase consisted of nine 12-hour sessions, but had variable numbers of food in each patch. Phase III was a series of fifteen 1-hour sessions with varying numbers of prey, and Condition IV consisted of nine 1-hour sessions with food amount being rotated in each patch. Sand was periodically intermixed to assure scent marking effects were controlled. Dependent measures were the number of pellets consumed, number of droppings, and evidence of urine for each patch.

Results indicated that subjects completely depleted most of the patches during Conditions I and II (12-hour sessions) and quickly located the nine food patches. Statistical analysis was used to determine the correlation between prey density and patch use. For two of the subjects, coefficients were -.41 and +.66, respectively, for the average over the first five sessions in Condition III, while averages over the final five sessions of Phase III were +.35 and +.71. For Condition IV, the density of prey in each patch was varied, and coefficients were +.85 and +.18, respectively.

This suggests that subjects overused low-density patches and underused high-density patches, which is not in accord with optimal foraging predictions regarding energy maximization. The rats did, however, sample all of the patches quite thoroughly but were too conservative in that they usually preferred some patches over others, even if the choice did not result in energy maximization. The authors suggest that learning where food is located and attributes of the food itself (i.e., complete information) may be independent functions in determining patch choice.

Baum (1981) studied travel cost with pigeons foraging in operant chambers. Each side key served as a patch, and an opaque partition was placed in the center of the chamber so that physical travel was required between the patches. Its length was increased during experimental conditions from 1" to 8". During baseline conditions, the partition was not present. Group 1 had to travel around a 1-8" partition in experimental conditions, while for Group 2, the maximum length was 4". Group 1 subjects also had to climb over a hurdle of heights ranging from 1.75" to 3.25". During the first 15 experimental conditions, the VI schedule was randomly varied between the two keys such that the subject had to obtain reinforcers on both side keys (a forced changeover procedure). The density of reinforcement (prey) was also varied across keys and conditions ranging from .25 to .75. VI schedules in three conditions were independent such that no changeover was required to switch patches, while the forced changeover was implemented in another. Group 1 subjects worked under a VI-41 sec. schedule and Group 2 a VI-20 sec. schedule. Sessions lasted until 50 reinforcers had been delivered.

Means across the last five sessions of each condition generally indicated that as partition length increased (and the hurdle was added for subjects in Group 1), the number of switches between patches decreased. Data is also presented regarding changeover durations and time spent on each of the keys. Partition lengths of up to 4" had little impact on changeover duration, but almost doubled when the partition was lengthened to 8" for Group 1 and the hurdle added for Group 2. After stability was obtained on changeover time, the schedules were varied producing underuse of profitable and overuse of unprofitable patches. Baum further suggests that overmatching may be the rule in the natural environment and that switching may be the result of the reinforcing consequences in each of the patches. Furthermore, the value of occasionally switching to less profitable patches, perhaps to sample patch quality, would be used to update information concerning various patches.

Dow and Lea (1987) conducted a study on choice between patch types (different key colors under adjusting random ratio schedules). One of the patches depleted based on reinforcers obtained, another was nondepleting, and a third had a constant number available, but once depleted, offered no additional food (called "sudden death"). The subjects allocated more time to (a) nondepleting patches, (b) replenishing rather than nonreplenishing patches, and (c) gradual depletion over sudden death. Moreover, GUTs were found to be longer in nondepleting patches and shorter in replenishing patches. Another interesting result is that it refutes predictions of the MVT, because as density in the patches increased, the GUTs also increased. The MVT would predict shorter GUTs with increased density.

Timberlake (1984) studied rats working in 24-hour sessions with two daily feeding opportunities. In the first feeding bout, the rats worked under a progressive ratio schedule. In the second opportunity (1-23 hours later), a fixed amount of food was freely available. In this study, patch choice relates to the decision to remain in a patch that depletes rapidly or switch to a more profitable one (i.e., the time horizon between work and food). Results suggested that the rats worked in depleting patches even when rich food patches always followed. Futhermore, intervals over 1 hour did not appear to affect current responding; thus, temporal limits were imposed upon animals foraging over long periods.

Timberlake, Gawley, and Lucas (1987) expanded on the previous study and further examined the forager's ability to compare patches across various temporal gaps (the "time horizon" or "memory window"). Results confirmed those obtained by Timberlake (1984) in that rats continued to work in depleting patches even when access to a rich patch always followed the depletion condition. The rat's "time horizon" was no longer than 16 minutes. Intervals longer than 16 minutes resulted in the rat overworking a depleting patch rather than waiting for a profitable patch. This study was also different from the first in that a physical barrier was added to the chamber to create two separate patches.

Timberlake (1984) failed to consider the possibility that the rats did anticipate the future rich patch but still continued working in the nondepleting condition. For intervals up to 32 and 64 minutes, the rats continued to work when the response cost per pellet was 20 times that of the rich patch. This study supports the view that animals have a relatively short time horizon with respect to temporally separated patch types. The results also point out the fact that optimality models need to further consider temporal gaps between guaranteed food now versus potential food later. The results provide support for the delay reduction hypothesis, suggesting that animals prefer food associated with a greater reduction time to eating, but refute the theory when temporal gaps of 16 minutes or less are involved. Future work will provide more conclusive data on the role of temporal factors in foraging and choice in animals and humans.

Hanson and Green (1984) studied choice between two patches of different types. Pigeons were provided two response keys of which only the left key was initially available (the search key). Responses to the left search key produced access to the terminal component of the chain (the handling key under a variable-ratio [VR] schedule). The subject could then reject the red or green colored keys (or patch types) offered or continue responding on the handling key. The red key was placed under a VR-2, while the green key was under a VR-20 schedule. Subjects were granted the option of rejecting any of the patch types offered and resume searching for other patches.

In the first experiment, the density of prey between patches were equal at .50, while the VR schedule was manipulated across experimental conditions. In this case, there should be indifference between the two patches. In the second experiment, the search cost was held at VR-20, while the density of the patches was varied. Experiment III manipulated search cost and more profitable patch density, while Experiment IV manipulated less profitable patch density. Results generally indicated that at low search value parameters, birds accepted profitable prey and rejected unprofitable prey. At high search costs, subjects accepted more of the less profitable prey. When search cost was constant but density was manipulated, subjects always accepted less profitable patches at .90 density. Only selected profitable prey at a probability of .50 did both for intermediate probabilities. When only the density of the more profitable type was varied as search cost was held constant, birds again accepted all prey at densities and rejected less profitable prey at low densities. Results support many optimality predictions, but only qualitatively.

Cheney et al. (1982) used a laboratory model of foraging to examine the effects of travel cost on GUTs. Pigeons responded under concurrent adjusting variable ratio schedules of reinforcement. The purpose of the study was to specify some variables which contribute to patch switching in an experimental apparatus containing two patches and a fixed number of prey. The cost of switching was then manipulated differentially to determine how this variable affected switching frequency. Subjects were first allowed to switch patches freely with replenishing and depleting patches identical to those described in forthcoming experiments. Center key switching responses were under fixed-interval or fixed-time schedules beginning after the first center key peck. Switching schedules ranged from FR 1-50, VR 5-50, FT 10-40 sec., and FI 10-40 sec. Each session lasted until 40 reinforcers had been dispensed or 30 minutes passed, whichever occurred first.

Results showed that the subjects averaged 71.5 switches between patches when no cost was required. The average number of reinforcers over the last five sessions of each condition revealed that as the travel cost schedule increased (in response requirement or time), the subjects switched in a decreasing fashion for both interval and ratio schedule types. Variables that were shown to affect absolute frequency of patch switching included both the cost of obtaining prey and the cost of switching between patches.

Summary

Which prey to include in the diet and which patches to exploit are two major questions that have been addressed in foraging research over the past 20 years. Early theories of prey choice (e.g., Emlen, 1966; MacArthur & Pianka, 1966; Royama, 1970; Schoener, 1969) and what later came to be known as optimal diet models were deterministic in that they assumed certain variables (such as search cost, energy gain, handling time, and travel time), held constant values. These variables were subsequently quantified to predict and explain foraging behavior. Early models also assumed that energy gain was a continuous rather than a discrete event (long- versus short-termed average rate maximization), and thus held true only for relatively high rates of energy intake. Later optimal diet models relaxed some of the traditional assumptions in an attempt to account for changing (stochastic) foraging environments. They also assumed that energy intake is not always the currency to be maximized, and that it was a discrete rather than continuous event (see Charnov, 1976a; Green, 1987; Iwasa et al., 1981; Kacelnick et al., 1987; McNair, 1979; Mellgren & Brown, 1987; Pulliam, 1974).

Semi-naturalistic field studies of prey choice have qualitatively supported many of the predictions promulgated by the optimal diet model, but have generally failed to support the model quantitatively. The most widely supported prediction is that predators choose prey that maximize E/h (Cambell, 1987; Davies, 1977a; Goss-Custard, 1977a, 1977b; Sutherland, 1982). Several studies have supported the prediction that prey choice is determined by the density of the more profitable prey and not the density of less profitable types (Davies, 1977b; Goss-Custard, 1977a; Hanson & Green, 1984; Krebs et al., 1977). Very little, if any, work in the field supports the prediction that diets should be all or none (that less profitable prey always be ignored regardless of density), or the prediction that partial preferences should not be observed (Goss-Custard, 1977a).

Studies of prey choice in the operant laboratory are more common than field studies and have sought to directly test optimal foraging models, or have been conducted to examine psychological theories of choice, such as the delay reduction hypothesis or the matching law (e.g., Fantino & Abarca, 1985; Herrnstein, 1970, 1974). Results of laboratory studies confirm many findings from the field; for example, that foragers maximize E/h (Erichsen et al., 1980; Lea, 1979; Peden & Rohe, 1984) and that prey choice depends only on the density of more profitable types (e.g., Krebs et al., 1974; Werner & Hall, 1974). Laboratory findings have failed to support predictions suggesting there should not be partial preferences (e.g., Emlen & Emlen, 1975; Zach & Falls, 1978).

Theories of patch use have been concerned with both patch residence time (RT) and patch giving-up time (GUT). Whereas RT is the interval between patch entry and patch exit, GUT is the interval of time between the last prey capture and patch exit. The Marginal Value Theorem (MVT) is a model of patch RT which predicts the optimal forager will abandon a food patch when the average rate of prey capture falls to a level equal to or below the average rate in alternative patches (Charnov, 1976b). The MVT has also been extended to account for optimal GUTs, although others argue that it is an inappropriate application (McNair, 1982, 1983).

Empirical studies of patch choice in the field have generally supported the MVT (Cowie, 1977; Krebs et al., 1974; Pyke, 1978a), although others would suggest that these were not valid tests (Gray, 1987). An early test by Krebs et al. (1974) used chickadees foraging for mealworms in artificial pinecones (the pinecones were the patches). Their results indicated that the chickadees abandoned a patch after a relatively fixed GUT; the value of which approximated the point at which it would be more prosperous to switch patches. Other studies of patch use in semi-natural settings have functionally related travel cost to choice of patches (i.e., as travel cost increases, switches between patches decrease) (Cowie, 1977; Pyke, 1978a). Patch choice has also involved manipulating the density of prey in two or more patches and determining the time allocated to each (Smith & Dawkins, 1971; Smith & Sweatman, 1974). The methods used to study patch choice are numerous, but most have, again, qualitatively but not quantitatively supported the predictions espoused by optimal patch-use models.

Laboratory studies of patch choice have used similar approaches, but under more controlled circumstances. For example, many of the studies using travel cost as the independent variable have used switches between patches as the dependent measure (e.g., Baum, 1982b; Cheney et al., 1982, 1985), but have also dealt extensively with patch RT and GUT. Experimental psychologists suggest that field investigations of RT and GUT are similar to operant studies of switching between two concurrent alternatives (usually schedules of reinforcement) by using a changeover delay or some other response requirement (e.g., pecks to a center key). Most laboratory studies have manipulated costs of obtaining prey and/or the density of prey available in two or more patches (Hanson & Green, 1984; Mellgren, 1982; Mellgren et al., 1984). Recently, studies of patch choice have expanded to incorporate replenishing and depleting cycles of prey within patches (Baum, 1987; Dow & Lea, 1987; Timberlake, 1984; Timberlake et al., 1987) and three-alternative choice (Fantino et al., 1987). Future research will determine the ultimate utility of laboratory approaches to studying foraging behavior, as operant investigators are gaining more understanding of foraging as it occurs in the wild.

CHAPTER III

GENERAL METHOD

Subjects

Twelve adult common pigeons (Columba livia) of unknown gender served in three experiments (four in each). Each subject was run six or seven sessions per week and maintained at approximately 80% free-feed weight for the duration of the studies. Subjects were food deprived at least 23 hours prior to each experimental session and housed in individual cages with continuous access to water. Supplemental feeding was delivered in the home cage approximately 30 minutes after the termination of that daily session. Purina racing checkers were used in the experimental chamber and for supplemental feeding.

Apparatus. A single, three-key, dual hopper Colbourn operant chamber was used as the experimental apparatus for all subjects and experiments. The chamber was enclosed in a sound and light attenuated box with an exhaust fan located on the back wall. The fan operated during all training and experimental sessions to both lower the temperature in the chamber and filter out extraneous noise. The chamber interior (28.5 x 29.0 x 24.0 cm) contained a houselight, three response keys, and two apertures for the delivery of food. The houselight (GE 1820 bulb operated at 25v dc) was located 28 cm above the chamber floor and 10 cm from the front and back sides of the chamber. Response keys were located 18.5 cm above the chamber floor and 8 cm apart. A response force (key peck) of approximately 5N (1 mm in distance) was required to close a microswitch and record a response. Each of the side keys was illuminated by a white, red, or green lamp (Industrial Electronics Engineers In-Line Digital Display Unit with Kodak Wratten filters) and the center key only by a white lamp. All response keys were inoperative during food presentations.

Food delivery consisted of 3-sec. access to checkers in one of the two 5.8 x 5.8 cm food apertures located directly below each side key and 3.75 cm above the chamber floor. A white hopper light (GE 1820 bulb) operated with each food presentation. Manipulation of the program was controlled by (a) a Commodore 64 microcomputer, (b) a G-link interface connected to the game port of the Commodore computer, and (c) an "intelligent" interface which runs on 28v dc and has a Z-80 central processing unit that runs at 4 MHz and controls communication between the Commodore computer, G-link interface, and the experimental chamber. The interface was also connected to essential electromechanical modules via parallel port (Crossman, Stephenson, & Lynch, 1980) and a 1541 Commodore disk drive. Critical experimental data was transcribed daily from the display monitor to preprinted data sheets.

Procedure

The general procedure is presented as a flow chart in Figure 2. When the subject's body weight was equal to or below 90% free-feeding weight, the following set of procedures were implemented.

Training. Four specific training procedures were presented to each experimental subject prior to formal baseline sessions. First, subjects were placed in the chamber individually with 5 g of checkers accessible in each of the two food apertures (aperture training). The

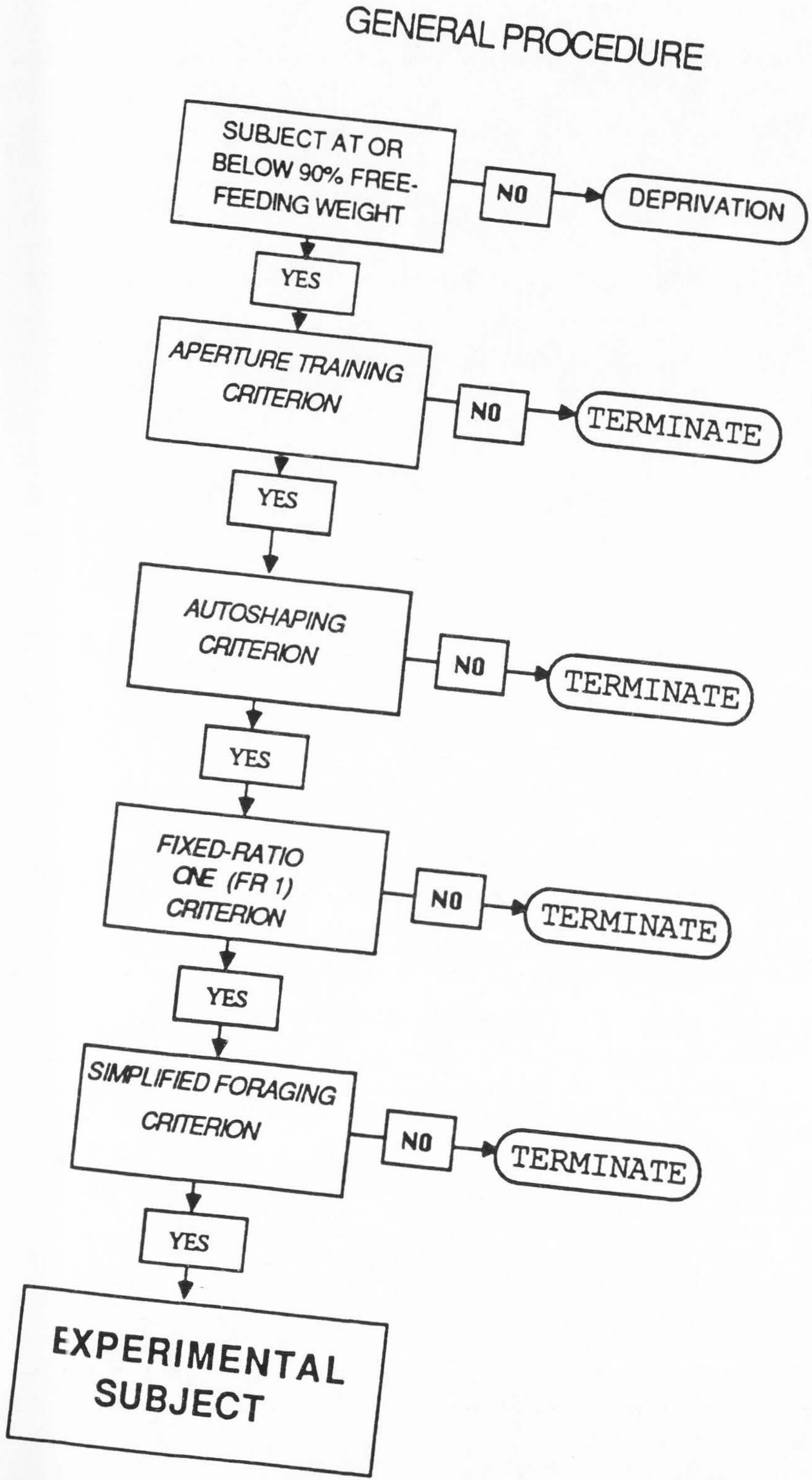


Figure 2. Flow chart representing the training criteria for experimental subjects.

seconds, beginning with the left side at the start of the session. One response to the illuminated key lead to a 3-second hopper operation. If the subject failed to respond within 6 seconds, the illuminated key was inoperative, and the opposite key illuminated for 6 seconds and continued in this manner until the session terminated (after 20 responses or 60 minutes, whichever occurred first). If the subject emitted 20 or more responses during this procedure, the subject advanced to a simplified version of the foraging program (see below). If the subject failed to meet the FR 1 training criterion, it was terminated from the experiment and a new subject was obtained.

Finally, subjects were exposed to a simplified version of the foraging program. In this procedure, the subject was required to respond only once on the center key to switch sides (patches) or return to the initial link, white key (rejection), and only once to gain access to reinforcement at the onset of the terminal link of the schedule. Figure 3 converts the series of three term contingencies displayed in Figure 1 into an experimental flow chart to aid in the design of the simulation schedule. Figure 4 further depicts the foraging schedule as a concurrent (simultaneously available) chain (dual component), adjusting probability schedule of reinforcement. The schedule adjusted only in the initial link of the chain to simulate replenishment and depletion of food from the prey patches.

As this program simulated an actual foraging environment, each side key served as a prey patch (to simulate spatially separated places to work and eat). The center key served to simulate travel cost between patches only during the initial link and required 10

Figure 3. The foraging episode represented as a flow chart. The subject first selects a patch, searches in the patch, and upon detection, either accepts, rejects, and continues foraging in the same patch or switches to the alternate patch. If the subject accepts the terminal link (prey) offered, the schedule terminates in a kill (reinforcement). The subject can then again resume searching in the same patch or travel to the alternate patch

FORAGING MODEL: CONCURRENT CHAIN

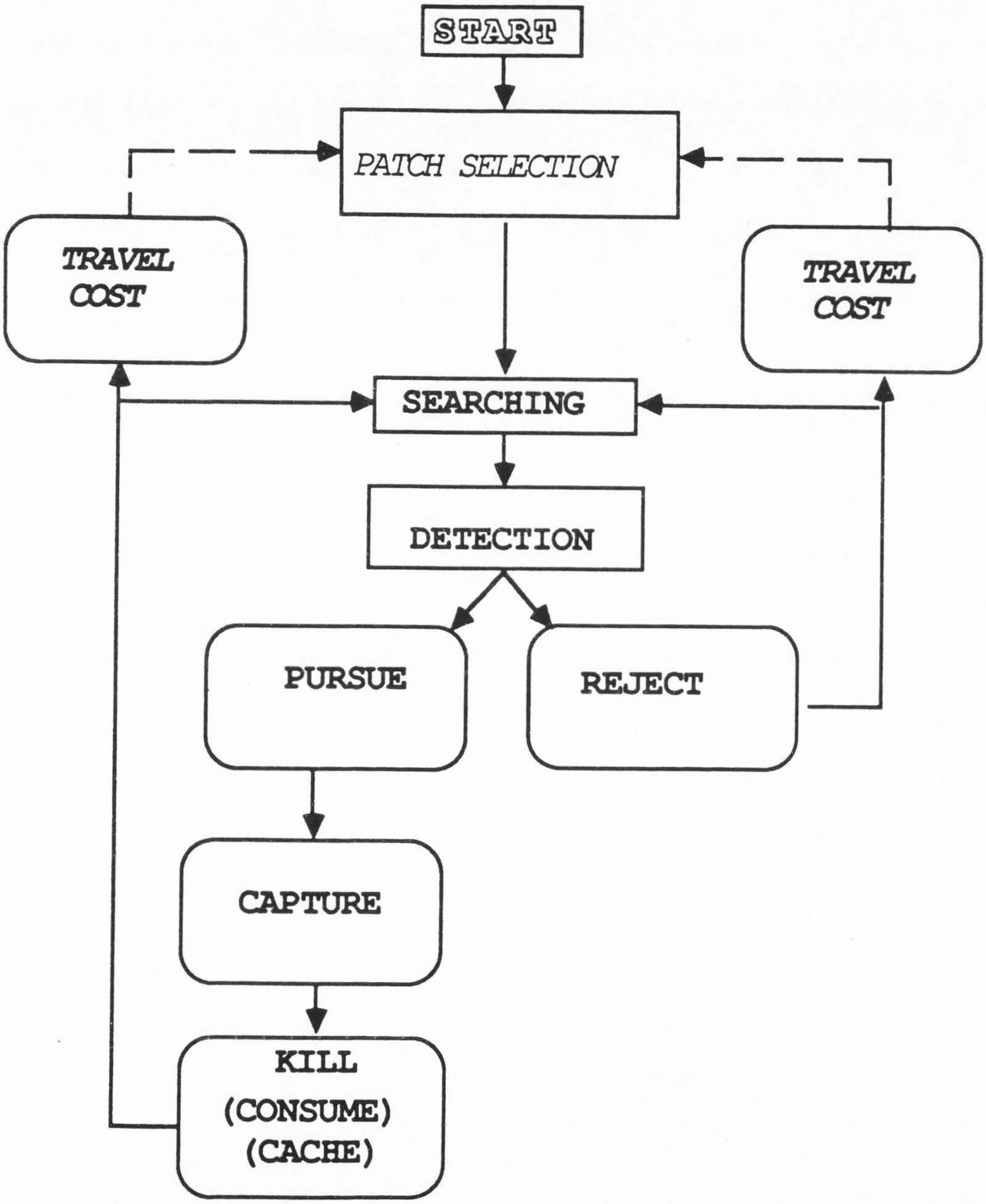
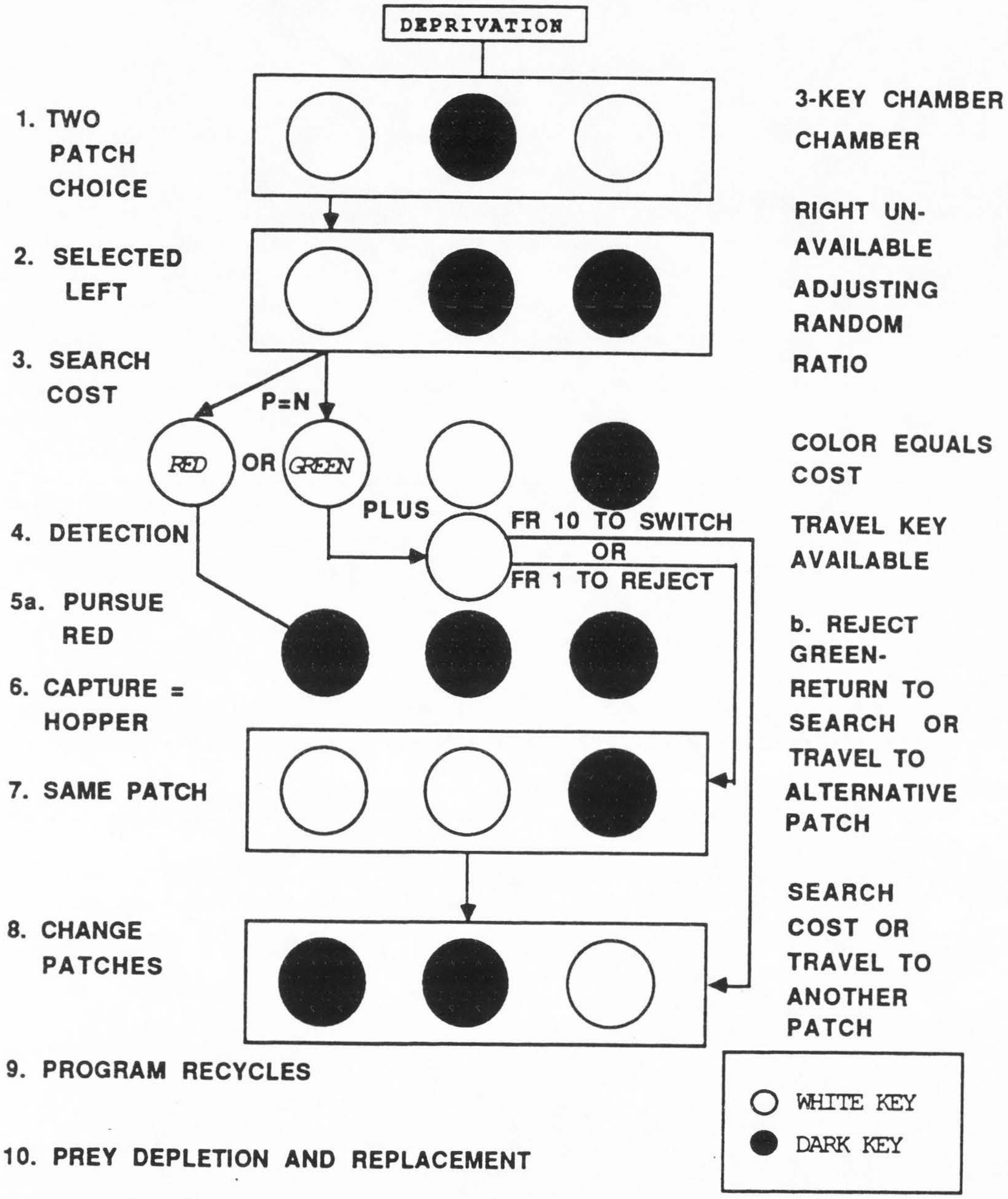


Figure 4. The foraging episode represented as a concurrent chain schedule of reinforcement. The subject begins by selecting a patch. Once the patch has been selected, the subject begins searching (white key). After the RR X schedule in the search phase is completed (the initial link), the key color changes to either red or green (the terminal link). At this point, the subject can either accept or reject the schedule offered. If the subject accepts the schedule, it will terminate in food reinforcement. If rejected, the animal can resume search or switch to the other patch.

FORAGING MODEL: EXPERIMENTAL SIMULATION



responses (FR 10) for a switch to the alternate patch. The center key also served as a prey rejection key when the terminal component was in effect on either side key, allowing the animal to peck the center key once to return the side key to the initial link (search) component (rejecting a prey item), but was never paired with primary reinforcement.

On each white side key, the initial component was a concurrent chain adjusting probability (random ratio) schedule. Random ratio schedules require each response to have an equal probability of resulting in reinforcement. The adjusting schedule increased by a factor of 5 each time the subject re-entered a patch after food presentation. For example, the first time the subject "worked a patch," the initial link is an RR 5 schedule. After a reinforcer had been delivered, the requirements advanced to RR 10, and so on, increasing as prey items were depleted from the patch. Concurrently, as the subject obtained prey on one side, prey were replenished on the opposite side by the RR schedule decreasing by a factor of 5 each time a reinforcer was obtained in the opposite patch, until replenishment reached RR 5 (i.e., foraging in one patch produced decreasing prey density in that patch, while density increased in the unexploited patch).

A red or green key color following the initial (white) link signalled that the terminal (colored) component was in effect. The change from a white key color to a colored key was the reinforcer for searching and considered equivalent to prey detection in this model of foraging. The travel center key was available to the subject at all times, with the exception of the first patch choice and directly after a switch between patches. Ten responses to the illuminated center white key allowed the subject to switch patches. When either terminal component was in effect, however, a single key peck to the center white key returned the subject to the initial link on that same side. A response of this type is termed a "terminal link prey rejection," and may occur when one terminal link is higher in cost than the alternative schedule. The terminal link consisted of one of two possible RR schedules, each associated with a different key color (red or green) and/or cost. This procedure more closely approximates an actual foraging episode because of the replenishing and depleting action during the search component contingent upon the animal working and the number of prey obtained from each patch.

CHAPTER IV

EXPERIMENT I: PREY CHOICE AS A FUNCTION OF VULNERABILITY

Purpose

The purpose of this study was to functionally relate terminal link (prey) rejections in the concurrent chain schedule to the size of the random ratio schedule in each terminal link. A functional relation describes the external conditions of which behavior is a function (i.e., a cause and effect relationship; Skinner, 1953). In ethological terms, the cost of obtaining one prey type was greater than the cost of obtaining another, but energy gain was equal for both. The question becomes, when the animal is randomly presented with both, will it consistently reject the high-cost prey and instead pursue the low-cost prey? The purpose was to determine how vulnerability (cost) relates to the forager's choice to pursue or reject prey.

Subjects and Apparatus

Four wild trapped adult common pigeons (Columba livia) of unknown age and gender served. The apparatus is described above in the General Method section.

Procedure

A single-subject reversal design (Sidman, 1960) was used to determine the effects of terminal link ratio size on prey rejections.

Baseline. All subjects were initially exposed to 20 sessions of baseline. In this condition, initial search links replenished and depleted according to the adjusting random ratio schedule beginning at RR 5. Terminal link pursuit schedules were equal (RR 20). The probability of either of the two colored terminal links occurring was .50. This condition represented a situation where there was no advantage to rejecting prey items offered or to work one patch more frequently than the other.

Experimental conditions. Table 1 summarizes the order of conditions for each subject. In the first experimental manipulation (B), the size of the random ratio schedules in the terminal links were manipulated differentially, with opposite key colors associated with high- and low-cost prey items. For two subjects, the size of the ratio in the red terminal link was 60 and 20 for the green terminal link (R = 60/G = 20). Relative ratio size was the same for the second set of subjects only with opposite key colors. In the second manipulation (C), the relative difference between ratios was greater for all subjects (R = 10/G = 100 and G = 100/R = 10). In the final manipulation (D), the relative size of the ratio was even greater (i.e., R = 10/G =150). The criterion used to determine stability was no new high or low values in the number of terminal link rejections for five consecutive sessions, with at least 10 sessions occurring in each condition. This stability criterion is commonly used to study steady-state operant behavior (e.g., Cheney et al., 1985; Mazur, 1974).

Results

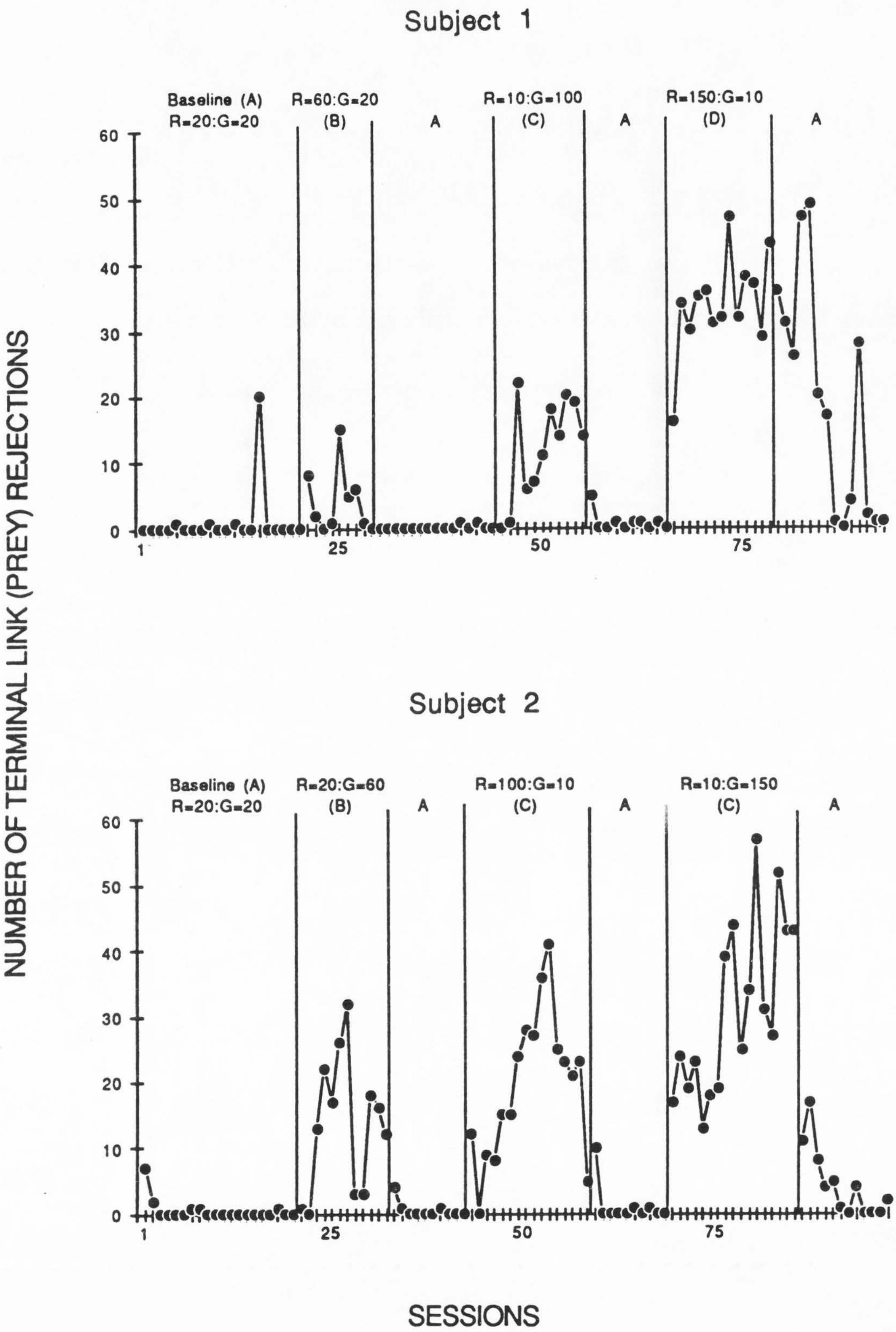
The total number of prey rejections for each subject and session are shown in Figures 5 and 6. Baseline conditions are shown in panels

Table 1

Terminal Link Ratio Requirements for Each Subject in Experiment I Under all Experimental Conditions

Subject	Condition A (1:1)	 B (3:1)	 C (10:1)	 D (15:1)
1	20R/20G	60R/20G	10R/100G	150R/10G
2	20R/20G	20R/60G	100R/10G	10R/150G
3	20R/20G	60R/20G	10R/100G	150R/10G
4	20R/20G	20R/60G	100R/10G	10R/150G

<u>Figure 5</u>. Number of prey rejections as a function of ratio size for red (R) and green (G) key colors in the terminal link of the concurrent chain schedule for Subjects 1 and 2 in Experiment I. Baseline conditions are displayed in panels marked A, while experimental manipulations with increasing cost differentials are displayed in panels marked B, C, and D.


Subject 1
Baseline (A)
R=20:G=20
R=60:G=20
(B)
A
R=10:G=100
(C)
A
R=150:G=10
(D)
A
60
50
40
30
20
10
0
1
25
50
75
Subject 2
Baseline (A)
R=20:G=20
R=20:G=60
(B)
A
R=100:G=10
(C)
A
R=10:G=150
(C)
A
60
50
40
30
20
10
0
1
25
50
75
NUMBER OF TERMINAL LINK (PREY) REJECTIONS
SESSIONS

marked A. Experimental manipulations with incremental terminal link schedule differences are shown in panels marked B, C, and D. Performance in terms of rejecting high-cost terminal links was apparent. When the relative response requirements were greater, the birds frequently rejected the high-cost terminal link requirement and returned to the initial link schedule to resume searching. Performance in all cases generally recovered during baseline conditions (i.e., the birds did not reject prey items encountered and return to the initial link search component).

As relative differences between size of the RR schedule on the terminal side keys increased, the probability of a rejection also increased. More specifically, rejections during the leaner random ratio component increased as the relative differences between ratio sizes in the two schedules increased. When the response requirement was increased threefold on one side key (e.g., G = 20/R = 60), subjects rejected at higher rates than that evident in the baseline condition. However, when the response requirement was increased tenfold for one terminal link, a substantial increase in rejections occurred (i.e., the birds rejected the RR 100 schedule and returned to the initial search state). In the third manipulation (D), the colors were reversed once again (i.e., the green key was correlated with a RR 150 schedule and the red key a RR 10 schedule). Rejections on the opposite key color occurred at an even higher rate than that during the B condition.

Table 2 summarizes the mean number of rejections over the last five sessions of each experimental condition, the mean number of

Table 2

Mean Number of Initial and Terminal Link Responses, Terminal Link Rejections, and Switches Between Patches Over the Last Five Sessions of Each Experimental Condition in Experiment I. Medians are Presented for Rejections and Switches

Subject 1	Initial Link Responses	Terminal Link Responses	Mean Rejections	Median Rejections	Mean Switches	Median Switches
A (20R:20G)	1009	836	0	0	6.4	8
B (60R:20G)	1122	1537	2.4	1	6.8	6
A (20R:20G)	967	811	0.2	0	6.6	5
C (10R:100G)	1374	1499	17.0	20	10.2	12
A (20R:20G)	1123	833	0.6	0	7.0	7
D (150R:10G)	1666	464	35.8	37	9.4	7
A (20R:20G)	918	788	7.2	2	8.4	4
Subject 2						
A (20R:20G)	1258	790	0.2	1	4.6	4
B (20R:60G)	1104	1568	10.4	18	6.6	6
A (20R:20G)	832	646	0.2	0	9.0	7
C (100R:10G)	2119	956	19.4	21	4.3	5
A (20R:20G)	1428	841	0.4	1	6.0	5
D (10R:150G)	1794	453	39.2	52	11.8	13
A (20R:20G)	891	739	1.2	0	6.8	8

(table continues)

Table 2 cont.

Subject 1	Initial Link Responses	Terminal Link Responses	Mean Rejections	Median Rejections	Mean Switches	Median Switches
A (20R:20G)	1013	760	0.8	2	7.2	7
B (60R:20G)	1150	1554	3.4	3	5.2	6
A (20R:20G)	1033	828	0.2	1	8.2	10
C (10R:100G)	1740	1454	14.4	13	5.2	6
A (20R:20G)	1249	792	0	0	6.6	5
D (150R:10G)	1998	578	37.4	38	10.2	7
A (20R:20G)	935	726	0.6	0	8.0	8
Subject 4						
A (20R:20G)	925	847	0.6	1	8.2	10
B (20R:60G)	1170	1291	20.2	21	8.2	6
A (20R:20G)	1008	791	1.0	1	6.6	6
C (100R:10G)	1607	626	31.6	35	8.4	9
A (20R:20G)	1016	705	2.0	1	7.0	7
D (10R:150G)	1449	559	37.2	31	9.8	9
A (20R:20G)	897	744	4.2	7	6.6	5

initial and terminal link responses, switches between patches, and medians for both prey rejections and patch switches. For three of the four subjects, the mean number of initial link responses increased across experimental conditions and remained stable over all baseline conditions. For the other subject, the mean number of initial link (search) responses were higher for the B condition than the C condition, but only slightly. The mean number of terminal link (pursuit) responses decreased across experimental conditions for all subjects and again remained generally stable over baseline conditions. The mean and median number of terminal link (prey) rejections also increased across conditions and remained low across baseline conditions for three of the four subjects, while the differences for the fourth were again minimal. Finally, switches between patches remained generally stable, with slight variability across subjects and conditions. This variability, however, was not predictable within or across subjects or conditions. Figure 7 depicts the mean number of rejections over the last five sessions of each condition and shows the incremental frequency of prey rejections as the relative differences between the two terminal links increased. Means for the incremental B, C, and D conditions are also shown in Table 2.

Discussion

Experiment I provided an experimental analysis of the pursuit component of the foraging chain by simulating two prey types possessing different costs, but equal pay-offs, and examining the resulting change in prey choice. Specifically, as the size of the terminal link random ratio schedule increased for one prey item, the

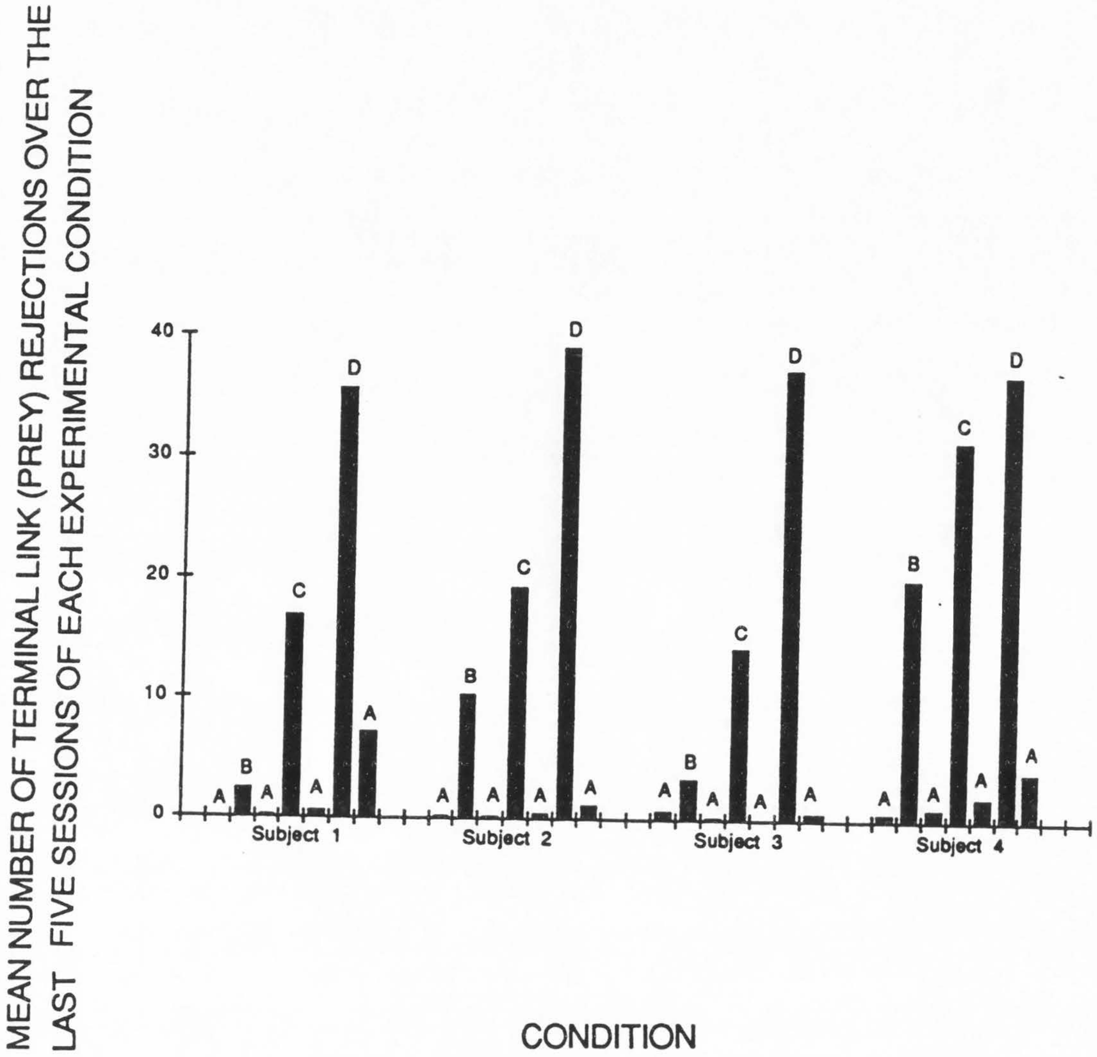


Figure 7. Mean number of terminal link (prey) rejections over the last five sessions of each experimental condition in Experiment I. Baseline conditions are marked A, while experimental manipulations with increasing cost differentials are labelled B (1:3), C (1:10), and D (1:15).

subjects consistently rejected those prey items and opted to return to the initial link schedule and resume searching for other prey items. This finding is interesting in that the subject responded to a stimulus which was never paired with unconditioned reinforcement, rather than one which had. This result is consistent with the notion that search behavior may be reinforcing in and of itself. Results showed that as the relative size of the ratios for two prey types increased, the probability of rejecting high cost prey also increased. That is, pigeons consistently pursued low-cost prey items but rejected high-cost prey. This general result has been supported in a number of studies using different subjects and procedures (e.g., Collier, 1977; Hanson & Green, 1984; Lea, 1979; Peden & Rohe, 1984).

The results of this study suggest that animals foraging for food will consistently pursue prey items that are associated with the fewest key pecks required for primary reinforcement. In addition, switching between patches occurred at a much more stable rate than rejections. Subjects would switch patches even when prey costs were equal, and few, if any, rejections were emitted (see Table 2). This suggests that the adjusting RR search schedule (simulating replenishment and depletion) was contacting the subject's behavior and influencing performance. Costs associated with colored red and green terminal links appeared interchangeable, and no order effects were apparent. Baseline performance generally recovered between and after experimental manipulations, thus accentuating control by the independent variable.

CHAPTER V

EXPERIMENT II: THE EFFECTS OF PREY VULNERABILITY AND DENSITY ON CHOICE

Purpose

The purpose of this experiment was to systematically expand on Experiment I by covarying the relative size of the random ratio schedule (pursuit cost) and the probability of encountering either of the two terminal link schedules (prey density). Thus, Experiment II posed the question, how does the density variable within the vulnerability and replenishment and depletion variables affect the forager's choice to pursue or reject prey? The data obtained from this study can be subsequently compared to results from Experiment I to determine if and how density and prey vulnerability affect choice.

Subjects and Apparatus

Four wild trapped adult pigeons (Columba livia) of unknown age and gender served. All other factors concerning housing, deprivation, and the experimental apparatus were identical to those described in the General Method section.

Procedure

An ABACA reversal design (Sidman, 1960) was used to assess the combined effects of prey vulnerability and density on prey choice.

Baseline. Baseline conditions were identical to those described in Experiment I in which the terminal link schedules were equal (RR 20), and there was no advantage to rejecting any of the prey items offered. That is, each color (red or green) had an equal probability of occurrence, and terminal link pursuit costs were identical. The initial link random ratio (search) schedule on both side keys depleted (increased in cost) and replenished (decreased in cost) as reinforcers correlated with either color were taken.

Experimental conditions. Table 3 shows the order of conditions for each subject in Experiment II. For Subjects 5 and 6, the first experimental condition (B) represented a high probability of the high-cost component occurring for the red terminal link and a low probability of occurrence for the low-cost green terminal link ($R = 40/G = 20$; $p(R) = .67/p(G) = .33$). That is, on the average, the high-cost component (red) occurred 67% of the time, and the low-cost (green) component occurred 33% of the time. In Condition C, the probabilities (densities) were reversed to create a situation with a high probability of low-cost prey and low probability of high-cost prey. For Subjects 7 and 8, the manipulations were identical in Conditions B and C, but the size of the terminal link schedules was relatively greater (1:3).

Table 3 also indicates the sequence of conditions for each subject in Experiment II. Baseline (A) conditions were run between each and after the final (C) manipulation. The stability criterion (Mazur, 1974) for advancement through conditions was that no new high or low values occurred in the number of prey rejections across the last five sessions of each condition, with at least 10 sessions required for each.

Results

Results appear in Figures 8, 9, and 10. Figures 8 and 9 display

Table 3

Terminal Link Ratio Requirements (Cost) and Probabilities (Density) for Each Subject and Experimental Condition in Experiment II

	Conditions[1]					
	A		B		C	
Subject	Cost	Prob.	Cost	Prob.	Cost	Prob.
5	20R/20G	.5R/.5G	40R/20G	.67R/.33G	40R/20G	.33R/.67G
6	20R/20G	.5R/.5G	40R/20G	.67R/.33G	40R/20G	.33R/.67G
7	20R/20G	.5R/.5G	20R/60G	.67R/.33G	20R/60G	.33R/.67G
8	20R/20G	.5R/.5G	20R/60G	.67R/.33G	20R/60G	.33R/.67G

[1] Condition A: Baseline
Condition B: High-Cost/High-Probability, N=2, 1:2
High Cost/Low-Probability, N=2, 1:3
Condition C: High-Cost/Low-Probability, N=2, 1:2
High-Cost/High-Probability, N=2, 1:3

Figure 8. Number of terminal link (prey) rejections as a function of ratio size and probability of encounter (density) for Subjects 5 and 6 in Experiment II. Terminal link key colors are represented by R (red) and G (green). Numeric values represent the average size of the ratio schedule in the terminal link. The probability (p) of each terminal link occurring is also shown for each condition

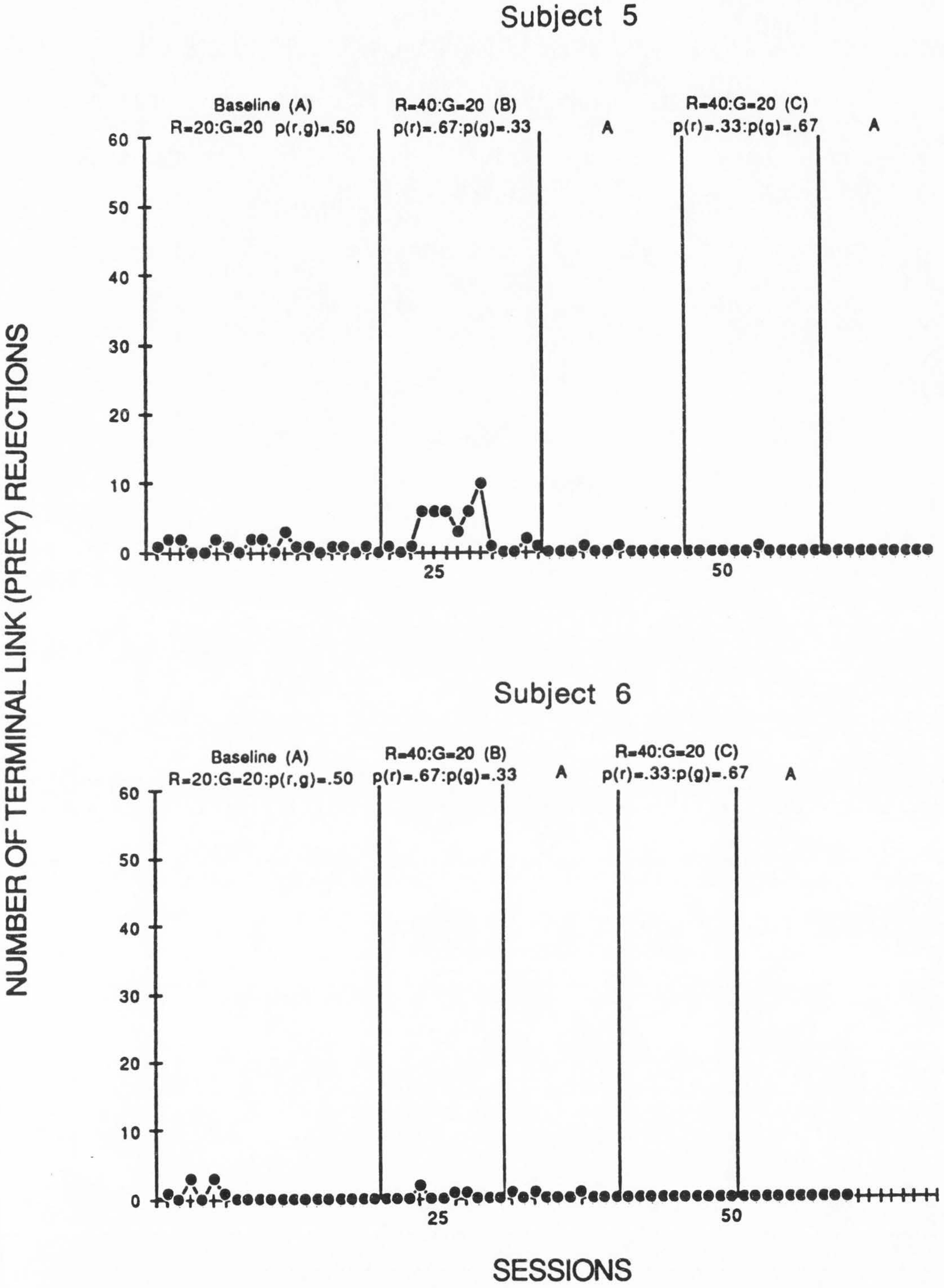
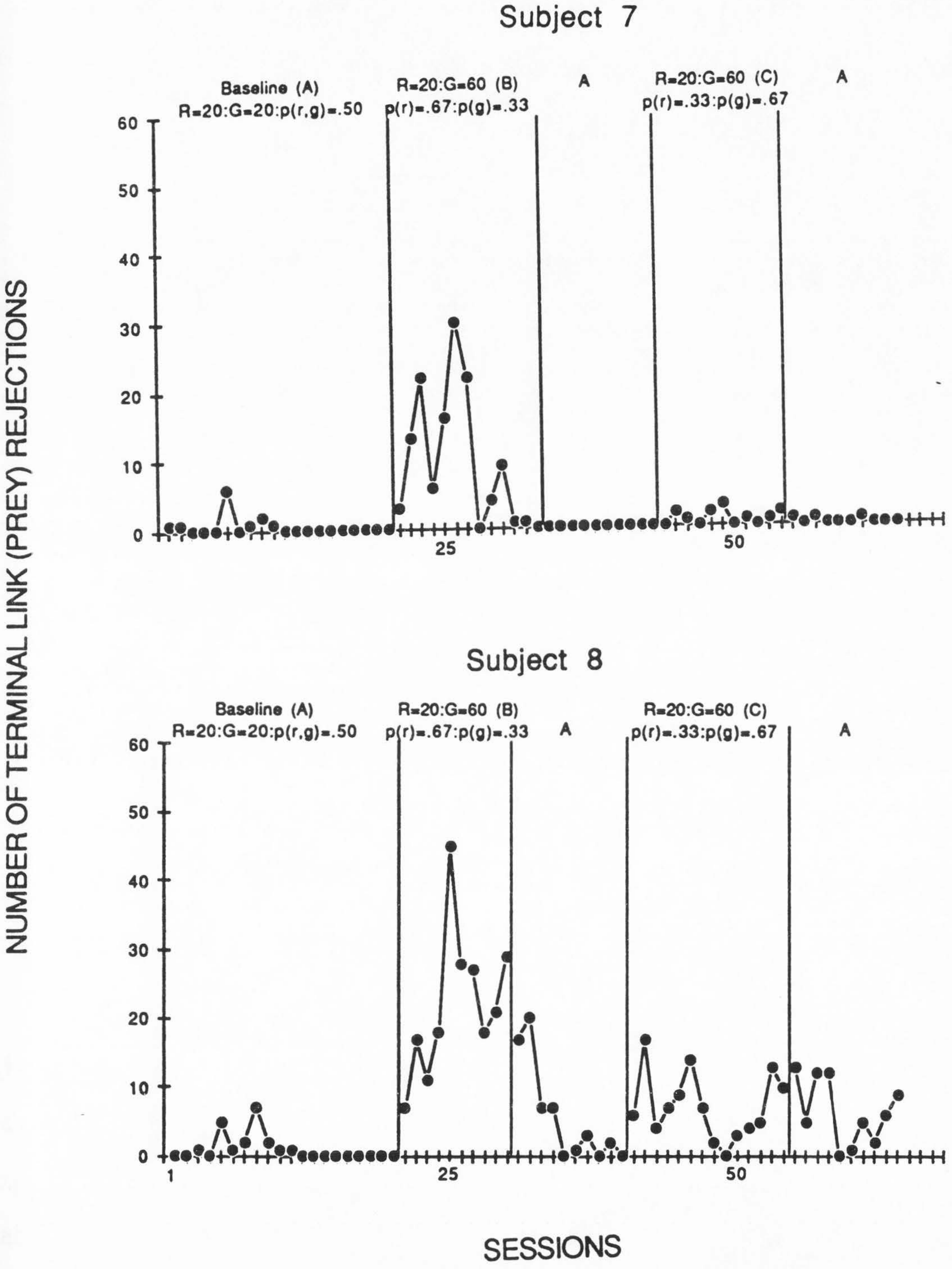

Subject 5
Baseline (A)
R=20:G=20 p(r,g)=.50
R=40:G=20 (B)
p(r)=.67:p(g)=.33
A
R=40:G=20 (C)
p(r)=.33:p(g)=.67
A
60
50
40
30
20
10
0
25
50
Subject 6
Baseline (A)
R=20:G=20:p(r,g)=.50
R=40:G=20 (B)
p(r)=.67:p(g)=.33
A
R=40:G=20 (C)
p(r)=.33:p(g)=.67
A
60
50
40
30
20
10
0
25
50
NUMBER OF TERMINAL LINK (PREY) REJECTIONS
SESSIONS

Figure 9. Number of terminal link (prey) rejections as a function of ratio size and probability of encounter (density) for Subjects 7 and 8 in Experiment II. Terminal link key colors are represented by R (red) and G (green). Numeric values represent the average size of the ratio schedule in the terminal link. The probability (p) of each terminal link occurring is also shown for each condition.


Subject 7
Baseline (A)
R=20:G=20:p(r,g)=.50
R=20:G=60 (B)
p(r)=.67:p(g)=.33
A
R=20:G=60 (C)
p(r)=.33:p(g)=.67
A
60
50
40
30
20
10
0
25
50
Subject 8
Baseline (A)
R=20:G=20:p(r,g)=.50
R=20:G=60 (B)
p(r)=.67:p(g)=.33
A
R=20:G=60 (C)
p(r)=.33:p(g)=.67
A
60
50
40
30
20
10
0
1
25
50
NUMBER OF TERMINAL LINK (PREY) REJECTIONS
SESSIONS

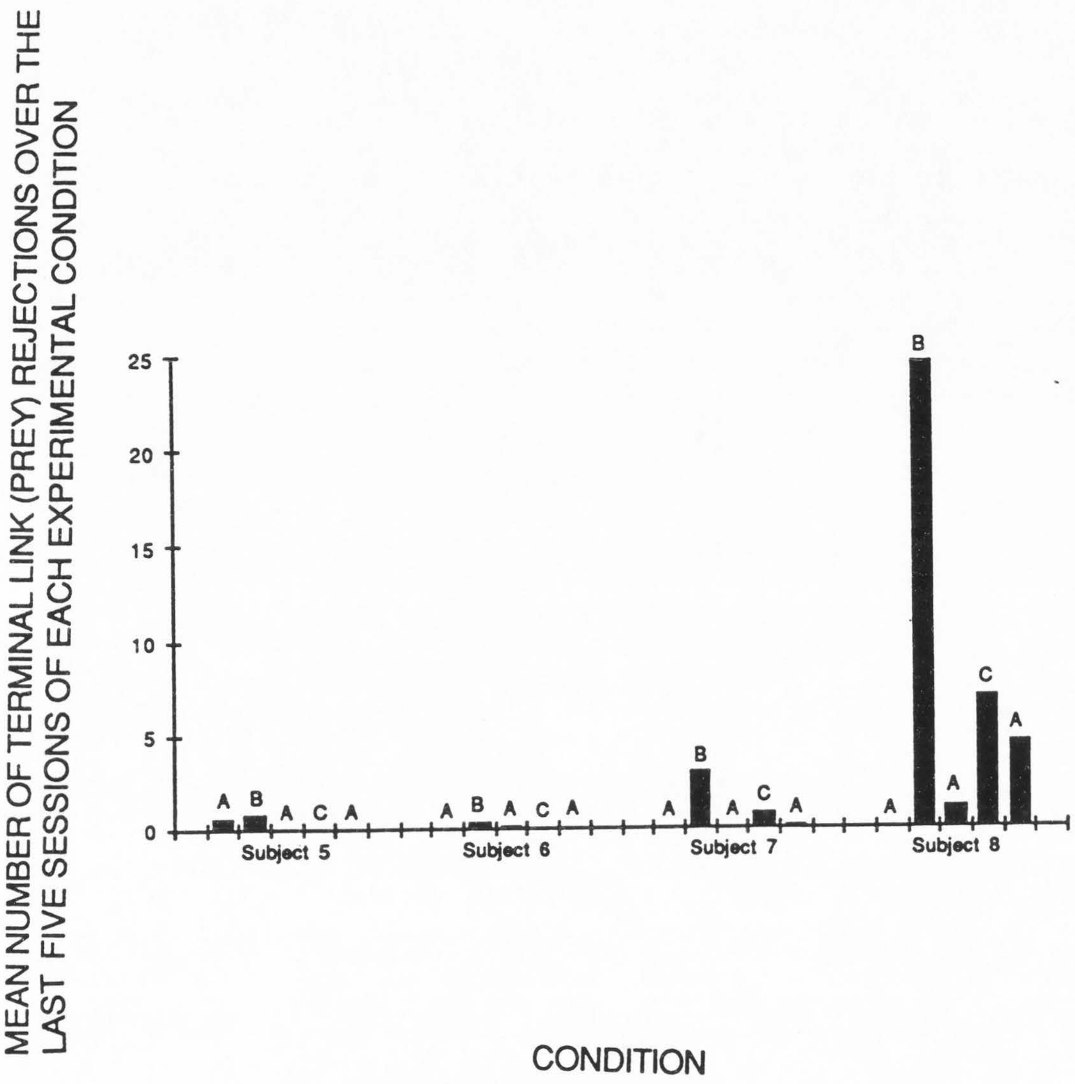


Figure 10. Mean number of terminal link (prey) rejections over the last five sessions of each experimental condition for all subjects in Experiment II. Baseline conditions are represented by bar graphs labelled A. Experimental manipulations are represented by bar graphs B, C, and D.

the total number of terminal link prey rejections for each subject and session in Experiment II as both cost and density were varied. For Subjects 5 and 6, the initial baseline condition resulted in relatively few prey rejections, averaging 0.6 and 0.0 over the last five sessions, respectively. Condition B showed no significant changes in the average number of prey rejections, averaging 0.8 and 0.4 for Subjects 5 and 6, respectively. Condition C also failed to show any major changes in the average number of prey rejections (0.0 for both subjects). The remaining baseline conditions also displayed indifference between prey.

Subjects 7 and 8 did not reject any terminal link schedules over the last five sessions of the first baseline condition. In Condition B, however, there was an average of 3.0 rejections for Subject 7 and 24.6 for Subject 8. These figures decreased when the probabilities were reversed (Condition C) to an average of 0.8 and 7.0 for Subjects 7 and 8, respectively. Performance recovered during subsequent baseline sessions for three of the four subjects, and rejections emitted by the fourth subject were previously high-cost/low-probability prey.

Figure 10 displays the mean number of prey rejections across the last five sessions of each condition. For Subjects 5 and 6, very few rejections were emitted across all baseline and experimental conditions when the differential was 1:2. For Subjects 7 and 8, the average number of rejections was relatively greater, as was the differences between the RR schedules in the terminal link (1:3). Terminal link rejections that occurred for Subjects 7 and 8 through experimental conditions were the low-probability/high-cost terminal links. Rejections for Subject 8 during the B condition was significantly higher (24.6) than comparable data from Subject 7 (3.0) under the same experimental conditions. Additionally, performance did not fully recover during the second or third baseline condition for Subject 8.

Table 4 presents additional data on the mean number of initial and terminal link responses, prey rejections, and switches between patches, as well as medians for both rejections and switches. Initial link search responses were generally stable across all subjects under baseline conditions, averaging 748, 945, 959, and 822 for Subjects 5-8, respectively. Terminal link responses during baseline were also highly stable across subjects, averaging 790, 823, 867, and 807 for Subject 5, 6, 7, and 8, respectively. Rate of prey rejections during baseline are low for all subjects, and switches between patches also occurred at stable rates throughout all baseline conditions, averaging 11.5, 9.3, 6.8, and 11.3 for Subjects 5-8, respectively.

The number of initial link responses over the first experimental condition was highly stable across subjects, averaging 1020, 1011 for Subjects 5 and 6 and 999 and 1478 for Subjects 7 and 8. Initial link responses in the C condition were also stable across subjects, averaging 786 and 757 for Subjects 5 and 6 and 760 and 817 for Subjects 7 and 8, respectively. Terminal link responses were also extremely stable over baseline conditions, averaging 790, 823, 867, and 807, but somewhat less stable over the B condition (1413, 1486, 2103, and 1492) and C condition (1066, 1013, 1427, and 1126). Prey

Table 4

Mean Number of Initial and Terminal Link Responses, Prey Rejections and Switches Between Patches Over the Last Five Sessions of Each Condition in Experiment II. Medians are Presented for Rejections and Switches.

	Initial Link Responses	Terminal Link Responses	Prey Rejections	Median Rejections	Switches	Median Switches
S5						
A 20R (.5):20G(.5)	734	797	0.6	0	13.4	15
B 40R (.67):20G(.33)	1020	1413	0.8	0	9.0	9
A 20R (.5):20G(.5)	702	811	0.0	0	14.2	13
C 40R (.33):20G(.67)	786	1066	0.0	0	8.0	9
A 20R (.5):20G(.5)	809	763	0.0	0	7.0	7
S6						
A 20R (.5):20G(.5)	1006	824	0.0	0	12.0	11
B 40R (.67):20G(.33)	1011	1486	0.4	0	11.0	14
A 20R (.5):20G(.5)	857	838	0.2	0	7.8	7
C 40R (.33):20G(.67)	757	1013	0.0	0	8.0	10
A 20R (.5):20G(.5)	972	806	0.0	0	8.0	10
S7						
A 20R (.5):20G(.5)	980	881	0.0	0	6.125	13
B 20R (.67):60G(.33)	999	2103	3.0	1	11.6	12
A 20R (.5):20G(.5)	985	839	0.0	0	8.2	7
C 20R (.33):60G(.67)	760	1427	0.8	0	9.4	9
A 20R (.5):20G(.5)	913	882	0.2	0	6.2	7
S8						
A 20R (.5):20G(.5)	843	873	0.0	0	13.0	14
B 20R (.67):60G(.33)	1478	1492	24.6	18	15.6	18
A 20R (.5):20G(.5)	625	810	1.2	0	13.0	10
C 20R (.33):60G(.67)	817	1126	7.0	5	11.6	13
A 20R (.5):20G(.5)	997	738	4.6	2	8.0	8

rejections over both experimental conditions were infrequent for Subjects 5 and 6 when the terminal link differential was 1:2 and more frequent for Subjects 7 and 8 when the differential was 1:3, although rate of rejection was significantly higher for Subject 8 relative to Subject 7. Finally, the number of switches between patches occurred at high rates for all subjects, averaging 11.7, 9.3, 9.0, and 10.7 for baseline, 9.0, 11.0, 11.6, and 15.6 for Condition B, and 8.0, 8.0, 9.4, and 11.6 for Condition C.

Discussion

The results for Subject 5 and 6 suggest that at RR terminal link values of 40 and 20, the birds accepted most higher-cost schedules when it was beneficial to do so (Condition B), but did not reject high-cost (RR 40) schedules even when it would have been more profitable (Condition C). This result suggests that differentials of 1:2 (low values) are not great enough for pigeons to reject higher-cost prey and return to searching for lower-cost prey. For Subjects 7 and 8, terminal link prey rejections generally did occur at differentials of 1:3 when it was profitable to do so (rejecting high-cost/low-probability prey; Condition B) and occurred at lower rates when high-cost prey had a higher probability of being encountered (Condition C).

The average number of prey rejections over the last five sessions of each condition (Figure 10) may be somewhat misleading at first look, but actually approximates appropriate behavior in all conditions except the last five sessions of the B condition and the entire C condition for Subject 7. For Subjects 5 and 6, all prey items should have been taken in Condition B, because the higher-cost prey had a probability of .67 of occurring. Yet the differences between the size of the terminal link schedules was not great enough for the bird to pursue this option. Some rejections would be expected in Condition C, but did not occur, suggesting that the terminal link schedule differentials were not great enough.

For Subjects 7 and 8, however, prey rejections should have been evident at approximately the rate displayed by Subject 8 rather than Subject 7 in both the B and C conditions. These subjects should have rejected all high-cost/low-probability prey at an average of about 20 per session. Interestingly, Subject 7 actually averaged nearly 10 rejections over all sessions of Condition B and emitted 30 rejections during one session. The data indicate that over the last five sessions, Subject 7 averaged only three rejections per session and averaged an extremely high (2103) number of terminal link pursuit responses in Condition B. Why this subject opted to accept high-cost/low-probability prey only toward the end of the condition needs to be examined more closely. It may have been simply a function of the animal oversampling less preferable prey items or possibly a result of the animal foraging in a generally efficient but not optimal (when defined by maximization of E/h) manner. For Condition C, it would have been more profitable for Subject 7 to reject high-cost/low-probability prey, but again, relative ratios may not have been great enough for the subject to specialize on low-cost/low-probability prey. An extension of this analysis would use pellets rather than chow in order to control the magnitude of reinforcement during each condition.

Further analysis suggests that initial link search and terminal link pursuit responses varied predictably with the size of the random ratio in the terminal component. That is, as pursuit cost increased, terminal link pursuit responses also increased, and as prey rejections increased, the number of initial link search responses also increased. Additional comparisons suggest that the average number of initial and terminal link responses did not vary significantly across subjects in the baseline or experimental conditions, except for the unexplained behavior of Subject 7 described above. The number of switches between patches occurred at high but stable rates, again suggesting the initial link-adjusting replenishment and depletion schedule was contacting the subject's behavior and influencing performance. Baseline performance generally recovered during reversals, except for a small number of rejections emitted by Subject 8 in the final baseline condition. Why pigeons continued to reject prey for several sessions when the costs were equal may again be a result of the bird having the immediate history of rejecting the preceding high-cost component rather than occasionally sampling prey and determining relative cost. Furthermore, costs associated with colored terminal components appeared interchangeable, and no order effects were apparent, accentuating control by the independent variables.

Other studies examining the effects of prey density have obtained similar results (e.g., Dow & Lea, 1987; Goss-Custard, 1977b; Krebs et al., 1974, 1977; Lea, 1979; Mellgren, 1982; Mellgren et al., 1984; Werner & Hall, 1974; Zach & Falls, 1978). Future research examining prey density and costs should consider time spent in a foraging bout as a potential variable influencing prey choice. One would expect that as the time available for foraging decreases, prey items would be added to the diet (Lucas, 1983, 1987). Future studies should consider a wider range of density parameters (such as .50 - .90) to more fully determine the precise point at which foragers change from being generalist to specialist feeders, and vice versa. Additionally, the use of pellets rather than chow would afford the experimenter the opportunity to collect data on reinforcer magnitude across patches and conditions.

CHAPTER VI

EXPERIMENT III: METHODS OF PATCH REPLENISHMENT

Purpose

Experiment III was designed to investigate how different rates of prey patch replenishment affect the subject's behavior regarding patch use. In Experiments I and II, when patches were not being exploited, they were replenished according to the number of prey (reinforcers) obtained in the exploited patch. That is, each reinforcer delivered on one side key increased the search schedule on that side by a factor of 5 (depleted) and decreased the search schedule requirement on the opposite side key by a factor of 5 (replenished). Experiment III posed the question, How will a fixed-time (FT) or temporally yoked schedule (approximately equal to the rate in the preceding baseline) of prey replenishment compare to a rate determined by the number of prey taken per patch? Examining different methods of patch replenishment will help determine the effect this variable may have on foraging behavior. Perhaps laboratory researchers, given the results of this manipulation, will design more biologically valid analogues of foraging by simulating the dynamic replenishment and depletion of prey from patches.

Subjects and Apparatus

Four wild-trapped adult common pigeons (Columba livia) of unknown age and gender served. Deprivation, housing, and the experimental apparatus were identical to those described in Experiments I and II.

Procedure

An ABACAD single-subject reversal design (Sidman, 1960) was used to determine how various methods of patch replenishment affect patch use behavior. Three parameters were chosen based on preliminary studies of the upper and lower rates of replenishment under the baseline procedure (Cheney et al., 1986): FT-15 sec., FT-60 sec., and FT schedule yoked to the average rate in the preceding baseline. Additionally, session times were equal across all preceding baseline and temporal rates of replenishment. To determine the mean temporal rate of replenishment in the FT yoking procedure, the mean session time over the last five sessions of each baseline was divided by the total number of replenishments obtained over those last five sessions. That is:

$$\frac{\bar{X}\ \text{Session Time (in seconds)}}{\bar{X}\ \text{Number of replenishments}} = \bar{X}\ \text{Rate of replenishment}$$

This provided a mean rate of baseline replenishment, and the same number of replenishments were then calculated to occur under the FT-yoked schedule with the same mean session time.

Baseline. Baseline sessions were identical to those described in Experiments I and II. The initial link search component was under the traditional adjusting RR (replenishing and depleting) schedule, while each terminal link schedule size was equal (RR 20), and there was no advantage to rejecting prey.

Experimental conditions. The primary independent variable was the rate of patch replenishment, either FT-15 sec., FT-60 sec., FT-yoked, or the baseline (reinforcer determined) method. The primary dependent measure was the number of switches between patches (center key responses during the initial link on either side). Other dependent measures included number of prey taken per session and condition, number of initial (search) and terminal (pursuit) link responses across the last five sessions of each condition, and prey rejections. The following conditions were conducted for all subjects in mixed order: Baseline, FT-15 sec., FT-60 sec., and the FT-yoked procedure. Baseline conditions were run at the beginning and between all experimental conditions. All FT schedule conditions had session times that were equal to the immediately preceding baseline condition. The stability criterion was no new high or low values in patch switches over the last five sessions of each condition (Mazur, 1974), with a minimum of 10 sessions per condition. Table 5 indicates the sequential order of conditions for all subjects.

Results

The total number of patch switches for all subjects across all baseline and temporal replenishment schedules are presented in Figures 11 and 12. Relevant comparisons include (a) those across all identical baseline and temporal rates of replenishment for each subject, and (b) those between temporal schedules yoked to the rate in the preceding baseline condition with equal session times. Results displayed in Figures 11 and 12 show that switching varied very little, with no major differences across sessions and conditions for all subjects. The average number of patch switches over baseline sessions ranged from a low of 5.6 to a high of 15.2, and averaged 12.8 for Subject 9; 6.9 for Subject 10; 8.5 for Subject 11; and 8.8 for

Table 5

Sequence of Patch Replenishment Schedules for all Subjects in Experiment III. Baseline Conditions (A) Refer to Replenishment as a Reinforcer Determined (RD) Rate, While Various Temporal Rates of Replenishment (B, C, and D conditions) are also Shown

	Conditions			
Subject	A	B	C	D
9	RD	FT-Y(RD)	FT-15s	FT-60s
10	RD	FT-15s	FT-60s	FT-Y(RD)
11	RD	FT-Y(RD)	FT-60s	FT-15s
12	RD	FT-60s	FT-15s	FT-Y(RD)

Figure 11. Number of patch switches for Subjects 9 and 10 in Experiment III. Baseline conditions are labelled A, and various FT replenishment schedules are shown.

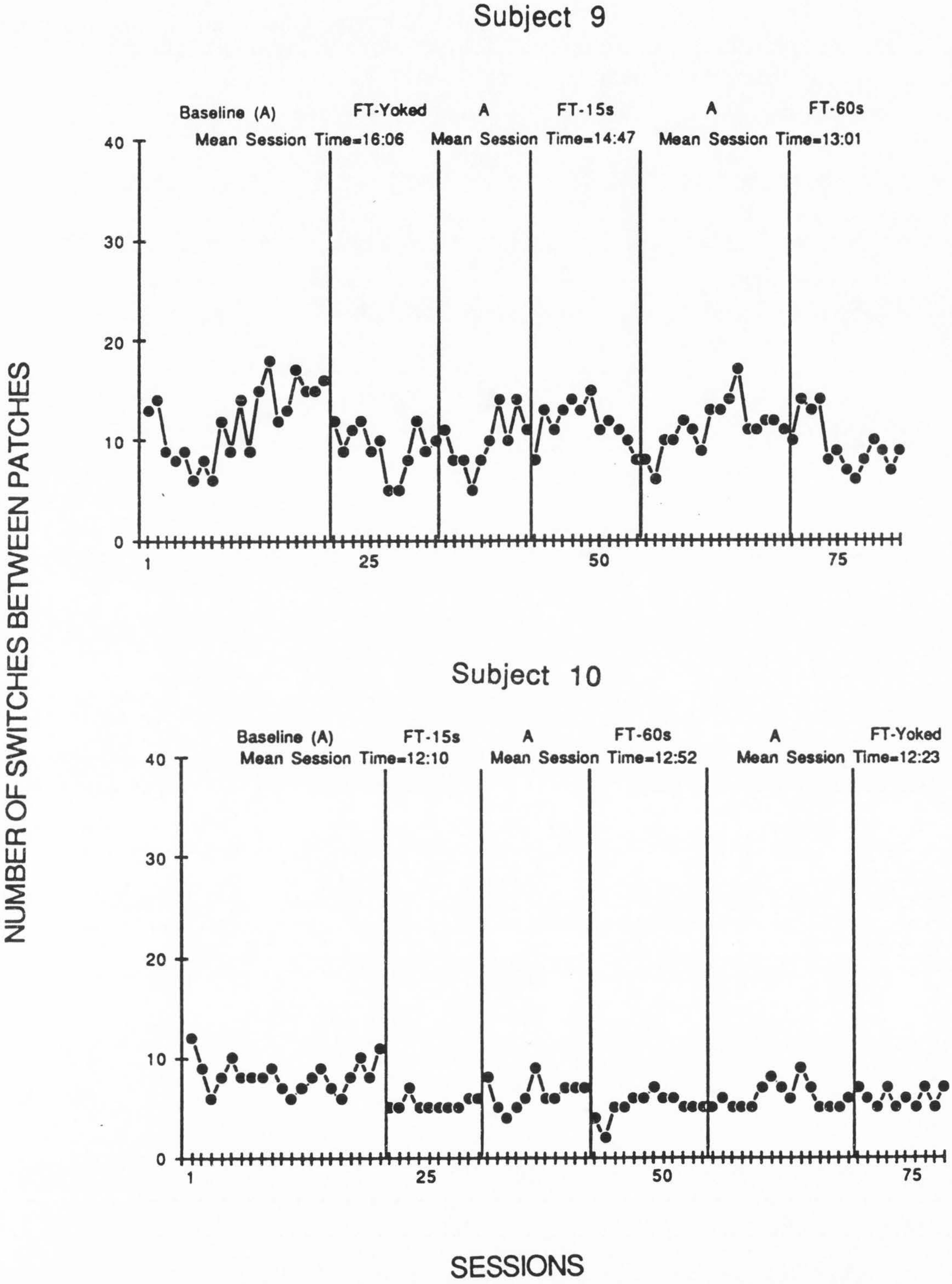
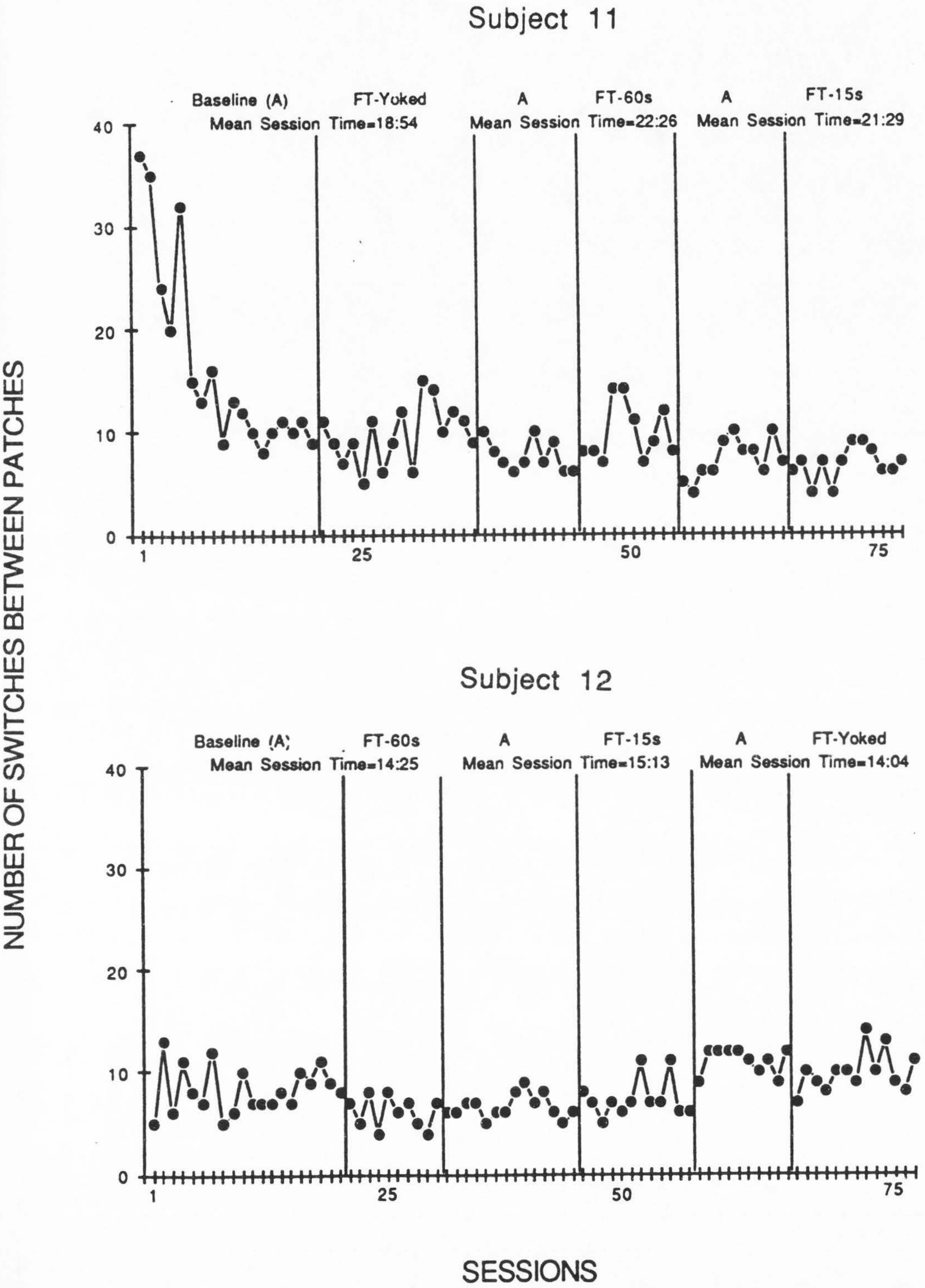

Subject 9
Baseline (A)
FT-Yoked
A
FT-15s
A
FT-60s
Mean Session Time=16:06
Mean Session Time=14:47
Mean Session Time=13:01
40
30
20
10
0
1
25
50
75
Subject 10
Baseline (A)
FT-15s
A
FT-60s
A
FT-Yoked
Mean Session Time=12:10
Mean Session Time=12:52
Mean Session Time=12:23
40
30
20
10
0
1
25
50
75
NUMBER OF SWITCHES BETWEEN PATCHES
SESSIONS

Figure 12. Number of patch switches for Subjects 11 and 12 in Experiment III. Baseline conditions are labelled A, and various FT replenishment schedules are shown.


Subject 11
Baseline (A)
FT-Yoked
Mean Session Time=18:54
A
FT-60s
Mean Session Time=22:26
A
FT-15s
Mean Session Time=21:29
40
30
20
10
0
1
25
50
75
NUMBER OF SWITCHES BETWEEN PATCHES
Subject 12
Baseline (A)
FT-60s
Mean Session Time=14:25
A
FT-15s
Mean Session Time=15:13
A
FT-Yoked
Mean Session Time=14:04
40
30
20
10
0
1
25
50
75
SESSIONS

Subject 12. The mean number of switches between patches during the baseline conditions preceding the FT-15 sec. condition were 11.8, 8.6, 7.8, and 6.4 for Subjects 9, 10, 11, and 12, respectively. FT-15 sec. averages (with equal session times) were 10.4, 5.4, 7.2, and 7.4 (differences of 1.4, 2.8, 0.5, and 1.0, respectively). The mean number of switches over the baseline conditions preceding the FT-60 sec. rate were 11.4, 6.6, 7.6, and 9.4, compared to averages of 6.0, 5.4, 9.4, and 5.8 in the FT-60 sec. temporal rate. The average number of patch switches in baseline conditions preceding the FT-yoked condition were 15.2, 5.6, 10.0, and 10.6 compared to yoked-temporal averages of 8.8, 6.0, 11.4, and 10.2. Table 6 presents the mean and median number of patch switches over the last five sessions of each experimental condition, as well as the average number initial and terminal link responses, mean number of reinforcers earned, prey rejections, and mean session time.

The number of initial link (search) responses varied slightly over baseline conditions, averaging 762, 874, 928, and 773 for Subjects 9-12, respectively. Initial link responses during the FT-15 sec. condition averaged 787 across all subjects, 1047 for the FT-60 sec. replenishment rate, and 794 for the FT-yoked condition. Terminal link (pursuit) responses during baseline averaged 816 for Subject 9, 821 for Subject 10, 880 for Subject 11, and 773 for Subject 12. Subjects averaged 802 terminal link responses over the FT-15 sec. condition, 712 for the FT-60 sec. condition, and 810 for the FT-yoked procedure. In general, the results indicate that the number of initial link search and terminal link pursuit responses covaried with

Table 6

Mean Number of Initial and Terminal Link Responses, Reinforcers, Terminal Link Rejections, Switches Between Patches, and Mean Session Time Over the Last Five Sessions of Each Condition in Experiment III

	Initial Link Responses	Terminal Link Responses	Reinforcers	Rejections	Switches	Mean Session Time
S9						
A (Baseline)	806	837	40.0	1.0	15.2	16:06
B (FT-Y)	853	917	42.0	0.0	8.8	16:06
A (Baseline)	782	866	40.0	0.2	11.8	14:47
C (FT-15s)	759	888	42.6	0.0	10.4	14:47
A (Baseline)	697	746	40.0	0.0	11.4	13:01
D (FT-60s)	868	683	32.0	0.0	6.0	13:01
S10						
A (Baseline)	933	840	40.0	0.0	8.6	12:10
B (FT-15s)	840	644	34.2	0.0	5.4	12:10
A (Baseline)	912	791	40.0	0.0	6.6	12:52
C (FT-60s)	1250	632	31.4	0.0	5.4	12:52
A (Baseline)	776	831	40.0	0.0	5.6	12:23
D (FT-Y))	917	724	38.0	0.0	6.0	12:23
S11						
A (Baseline)	800	911	40.0	1.0	10.0	18:54
B (FT-Y)	753	781	43.0	0.6	11.4	18:54
A (Baseline)	1076	795	40.0	0.0	7.6	22:26
C (FT-60s)	1131	892	45.2	0.0	9.4	22:26
A (Baseline)	907	935	40.0	1.2	7.8	21:29
D (FT-15s)	852	855	41.6	0.0	7.2	21:29
S12						
A (Baseline)	835	766	40.0	0.0	9.4	14:25
B (FT-60s)	938	640	32.2	0.0	5.8	14:25
A (Baseline)	764	807	40.0	0.4	6.4	15:13
C (FT-15s)	698	819	37.8	0.0	7.4	15:13
A (Baseline)	721	809	40.0	0.0	10.6	14:04
D (FT-Y))	652	817	41.0	0.2	10.2	14:04

higher and lower replenishment rates, but were not significantly different across subjects.

Figure 13 presents the mean number of patch switches over the last five sessions of each condition. The mean number of switches between patches across baseline (A) conditions varied slightly across, but not within, subjects. The number of patch switches also varied across subjects and conditions, but not within baseline and temporal rates of replenishment with equal session times. Figure 14 shows that the average number of reinforcers (prey) obtained during all baseline sessions was always 40 and averaged 39.05 for the FT-15 sec. condition, 35.2 for the FT-60 sec. condition, and 41 for the FT-yoked condition across all subjects. Prey rejections did occur at low rates, even when there was no advantage to doing so, but never averaged more than 1.2 over the last five sessions of any condition for any subject.

Discussion

Many types of patches in the wild are depleted according to the number of prey taken from the patch and replenished based only on time (Baum, 1983). The purpose of this study was to determine if patches replenished according to the number of prey (reinforcers) taken from alternative patches differed highly from various temporal rates of patch replenishment. Temporal rates of patch replenishment were 15 sec., 60 sec., or based on an FT procedure yoked to the individual subjects baseline rate. These parameters were chosen because of the upper and lower limits observed during the baseline reinforcer determined replenishment procedure. The yoking procedure was chosen

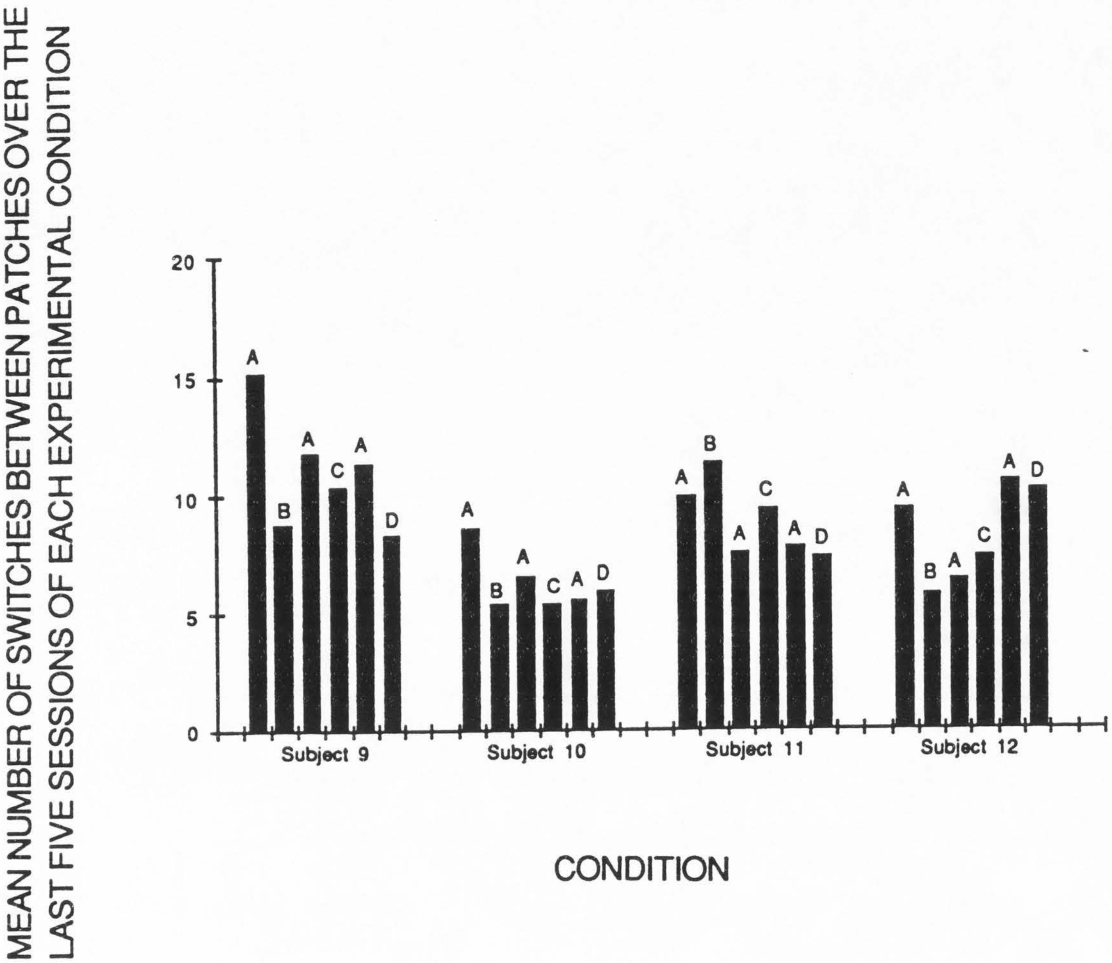


Figure 13. Mean number of switches between patches over the last five sessions of each experimental condition for all subjects in Experiment III. Baseline conditions are represented by bar graphs labelled A. Experimental manipulations (various temporal rates of replenishment) are represented by bar graphs B, C, and D.

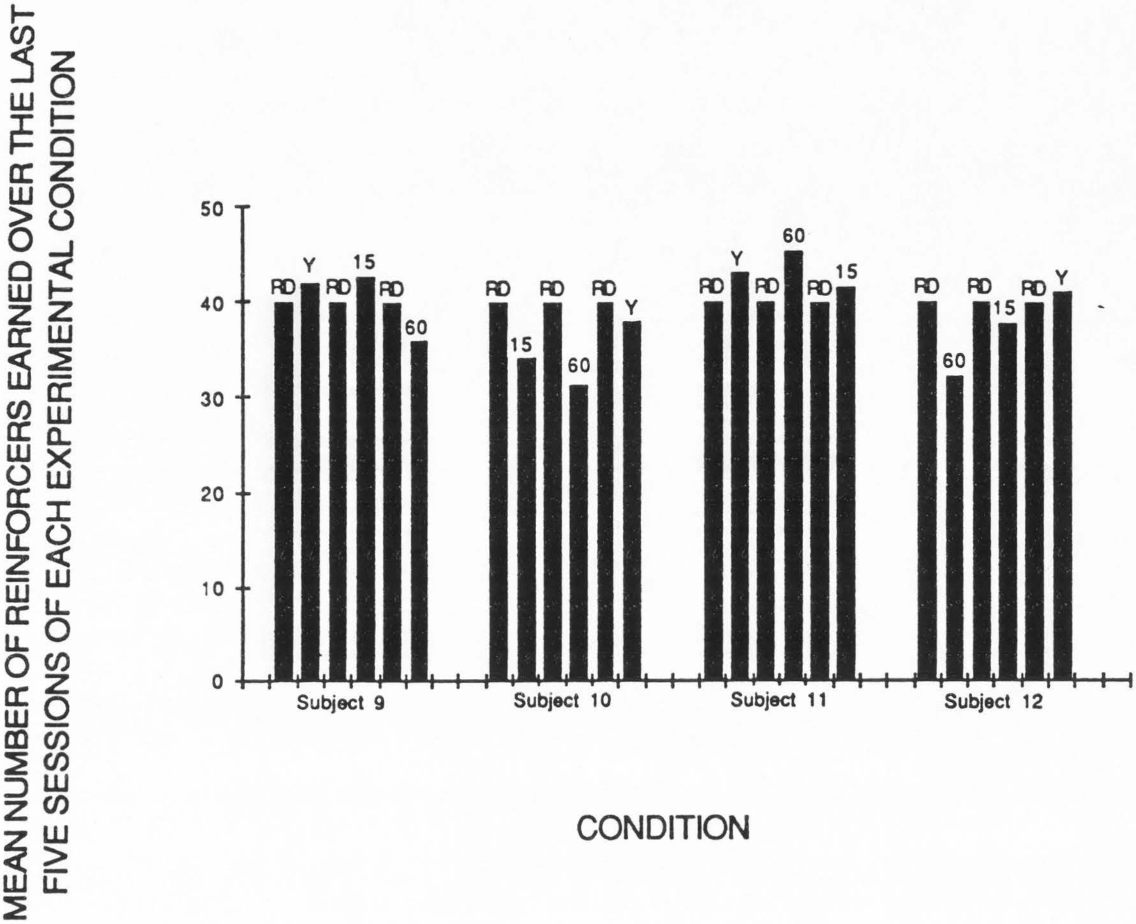


Figure 14. Mean number of reinforcers earned over the last five sessions for each subject and experimental condition. Baseline conditions (regressive random ratio schedule) are represented by bar graphs labelled RD (reinforcer determined), and various FT replenishment schedules are labelled either 15 sec., 60 sec., or yoked (Y).

to make the two methods as equal as possible while still replenishing patches in temporal fashion.

The results showed that there were no major differences within subjects in number of switches between patches across preceding baseline and subsequent temporal rates of replenishment with equal session times. For three of the four subjects, more reinforcers were earned in faster replenishing patches (e.g., 15 sec.) and less were earned in slower replenishing patches (e.g., 60 sec.), suggesting that the rate at which patches replenish can be an important variable to consider when studying patch use behavior.

The goal of behavior analytic studies of foraging is said to be simplicity and completeness (e.g., Collier & Rovee-Collier, 1981; Lea, 1981). Experiment III appears to make a unique contribution towards achieving this goal, as little empirical work in the laboratory has investigated methods of patch replenishment. Recent reports (e.g., Baum, 1987; Stephens & Krebs, 1986) have begun to pay closer attention to aspects of depletion and replenishment, as laboratory researchers strive toward achieving increased biological validity in their studies. Results of Experiment III suggest that a valid method of replenishing and depleting prey from patches can be accomplished in the operant laboratory using both reinforcer-determined and temporal schedules. This would not be the case if major differences were observed under the two replenishment conditions. Future work in this area may, for example, examine other methods of simulating depletion and replenishment of patches as they are thought to occur in the wild, and to examine the precise point at which animals switch patches altogether. Psychologists studying adjusting (progressive and regressive) random ratio schedules under the concurrent chains procedure are beginning to make significant advances in better simulating features of replenishment and depletion in the laboratory (Baum, 1983, 1987).

CHAPTER VII

GENERAL DISCUSSION AND CONCLUSIONS

The results of these experiments extend and support many earlier investigations of foraging both in the field and in the laboratory. The results of Experiment I indicated that as the relative cost of obtaining one of two prey items increased, the probability of the subject rejecting that prey also increased. This result showed that pigeon subjects were sensitive to this independent variable and that they tended to pursue only low-cost prey. This result supports several field- (e.g., Cambell, 1987; Davies, 1977a; Goss-Custard, 1977a, 1977b; Sutherland, 1982) and laboratory-based (e.g., Lea, 1979; Hanson & Green, 1984; Krebs et al., 1977; Peden & Rohe, 1984; Shettleworth, 1985) investigations.

The results of Experiment II showed that as the cost of obtaining prey increased together with density, the probability of rejecting prey remained stable. In other words, when high-cost prey were relatively abundant, three of the four subjects generally pursued these rather than rejecting and returning to search for less costly and less-probable prey, as was evident in Experiment I. Although OFT would predict that the animal should never specialize on (less-preferred) prey, the results of this study suggest otherwise, as do Erichsen et al. (1980), Lucas (1983, 1987), and other second generation OFT models.

Experiment III was designed to test the prediction that a valid method of replenishing patches in laboratory analogues of foraging is to decrease the search cost (initial link) in a patch not being exploited, as prey are taken from other patches. Patches in the wild are generally thought to replenish based solely on time (Baum, 1983, 1987). Little empirical work has been conducted on this aspect of foraging in the field or in the laboratory, although recent studies suggest that this trend is beginning to change (Baum, 1987; Dow & Lea, 1987).

Perhaps more importantly, these experiments suggest that several aspects of foraging in the wild can be simulated simply, extensively, and under well-controlled conditions in operant simulations. There are numerous advantages to using an operant laboratory approach over field work. First, the experiments are conducted under well-controlled circumstances, which set the occasion for clear establishment of functional relations among specific independent and dependent variables. Second, independent and dependent measures can be specified alone or in combination, and shown to control several aspects of prey and patch choice. Third, operant analogues of foraging are virtually unlimited in terms of allowing flexibility and potentially interesting independent (e.g., manipulation of search cost, handling cost, travel cost, density of one or more prey types, reinforcer duration, and time allocation, to name but a few) and dependent variables (the most common being prey choice based on size or capture cost and patch choice based on RT or GUT). Finally, operant simulations of foraging can facilitate interdisciplinary interaction among field and laboratory researchers from such disciplines as psychology, behavioral ecology, ethology, and others. Researchers in these disciplines have shared common interests in the past, but have also disagreed about many issues (e.g., Kamil, 1983). The study of foraging has and will continue to flourish if researchers continue to use convergent methodologies and communicate freely.

The laboratory simulation is also an excellent method of testing ecological models of prey and patch selection (i.e., the optimal diet models, the marginal value theorem, etc.) and psychological models of choice among and constraints on alternative sources of reinforcement and time allocation. Optimal foraging theory makes several rather specific predictions regarding prey and patch choice. Laboratory results both confirm and refute many of the predictions promulgated by optimal foraging theory. Several more predictions are supported qualitatively than they are quantitatively, suggesting that animals do not forage in a quantitatively optimal manner, only efficiently.

Future simulations of foraging conducted in the operant laboratory should consider four factors of foraging which will be of vital importance in generalizing to naturally occurring foraging situations. These include: (a) patches simulated as separate places to work and obtain food (spatially separated operanda), (b) concurrent chained schedules with adjusting random ratio initial link schedules and fixed random ratio terminal link schedules to simulate replenishing and depleting patches and relative costs of prey, (c) travel between patches requiring some cost and a period of nonreinforcement, and (d) the use of pellets rather than chow to allow measurement of energy gain across patches and experimental conditions. Operant researchers meeting these criteria will not only have increased external validity to naturally occurring foraging behavior, but will likely be met with enthusiasm and support from researchers in other disciplines.

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VITA

April, 1988

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ADDRESS

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EDUCATION

B.S. (1984)
Northern Michigan University
Major: Psychology (Behavior Technology)
Minor: Business Administration

Ph.D. (1988)
Utah State University
Major: Analysis of Behavior
Dissertation: The Effects of Prey Vulnerability, Density, and Patch Replenishment in an Operant Analogue of Foraging

PROFESSIONAL ORGANIZATIONS

Association for Behavior Analysis
Council for Exceptional Children
Student Affiliate, American Psychological Association

TEACHING EXPERIENCE

August, 1981-December, 1981
General Psychology. Duties included test administration, correction of weekly assignments, and tutoring students. Under the supervision of Dr. Edward J. Barton.

August, 1981-December, 1981
Child Psychology. Duties included correction of observational reports and tutoring students. Under the supervision of Dr. Connie Hamm-Duncanson.

January, 1984-April,1984
Behavioral Assessment and Evaluation. Duties included supervision of practicum students in local agency settings. Under the supervision of Dr. Robert Stromer.

January, 1984-April, 1984
Psychological Statistics. Duties included correction of weekly quizzes and tutoring. Under the supervision of Dr. Steven Platt.

May, 1984-August,1984
Psychological Statistics. Duties included correcting homework assignments, quizzes, tests, and tutoring. Under the supervision of Dr. Sheila Burns.

September, 1985-June, 1986
Developmental Psychology. Duties included six lectures, leading discussion groups, and supervising testing sessions. Under the supervision of Dr. Edward K. Crossman.

January, 1987-March, 1987
Practicum. Duties included supervision of special education undergraduates in agency settings implementing behavioral programs with adult mentally handicapped persons, functional analysis, generalization and maintenance training. Under the supervision of Dr. Charles Salzberg.

January, 1988-March, 1988
Behavioral Dimensions in Management (Organizational Behavior). Duties included supervising and leading discussion groups engaging in business decisions. Under the supervision of Dr. Glenn McEvoy.

March, 1988-June, 1988
History and Systems of Psychology. Duties included grading quizzes and supervising students. Under the supervision of Dr. Carl Cheney.

CLINICAL EXPERIENCE

October, 1981-December, 1981
Student Therapist. Behavioral Assessment and Evaluation. Duties included conducting informal observations in a special education classroom and recommending behavioral interventions for two clients. Under the supervision of Dr. Harlynn Hamm.

January, 1982-April, 1982
Student Therapist. Practicum. Duties included data collection and analysis, experimental design, implementation of intervention, evaluation of intervention and generalization. Under the supervision of Dr. Edward Barton.

August, 1983-December, 1983
Student Counselor. Student Counseling Center, Northern Michigan University. Duties included advisement of effective study methods, time management and a variety of other academic and personal issues. Under the supervision of Dr. Harlynn Hamm.

January, 1987-March, 1987
Clinical Services Internship. Developmental Center for Handicapped Persons, Utah State University. Duties included interdisciplinary assessment and evaluation, psychoeducational assessment, and coordination of cases. Under the supervision of Dr. Phyllis Cole.

September, 1985-May, 1987
Interdisciplinary Training. University Affiliated Facility. Developmental Center for Handicapped Persons, Utah State University. Under the supervision of Dr. Richard West, Director, Interdisciplinary Training Division.

RESEARCH EXPERIENCE

September, 1983-April 1984
Paid Research Assistant, Department of Psychology, Northern Michigan University, Marquette, Michigan. Duties included setting up and organizing laboratory equipment, reviewing stimulus control literature, assisting in the conduct of human operant research, and developing research software. Under the supervision of Dr. Pryse Duerfeldt (Department Head) and Dr. Robert Stromer.

September, 1985-July, 1987
Hi-Tech Project. Research and Evaluation Assistant. Outreach, Development, and Dissemination Division, Developmental Center for Handicapped Persons, Utah State University. Duties included supervision of applied research study involving preservice teachers and handicapped preschool children in project sites, cost analysis of the project, and grantsmanship in outreach projects. Under the supervision of Drs. Joseph Stowitschek, Sarah Rule, and Charles Salzberg.

July, 1987-September, 1987
Co-Worker Research and Training Project. Research and Evaluation Assistant, Outreach, Development and Dissemination Division, Developmental Center for Handicapped Persons, Utah State University. Duties included conducting research in a local business on co-worker training strategies for adult handicapped persons, development of observational system, data collection and supervision. Under the supervision of Dr. Charles Salzberg and Dr. Rita Curl.

October, 1984-January, 1988
Foraging Behavior. Studying the effects of prey vulnerability, density, and patch replenishment on prey and patch choice in an operant analogue of foraging.

PUBLICATIONS

DeWulf, M.J., Hamm, H.D., & Barton, E.J. (1982). Qualitative analysis of a behavioral program designed to modify intense tantrum behavior. In E.J. Barton (Ed.), Psychology Practicum Summary (Vol. 5.). Marquette: Northern Michigan University.

DeWulf, M.J., Biery, T., & Stowitschek, J.J. (1987). Modifying preschool teacher behavior through telecommunications and graphic feedback. Teacher Education and Special Education, 10, 171-180.

Rule, S.E., DeWulf, M.J., & Stowitschek, J.J. (in review). Economic evaluation of teacher training: Telecommunications versus on site training. The American Journal of Distance Education.

GRANTS

Rule, S., & DeWulf, M.J. (1986). The Social Integration Outreach Project. Office of Special Education (unfunded), $145,840.

PRESENTATIONS

DeWulf, M.J., Bonem, E.J., & Cheney, C.D. (1986, November). An Experimental Analysis of Foraging. Poster presented at the meeting of the Association for Behavior Analysis. Milwaukee, WI.

Rule, S., DeWulf, M.J., Stowitschek, J.J., & Pitcher, S.E. (1986, October). Enhancing training and outreach through telecommunications: Research and demonstration. Paper presented at the meeting of the National Early Childhood Conference on Children with Special Needs, Lousville, KY.

Cheney, C.D., DeWulf, M.J., & Bonem, E.J. (1986, May). The Effects of Prey Vulnerability in a Foraging Simulation. Paper presented at the meeting of the Psychonomic Society. New Orleans, LA.

Stowitschek, J.J., DeWulf, M.J., & Rule, S. (1987, May). Telecommunications and the Development of Preschool Teaching Skills. Poster presented at the meeting of the Association for Behavior Analysis, Nashville, TN. Outstanding Poster Award, Staff Interventions in Human Service Organizations.

Rule, S., Stowitschek, J.J., & DeWulf, M.J. (1987, May). Use of Interactive Television to Train Staff in Remote Locations to Apply Specific Instructional Techniques. Paper presented at the meeting of the Association for Behavior Analysis. Nashville, TN.

DeWulf, M.J. & Rule, S. (1987, September). A Cost Analysis of Teacher Training Alternatives. Poster presented at the meeting of the Utah Council for Exceptional Children, Park City, UT, and at the meeting of the Association for Behavior Analysis (May, 1988) Philadelphia, PA.

WORK EXPERIENCE

September, 1983-August, 1984

Work-Study, Department of Psychology, Northern Michigan University. Duties included assisting faculty and staff in various jobs and caring for laboratory animals. Under the supervision of Drs. Pryse Duerfeldt (Department Head) and Robert Stromer.

October, 1984-May, 1985

Animal Caretaker, Basic Behavior Laboratory, Department of Psychology, Utah State University. Under the supervision of Dr. Carl Cheney.

January, 1985-March, 1985

Private Tutor for Statistics in Psychology and Education. Under the supervision of the Utah State University Disabled Student Center.

May, 1985-October, 1985

Laboratory Manager and Animal Caretaker. Basic Behavior Laboratory, Department of Psychology, Utah State University. Under the supervision of Dr. Carl Cheney.

September, 1987-May, 1988

Editor, Parent News and Exceptional News. Outreach, Development and Dissemination Division, Developmental Center for Handicapped Persons, Utah State University. Duties included information dissemination, collection of articles, ideas, announcements, and development and marketing of mini-posters for joint publication between the Developmental Center for Handicapped Persons and the Department of Special Education. Under the supervision of Dr. Sarah Rule.