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# LEARNING, SAMPLING AND THE ROLE OF INDIVIDUAL VARIABILITY IN THE FORAGING BEHAVIOR OF BLUEGILL SUNFISH

By

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Submitted to
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# ABSTRACT

# LEARNING, SAMPLING AND THE ROLE OF INDIVIDUAL VARIABILITY IN THE FORAGING BEHAVIOR OF BLUEGILL SUNFISH (*LEPOMIS MACROCHIRUS*)

By

Timothy J. Ehlinger

This thesis deals with two ways that learning affects foraging behavior. On one hand, feeding experience on a prey type within a habitat improves a forager's ability to locate and capture that prey. Secondly, a forager may use the information it gathers while foraging to make better decisions about where to forage. Laboratory experiments were conducted with bluegill sunfish (*Lepomis macrochirus*) to investigate the role of both aspects of learning.

In the first set of experiments, bluegills were fed *Daphnia* in an openwater habitat or damselfly nymphs in a vegetated habitat. Each fish had two 5min. feeding trials per day. In the second set of experiments, the density of one prey type was held constant while the prey density in the other habitat was varied over a period of eight weeks. Results indicate that foraging efficiency improved as bluegills gained experience feeding on a prey type. Furthermore, inclusion of a second prey type in the diet resulted in a loss of foraging ability on the other type. Analysis indicated that fish switched to a new habitat when the actual energetic return rate of that habitat exceeded the return rate of the other.

However, patterns constructed by averaging the data for all fish did not accurately represent the behavior of individual bluegills. Cluster analysis confirmed the existence of "early" and "late" switching types.

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Switching types also differed in searching techniques. Early switchers hovered for shorter durations while searching and gave up searching sooner after not finding a prey than did late switchers. As a result, early switchers moved between habitats more frequently and showed an increased propensity to discover a second prey type in the environment.

A mechanistic model of habitat switching was constructed which suggests that either switching type might perform better than the other depending on the rate and frequency of changes in prey abundances. Sampling a second habitat decreases capture efficiency within a habitat, but also raises the probability that a forager will switch to a better habitat. This raises the possibility for frequency dependent selection to influence the distribution of switching types within environments.

To Kathy, Aaron and Sasha

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# CHAPTER 1

# FORAGING BEHAVIOR AND LEARNING: AN INTRODUCTION

## Optimal Foraging and Learning

The study of foraging, per se, holds a prominent position within behavioral ecology and evolutionary biology. This is not surprising, given that all animals must procure energy and nutrients for growth and reproduction. Furthermore, foraging provides an attractive system for study of the adaptedness of behavior since the potential costs and benefits that accrue from a particular course of action are often identified and measured easily (Kamil and Roitblat 1985, Staddon 1980, Hinde 1966, Bitterman 1971, cf Peters 1976). However, the correlations between foraging success and fitness are not always elucidated as easily (see Pyke 1984 for review) and it is not always straightforward how foraging may act in consort with other aspects of an organism's life history to produce adaptive behavior (e.g. Werner and Gilliam 1984).

Optimization models are among the most widely used techniques for predicting foraging behavior (Pyke 1984, Krebs et.al. 1983), usually maximizing some currency of utility to a forager, such as energetic intake rate. These models begin with the tennet that natural selection maximizes fitness and then go on to reason that foraging, as a component of fitness, should also be optimized (Krebs and McCleery 1984). Although the idea of using optimization theory to study foraging had been around for some time (e.g. Hinde 1959), MacArthur and Pianka (1966) are credited with the first mathematical formalization of an "optimal-foraging" model. These early models predict where a predator should forage and/or what prey a predator should select in order to maximize its rate of energy intake. For example, when multiple prey types co-occur within a habitat, these models often predict that certain highly profitable prey types should always be attacked while other less profitable types should always be ignored (Pyke et.al. 1977 for review). On another level, when prey types are distributed non-uniformly within the environment (either among habitat types or clumped into patches of varying density) predators should spend more time in the patches with high profitability and less time in the patches with low profitability (Charnov 1976b, see also McNair 1982).

In spite of their broad assumptions about natural selection, the predictions of these models often agree quite well with actual foraging behaviors. This supports the simple notion that foragers are sensitive to energy intake. The models have been most successful when applied in simple environments where experiments involved size selection among one prey type (Werner and Hall 1974, Cowie 1977, Smith and Follmer 1972, Krebs 1974). Results have been more equivocal in multiple prey and field situations when environments included such complicating features as prey clumping, depletion and temporal changes in prey distributions (see Schluter 1981 and Pyke 1984 for reviews). The realization that these features play an important role in diet selection has led theorists and empiricists alike to be more sensitive to an additional array of factors potentially important in the measures of prey 'value'. These factors include variability in prey abundance (Caraco 1980, Real 1980, 1981), nutritional constraints (Pulliam 1975) and crypsis (Pietrewicz and Kamil 1981) to name just a few (see also Hinde 1966, Krebs et. al. 1983, Pyke 1984, Green 1984, Breck 1978).

## Effects of Experience on Foraging

The potential effects of experience on foraging can be explored using the general situation represented in Figure 1.1. In this case two habitats are separated spatially and prey densities within the habitats change across time; the prey density in habitat 1 declines across time whereas prey density in habitat 2 increases. To apply a foraging model one first converts prey density into the maximum rate of energy intake (E/T) a forager could experience feeding in each habitat given that the forager choses the optimal diet within the habitats (Figure 1.1a). Such early optimal foraging models assume that foragers are omniscent, i.e., they possess perfect knowledge about the distributions, abundances and profitabilities of prey within their environment. Secondly, they assume that foragers use this knowledge to make rational decisions about where to forage and what prey to select. If foragers make decisions that maximize their energy intake, then they should invest all of their foraging effort in the habitat with the highest E/T and should switch abruptly between habitats whenever the profitabilities of the habitats cross (Figure 1.1b - omniscent).

Relaxing the assumption of omniscience will affect foraging decisions in several ways. First, the conversion of prey density into E/T ignores any improvement in feeding rate that might result from foragers learning how to more efficiently locate and capture prey within habitats. As such, the E/T assigned to the habitat is the maximum rate foragers could attain and not necessarily the rate actually experienced. Therefore, the actual E/T would most likely be lower than the predicted E/T for a habitat. Secondly, it is not possible for foragers to know

Figure 1.1 Schematic representation of (a) the changes in foraging return rates on prey (E/T) across time in two habitats, and (b) the percentage of a forager's diet eaten from the second habitat (%2) across time for an onmiscent forager and a non-omniscent forager. See text for more details.

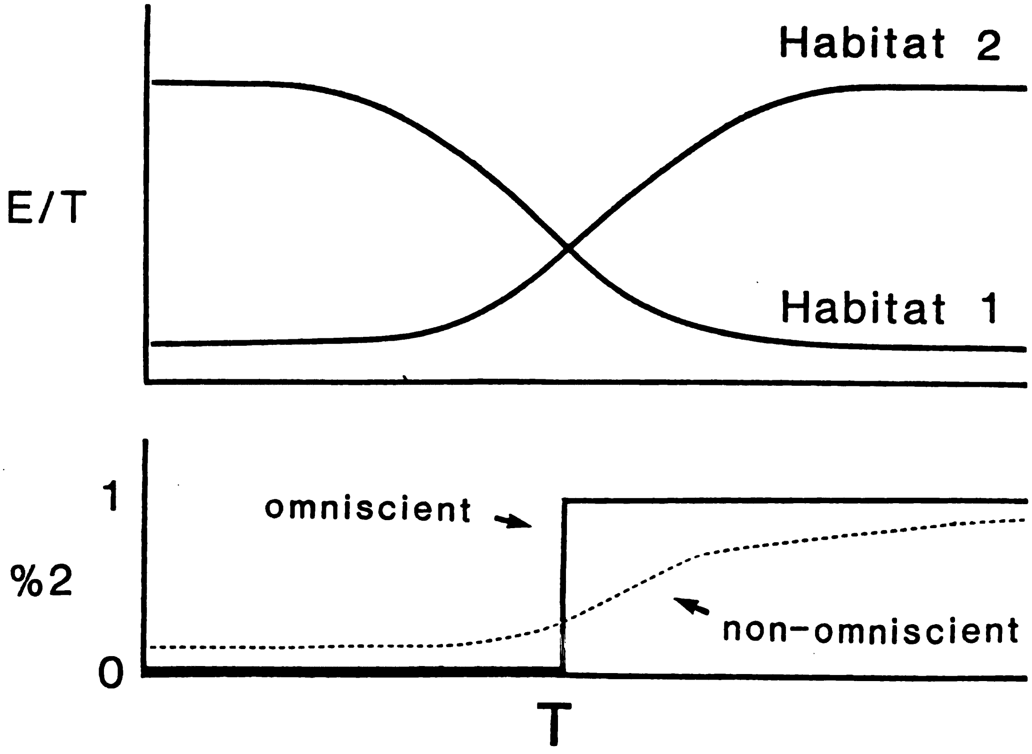


Figure 1.1

when the profitability of another habitat exceeds that of the current habitat unless they sample the other habitat from time to time. As a result of the need to sample, foragers might never commit to a single habitat exclusively, always spending some foraging time in other habitats (Figure 1.1b non-omniscent). Further, even with sampling, foragers may require several samples to form accurate estimates of the E/T of a habitat. As such, there might be a lag between when the E/T of the second habitat exceeds that of the first habitat and the time that foragers actually switch habitats.

Krebs et.al. (1983) make a similar distinction between foragers' learning 'how' to exploit prey and learning 'about' prey distributions and abundances. Learning 'how' refers to direct changes in predators' abilities to locate and/or capture prey within a habitat that result from experience with that particular prey type. For example, under circumstances where prey are cryptic, learning 'how' to recognize prey as distinct from non-prey (Hughes 1979, Pietrewicz and Kamil 1979, Getty and Krebs 1984, Getty 1984) and changing velocity while searching (Gendron and Staddon 1983, Gendron ms.) can significantly affect searching success. If prey are difficult to capture and/or handle, learning 'how' to apprehend, subdue, or manipulate prey effectively can also increase foraging success (e.g. Heinrich 1979, Winfield 1983). In this respect, learning 'how' is similar to changes in ability brought about from simple practice and to the training effects referred to by McNair (1982).

When prey are distributed in patches, it is advantageous to learn 'about' the prey, i.e. to be able to assess the availability of prey within a patch and compare it to the prey density in other patches before choosing a feeding location (Pyke et al. 1977, Krebs et al. 1978, Werner and Hall 1979). When prey are changing in distribution and abundance temporally, it is useful not only to be able to assess and compare the present prey availabilities between and within habitats, but also to compare present to past estimates to identify the direction of changes (see Lester 1984, Harley 1981). In each case, foragers must be able to recall past information and use it in making current foraging decisions. Learning 'about' will, in and of itself, have no affect on foraging success. Only if the knowledge gathered about the prey is used to make proper decisions about how to allocate foraging effort will foraging return rate in the environment as a whole be increased (e.g. Ringler 1979).

Krebs et al. (1983) consider learning 'about' to be "more or less the information problem". However, if learning 'about' prey involves assessing prey abundance and return rates, then changes in encounter rates and handling times due to learning 'how' could produce a shift in the perceived prey abundance and return rate (Tovish 1982). The potential feedback between the two types of learning cannot be overlooked, and as such, learning 'how' should not be ignored when considering the effects of information acquisition on foraging behavior. This will be the case especially when different suites of prey are located within habitats of differing physical structure and when specific search and capture skills are necessary for each prey type (Werner et al. 1981). In such situations, spending time and learning how to feed on a new prey type in a new habitat may interfere with what has been already learned on the other prey type. As a result, the forager may experience a decrease in foraging rate on the old prey type while return rate on the new type increases (Dill 1983). This interaction between learning 'how' and 'about' prey has the potential to affect the predictions of diet selection and habitat choice in optimal foraging models substantially (Dill 1983, Tovish 1982).

It is, therefore, better to consider the overall information problem for foragers as consisting of three interacting parts: (1) ADJUSTING the components of capture efficiency for particular prey types, (2) ASSESSING prey distributions and abundances, and lastly, (3) ALLOCATING foraging effort among prey types and habitats based upon the information gathered. Distilling the form of each of these parts of the information problem may prove difficult operationally. Each component involves a different level of derived knowledge, gathered and stored in different ways. Adjustments in searching and handling behaviors may be the result of simple trial and error. Assessments of prey density may depend greatly upon foragers' abilities to remember foraging return rates. If we assume that foraging behavior is influenced by natural selection, the way foragers decide to allocate their foraging effort may be a product of their genetic makeup.

## Ecology vs. Psychology: Historical Perspectives

The study of choice and decision behavior has traditionally been the realm of the psychologist. The failure to discover general rules for learning in animals has led many psychologists to ask whether the ecological context of learning in foraging can add new insight to the development of learning theory (Johnston 1981, Bitterman 1971). It is hoped that establishing the ecological and evolutionary significance of learning abilities in animals will help uncover principles of learning applicable across taxa (Johnston 1981, Shettleworth 1984, Arnold 1978).

Incorporating learning theory into the study of foraging has not been without its controversy. Much confusion in the literature can be attributed either to the difficulties of providing precise definitions for what is considered to be learning or to the overuse of the adaptionist paradigm in describing specializations (Hinde 1975, Gould and Lewontin 1979, Staddon 1984).

Johnston (1981) defines learning as any process in which, during normal, species-typical ontogeny, the adaptive organization of an animal's behavior is in part determined by some specific prior experience. In the absence of the experience, the behavior will be lacking or its organization less adaptive. Herein I consider experience to be time spent actively involved in the task under consideration (e.g. time actually spent foraging on a particular prey type or in a particular habitat). This definition shifts the emphasis away from the highly unnatural learning tasks used in many psychology experiments toward situations that mimic problems faced by organisms in nature.

By this definition, the context of the task is as important as the learning process itself. The optimal behavior with respect to a goal can only be assessed relative to the options available to the forager within the specific environment. One can start with the premise that the animals behave optimally, then add in the limitations imposed by their learning abilities. Alternatively, one can begin with empirically described learning abilities and ask What is the best that the animal can do in a given environment?". This may appear to be a trivial distinction, but it does characterize the historical differences between the ecological and psychological approaches to the study of learning.

By defining learning in terms of adaptation, it is important to recognize that not all attributes of an organism necessarily serve to increase its adaptedness to the environment (Gould and Lewontin 1979, Sahlins 1977). Simply demonstrating that behavior can be molded by experience does not confirm that either learning or the acquired changes in behavior are adaptive (Johnston 1981, 1982, compare Menzel and Wyers 1981). In order to judge the adaptedness of learning relative to not learning properly, it is necessary to show that foragers adjust their behavior in ways that result in net reproductive success increased over that which any single inherited behavioral rule could provide (Freeman and McFarland 1982, McNamara and Houston 1982). This is a tall order. As first steps in assessing fitness it is necessary to identify: (1) the appropriate currencies for cost and benefit measures, (2) the importance of other conflicting demands such as predator avoidance, reproduction and/or defense of a territory and (3) the relevant time horizon over which to integrate the forager's performance. In this regard, there is no substitute for an in-depth understanding of the natural history and ecology of the forager and the specifics of the foraging environment.

An interdisciplinary approach to the study of learning may lead to new hypotheses about both the proximate mechanisms for learning and the ultimate explanations for the nature of learning phenomena. It is clear that training effects in foraging (e.g. Ivlev 1961) bear striking similarity to conditioning effects in many psychology experiments (Lea 1982). The potential benefits of integrating the psychological and ecological approaches to learning and foraging are, however, more than the discovery of 'real world' examples of psychological constructs and the vindication of nice mechanistic models; more than the discovery of interdisciplinary support for existing theories and hypotheses (Houston 1983, Kamil et. al. 1982). Combining the psychologists' emphasis on the process of how learning occurs with the evolutionary ecologists' preoccupation with the whys of nature is providing fertile ground for new ideas on the adaptive function and structure of learning in animals (Houston 1980, Johnston 1983, Staddon 1983, Kamil and Yoerg 1983).

Learning allows foragers to adjust to changes in some critical aspects of their environment (e.g. Plotkin and Odling-Smee 1979) and it is generally agreed that this ability often confers some selective advantage (Istock 1984, Johnston 1984, Arnold 1984, Fretwell 1972, Dingle 1983, Levins 1968, Slobodkin and Rappoport 1974). As such, some find it surprising that greater attention has not been paid to the role of learning in the development and application of foraging theory (Glasser 1985). Such criticisms are valid if one is attempting to validate hypothesized mechanisms of diet selection by using the agreement between predicted and observed diets (Krebs et.al. 1983). When theory is used in this manner, it is of paramount importance to consider alternate mechanisms that could result in the observed patterns of diet selection. However, when the questions of interest are not the mechanisms of prey selection, but rather the implications of prey selection for population and community level processes, it is the qualitative agreement of the observed with the predicted diet that is important (Werner and Mittelbach 1981). In this latter case, learning is important in so far as it changes the qualitative predictions of foraging theory (e.g. Houston et.al. 1982, Hughes 1979, Inoue 1983, Dill

1983). A proper assessment of the importance of the qualitative and quantitative effects of learning in foraging will come about gradually through further research.

## An Example of Optimal Foraging and Habitat Selection

Werner and Hall (1974) proposed an optimal foraging model to predict prey selection for bluegill sunfish (*Lepomis macrochirus*). Using searching and handling times determined from laboratory experiments together with prey samples from the field, the model predicts prey selection patterns in controlled pond experiments (Werner et al. 1983, Werner and Hall 1979) and in small lakes (Mittelbach 1981) with good qualitative success. As prey abundances and size distributions change during the course of a season, relative foraging return rates among habitats also change. Since specific suites of prey types are often associated with specific habitats, it is often possible to estimate the energetic return rate (also termed E/T or 'profitability' of the habitat) attainable if bluegills fed within a given habitat choosing the optimal diet. Given that bluegills have perfect knowledge of prey distributions within and between habitats and behave in complete accordance with the model, fish should shift their foraging effort to a new habitat if and when its profitability exceeds that of the current habitat. Mittelbach (1981) demonstrated that bluegill sunfish in several small Michigan lakes switched from the vegetation to the openwater when the profitability of the openwater zooplankton rose above that of the prey in the vegetation. Controlled pond studies have come to similar conclusions (Werner and Hall 1979, Werner et. al. 1981, Werner et al. 1983).

There are, however, several cases where the predictions of the model were clearly not met by what the fish were actually doing. First, fish shifted habitats consistently several days to a week later than predicted by the optimal foraging model (Mittelbach 1981, Werner et al. 1981, Werner and Mittelbach 1981). Although this could be due to failure on the part of the investigators to sample the prey available to fish in each of the habitats accurately or to some inherent bias within the model, the lags between predicted and actual habitat shifts suggest that some time is required for fish to learn that the other habitat is actually a better place to forage and to adjust their behavior accordingly. Fish behavior also deviated from the model in that fish did not show exclusive choice after switching to the new habitat. The optimal foraging model predicted that they should feed completely within the habitat with the greater return rate and avoid the less profitable habitat completely. Although some individuals did take all their prey from the predicted habitat, a significant proportion of bluegills continued to take some small portion of their daily ration from the sub-optimal habitats. It is difficult, if not impossible, to know from this field data what function, if any, this non-exclusive habitat usage may serve, but intuition suggests that it is difficult to know what potential return exists in a habitat unless some amount of foraging effort is expended there. This non-concordance with predictions may reflect sampling behavior by bluegills.

Furthermore, bluegills increase capture success and capture rates as they gain experience with novel prey (Werner et al. 1981, Vinyard 1980) and in this regard learn 'how' to eat prey. The predictions of the optimal foraging model used by Mittelbach (1981) were based upon capture rates from experienced bluegills. If learning influenced the actual return rates that bluegills received in the habitats, it is possible that fish switched when the profitabilities they experienced in the second habitat exceeded the first. Furthermore, if bluegills require time to learn both 'how' to feed on the new prey types as well as properly learn 'about' the relative habitat profitabilities, the non-concordance of observed diets with predictions of the model may be amplified. Learning in terms of both capture efficiency and decisions about where to forage may be important constraints on the foraging behavior of bluegills and interact to determine patterns of prey selection.

## Thesis Organization

This study explores the relationship between learning and the foraging behavior of the bluegill sunfish (Lepomis macrochirus). The thesis is divided into four chapters. This first chapter provides an introduction to the general questions concerning learning and foraging. The second chapter describes, in detail, the components that determine return rates within habitats and the manner in which return rates change as bluegills gain experience with a single prey type. Chapter 3 presents a laboratory study showing how bluegills allocate their foraging effort between habitats in response to the return rates of the habitats, incorporating the effects of learning. Chapter 4 examines how foraging return on a prey type changes when foraging effort is split between two prey types and explores the behavioral mechanisms that might cause the observed allocation patterns of foraging effort. The final section explores the significance of individual variation in foraging techniques and the consequences of differences between individual fish with respect to how they use their past experience to allocate their foraging effort in changing environments.

# CHAPTER 2

# THE EFFECTS OF EXPERIENCE ON THE COMPONENTS OF CAPTURE TIME: FORAGING ON A SINGLE PREY TYPE

## INTRODUCTION

As mentioned in the previous chapter, experience may affect foraging in two distinct ways: (1) through alterations in foragers' abilities to locate and capture prey types within a given habitat (learning "how", sensu Krebs et al. 1983), and (2) by providing foragers with additional information about the return rates within and among habitats (learning "about", sensu Krebs et al. 1983). Learning 'how' directly affects return rates within habitats via improvements in capture efficiency. Learning 'about' will increase a forager's overall return rate only if the forager in turn chooses to spend more time foraging in the more profitable habitat. This chapter is concerned with learning 'how', i.e., the effects of experience on the components of capture efficiency within habitats.

It has long been known that fish often increase their capture rates as they accumulate feeding experience with novel prey types (Ivlev 1961, Ware 1971, Mittelbach 1981, Winfield 1983). Only recently has there been an active discussion in the literature as to how experience-induced changes in capture rates might affect diet and habitat choice by fish (e.g. Dill 1983, Werner et al. 1981, Vinyard 1980). This discussion has been motivated in great part by the mathematical incorporation of learning effects into general models of diet selection (Hughes 1979, McNair 1982). These models have given rigor to the general idea that learning can influence prey and habitat selection. In turn, these models have also allowed for increased speculation about the magnitude and importance of learning in the foraging behavior of fish (Dill 1983, Glasser 1984, Shettleworth 1984, Stephens and Krebs 1986). However, it has often been necessary to make simplifying assumptions about how learning actually occurs and the specific roles that it may play in foraging. For example, some foraging models assume a continuous exponential curve for learning as a function of experience (e.g. Hughes 1979). This appears to be a reasonable assumption. However, some studies have shown that learning may often occur with discrete jumps in performance level (e.g. Dawkins 1971).

It is not entirely clear how these assumptions about the nature of learning 'how' will affect the predictions of habitat choices based upon learning 'about' prey. It is difficult to know what foragers actually learn when foraging (see Krebs 1973, Lawrence and Allen 1983) and there are few empirical studies of the effects of experience on the specific behavioral changes that translate into increased capture rates (cf Vinyard 1980, Laverty 1980).

This chapter is a detailed analysis of the effects of learning on the foraging behavior of bluegill sunfish (Lepomis macrochirus). My main purpose is to explore how the component behaviors of prey location and capture change as naive bluegills gain experience feeding on a novel prey type. Subsequent chapters will examine the affect of this learning on the ability of bluegills to make decisions about where to forage.

## Components of Capture Time for Bluegills

Since foraging is a multifarious activity, it is imperative to decompose capture time into component parts which are easier to describe empirically. Predators that feed on individual prey items one at a time must first locate a prey item, then catch and ingest the prey. All activities associated with locating prey are termed "searching behaviors". Likewise, once prey are located, all activities involved with apprehending and ingesting prey are called "handling behaviors".

Unlike many other planktivorous fish, bluegills do not swim constantly while searching for prey (Janssen 1976). Bluegills use a very stereotyped searching pattern similar to the travel-pause technique described by Andersson (1981) for raptors. Bluegills hover motionless while searching an area. If no prey item is detected, they move a distance to another spot and again hover (Figure 2.1). The location and duration of hovers are easily measured in experiments, as is whether or not a particular hover was followed by an attack on a prey item.

The process of handling for bluegills can be divided into 5 phases (Figure 2.1). If a prey item is detected while hovering, fish stop hovering and pursue the prey. When bluegills reach within striking distance of the prey, they slow down (sometimes even stopping completely) and position the body for an attack. The dorsal fin is erected and the pectoral fins are flaired. The body and tail fin are drawn into a curved position resembling either an 'S' or 'C' shape when observed from above (see Brown and Colgan (1984) for more detailed descriptions). The 'C' attack posture is used most often in captures of relatively non-evasive prey such as <u>Daphnia</u>, whereas the 'S' posture is

Figure 2.1 Sequencing of behavioral components for searching and handling time for bluegill sunfish. See text for further descriptions of each component.

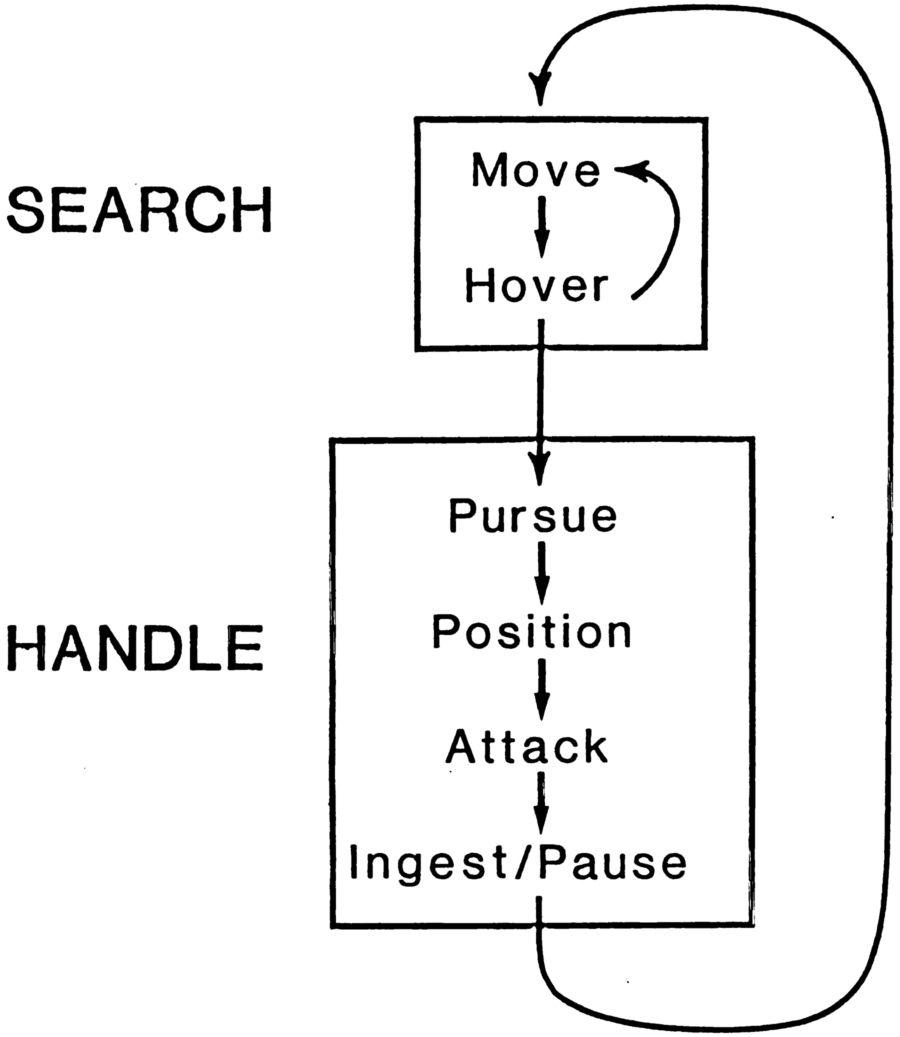

SEARCH
Move
Hover
HANDLE
Pursue
Position
Attack
Ingest/Pause

Figure 2.1

used most often with more mobile and evasive prey such as Chaoborus larvae, copepods and some mayfly nymphs. Attack postures reflect strongly both experience effects (Vinyard 1980, 1982) and ontogenetic patterns in development (Brown and Colgan 1984).

Once positioned, a bluegill attacks and ingests the prey. With small prey the actual time to apprehend a prey can take less than 0.1 second. With larger and/or more evasive prey types this time can be considerably longer. Once a prey is captured (i.e. the prey is entirely within the mouth and out of view) it is swallowed and the fish pauses momentarily before resuming search.

## Relationships among the Components of Capture Time

When foraging, all time is spent either searching for or handling prey. Thus, by definition

$$C_i = S_i + H_i \qquad (1)$$

where $C_i$ is the time per capture, $S_i$ and $H_i$ are the searching time and handling time, respectively, for a predator feeding on prey type 'i'. In this formulation, $1/S_i$ is equivalent to "encounter rate" as defined by Mittelbach (1981). Operationally, search time and handling time can be calculated either for an individual capture or averaged over many captures to provide an expected capture rate for the predator on prey type 'i'.

The number of prey captured ($N_i$) within a given period of time ($T_i$) at a given prey density ($D_i$) is given by the Holling's famous 'disk equations' (Holling 1959, 1968) where,

$$N_i = \frac{A_i * D_i * T_i}{1 + A_i * D_i * H_i} \qquad (2)$$

In this equation, $A_i$ is the "rate of successful search" (Holling 1959, 1968) and is equivalent to encounter rate (i.e. $1/S_i$).

It is possible to imagine a myriad of factors that might affect searching success. Predator size, prey type, prey size and, most obviously, prey density constrain the maximum encounter rate possible for a predator on a prey. If we consider a single size predator and prey, then, generally speaking, the maximum encounter rate attainable on prey type 'i' (i.e. the best it can do with infinite experience) is directly related to prey density by the equation

$$A_i \max = B_i * D_i \qquad (3)$$

where $B_i$ is an empirically determined constant. This relation, though quite general for asymptotic performance, masks the behaviors that contribute to successful search within the constant, $B_i$, (Gendron and Staddon 1983). When considering the effect of experience on searching ability, $B_i$ will become a variable. There are several examples in the literature where $B_i$ has been decomposed into smaller contributing parts (see for example Holling 1968 for mantids, Beukema 1968 for sticklebacks). Thus, $B_i$ is a function of 4 components of search: (1)

the efficiency of the search path, (2) the rate of searching, (3) the forager's ability to detect prey items that occur within its visual field, and (4) the probability that it pursues detected prey.

This study examines how these component behaviors of searching and handling ability change as bluegills gain foraging experience with single prey types.

## METHODS

It is difficult to know a priori how searching and handling abilities will be affected by experience with a prey type. Effects are likely to be very specific to the particular predator, prey and habitat types being considered. Therefore, it is important to exercise the greatest amount of control possible over the experimental conditions and the past foraging history of the experimental fish.

### Experimental Tanks

Each experimental tank contained an 0.8m x 0.8m x 0.25m arena with 4 holding rooms for housing one fish each (Figure 2.2). The bottom of the arena was covered with 2cm of washed silica sand. One half of the arena contained artificial nylon fabric plants similar in morphology to Potamogeton crispus (a common local aquatic plant) at a density of 180 stems/m$^2$. The other half of the arena contained sand bottom only. These habitats are referred to as the vegetation and openwater habitats, respectively. Tanks were constructed from white opaque plexiglass except that the front panel looking into the openwater habitat was made

Figure 2.2 Schematic view looking down on an experimental aquarium showing holding rooms and experimental arena. Damselfly nymphs were used as prey in the vegetated habitat and *Daphnia pulex* were used as prey in the openwater habitat.

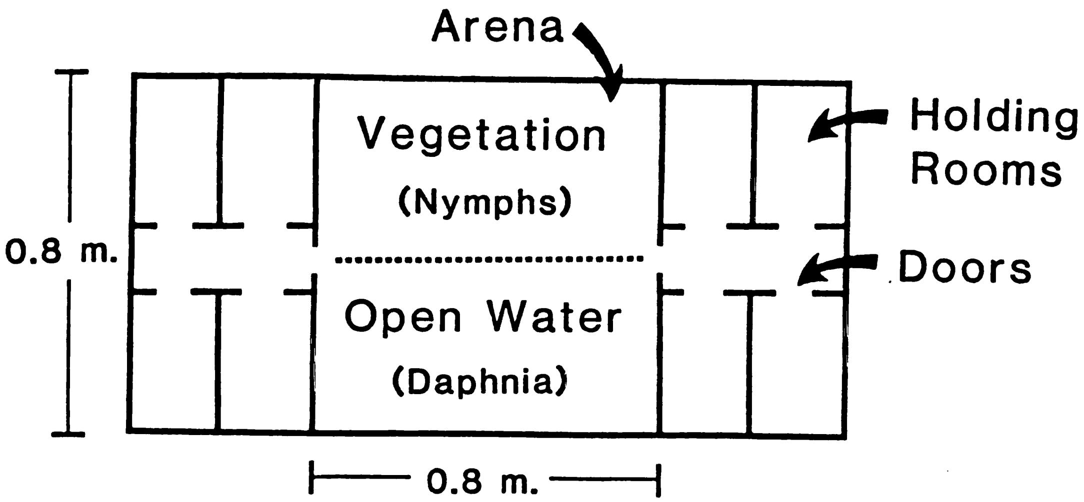

Arena
Holding Rooms
Vegetation
(Nymphs)
Doors
Open Water
(Daphnia)
0.8 m.
0.8 m.

Figure 2.2

from clear plexiglass to allow for observation of the experiments. A mirror suspended above the arena allowed for a view from above. The back panel of the arena was marked with a 2.5cm grid to facilitate distance measurements during experiments. Water in the tanks was maintained between 23°C and 25°C. Light was supplied by two 20 watt flourescent lights suspended 1m above the arena on a 16h:8h Light:Dark cycle.

### Fish

Bluegill sunfish were seined from Warner Lake in Allegan County, Michigan in May of 1982 and 1983. Fish between 57mm and 58mm standard length were retained. Fish were kept together in holding tanks and fed TETRAMIN (tm) artificial fish food. After fish adjusted to the laboratory as evidenced by their readiness to feed upon the artificial food (after approximately 2 weeks in captivity), 24 fish were randomly selected for experiments and placed into the experimental tanks (see below). Age was determined by examining annuli from scales (see Jearld (1983) for methods). All fish were entering their third summer (i.e. 2+ years old).

Individual fish were sorted into their own holding rooms in the experimental tanks (Figure 2.2). Twice each day TETRAMIN was spread evenly across the water surface of the experimental arena and individual fish were coaxed from their holding rooms into the experimental arena to feed for 5 minutes. This procedure was repeated for one month prior to the beginning of the experiments. The fish acclimated readily to the procedures, swimming freely out to feed in the arena. Fish showed no preferences for either habitat section by the end of this pre-trial conditioning, spending roughly half of their feeding trials feeding in either habitat.

## Experimental Prey

Damselfly nymphs (Coenagrionidae) and *Daphnia pulex* were used as prey in the vegetation and openwater habitats respectively. Nymphs were collected daily from local ponds using dip nets and *Daphnia* were cultured in the laboratory. Only one size class of each prey type was used; 8.1 ± 0.3mm SE for nymphs (length from the ocelli to the posterior tip of the abdomen) and 2.2 ± 0.1mm SE for *Daphnia* (length from head to posterior of carapace excluding tail spines). *Daphnia* were sorted serially through nytex seives and individuals carrying ephippia (dark resting eggs) were not used for experiments due to their enhanced visual contrast. Nymphs were sorted by hand. Subsamples of each prey type were measured using an occular micrometer on a dissecting microscope, dried and weighed (0.38 ± 0.07mg SE for nymphs and 0.078 ± 0.012mg for *Daphnia*). Prey types were equivalent in caloric content per mg dry weight (approx. 21 Joules/mg, from Cummins and Wuycheck 1971).

## Experimental Procedures and Treatments

Treatments consisted of sequential feeding trials of a set density of only one prey type. Four fish were randomly assigned to each prey type/prey density treatment group (Table 2.1). The density of the prey type was changed across 3 sequential treatment blocks as shown in Table

Table 2.1. Prey densities for experiments with one prey type available. For *Daphnia*: Low = 0.25/l, Med = 0.50/l, High = 1.00/l. For nymphs: Low = 0.125/l, Med = 0.25/l, High = 0.375/l. Four fish were used in each group (N = 24).

| BLOCK | | I | II | III |
|---|---|---|---|---|
| TRIAL NUMBER | | 1-8 | 9-12 | 13-16 |
| DAPHNIA | | | | |
| | Group 1 | Low | High | Med |
| | 2 | Med | Med | Med |
| | 3 | High | Low | Med |
| NYMPHS | | | | |
| | Group 1 | Low | High | Med |
| | 2 | Med | Med | Med |
| | 3 | High | Low | Med |

,2.1. During the first block each group had 8 feeding trials. In the second and third block of trials densities were manipulated to test whether the components of searching and handling responded to changes in prey density. Fish that fed on high prey density were presented with low prey density and vice versa. The medium density group continued on medium density across all trials and served as a control. In the final block all fish faced medium prey density.

Before each trial, known numbers of each prey type were introduced into the appropriate habitat. Nymphs were placed on vegetation in as even a spatial distribution as possible. Daphnia were placed into the openwater habitat and allowed to disperse. Daphnia remained in the openwater habitat throughout the trials (due in part to the higher light levels in the openwater combined with the positive phototactic response of the Daphnia). Nymphs remained attached to the vegetation, with less than 2% of all captures by bluegills occuring on unattached nymphs. Captures of unattached nymphs were coded separately and were not used in the analysis.

When prey had dispersed evenly throughout the habitat (usually within 2 minutes) the door to a holding room was opened and one fish allowed to swim into the arena to feed. After feeding for 5 minutes, the fish was guided back to its room, prey were replenished and another fish was let into the arena. Each fish experienced 2 trials per day (1st. trial 8:00-9:00, 2nd. trial 16:00-17:00). After the evening trial all fish were fed to satiation with TETRAMIN to equalize hunger levels for trials the next day. The TETRAMIN meal never accounted for more than 10% by weight of any fish's daily ration.

Trials were observed from the side of the arena. Each search move, search hover, pursuit, attack positioning, attack, post-capture pause, location and missed capture were recorded in timed sequence on an electronic event recorder ("MORE" trademark). Selected trials were video-taped from a lateral view. Pursuit, attack and search distances and velocities were determined from slow motion replay of these videos. By mapping the sequences of hovers in a feeding trial, it was possible to chart 2 dimensional search paths taken by bluegills.

## RESULTS

### I. Changes in Capture Time with Experience

The time required per prey capture decreased across trials for all fish. Figures 2.3 and 2.4 show examples for 6 fish of how cumulative prey captures across time changed both within and between trials in Block I. An ANOVA of the mean time required per capture indicated significant effects of prey density and trial for both prey types (split plot ANOVA with repeated measures [Gill 1978b] using captures up to the 25% prey depletion level in each trial, see Tables 2.2 and 2.3). However, the significant effect due to individuals and the interaction between density and trial for _Daphnia_ make interpretation of main effects from the ANOVA difficult. The fact that individual differences were present with _Daphnia_ but not with nymphs suggests that there was some difference in learning how to feed on nymphs in the vegetation compared to _Daphnia_ in the openwater which accentuated the differences among individual fish. The strong interaction between trial and density

Figure 2.3 Examples of the accumulation of _Daphnia_ captures within trials for 3 fish. (a) Low density, fish 12A. (b) Medium density, fish 9A. (c) High density, fish 14A. % depletion = (number of _Daphnia_ captured in the trial up to that time divided by the total number of prey available in the arena at the beginning of the trial) * 100.

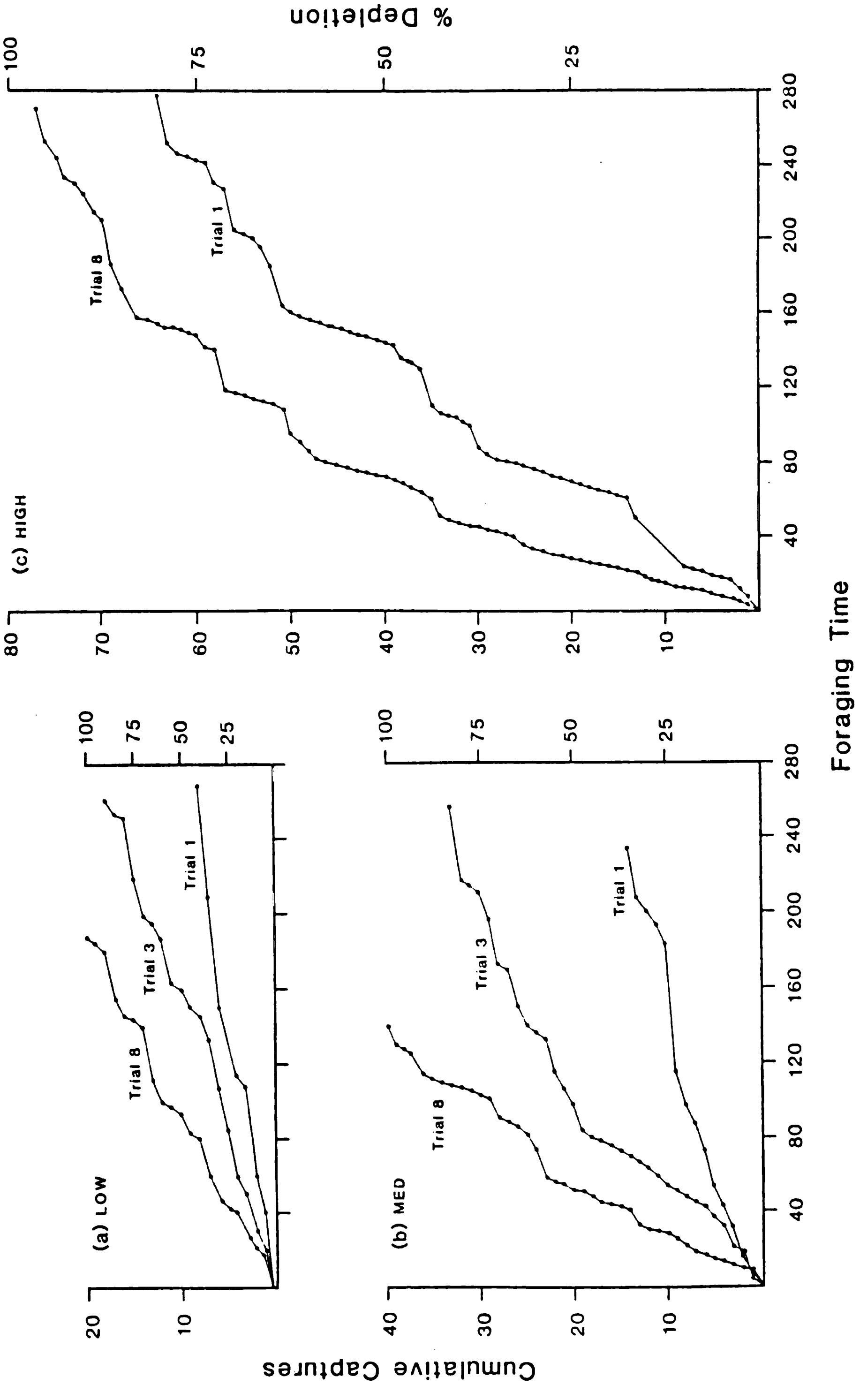

(a) LOW
Trial 8
Trial 3
Trial 1
(b) MED
Trial 8
Trial 3
Trial 1
(c) HIGH
Trial 8
Trial 1
Cumulative Captures
% Depletion
Foraging Time
20
10
40
30
20
10
80
70
60
50
40
30
20
10
100
75
50
25
40
80
120
160
200
240
280

Figure 2.3

Figure 2.4 Examples of the accumulation of nymph captures within trials for 3 fish. (a) Low density, fish 17A. (b) Medium density, fish 17A. (c) High density, fish 1A. % depletion calculated as in Figure 2.3.

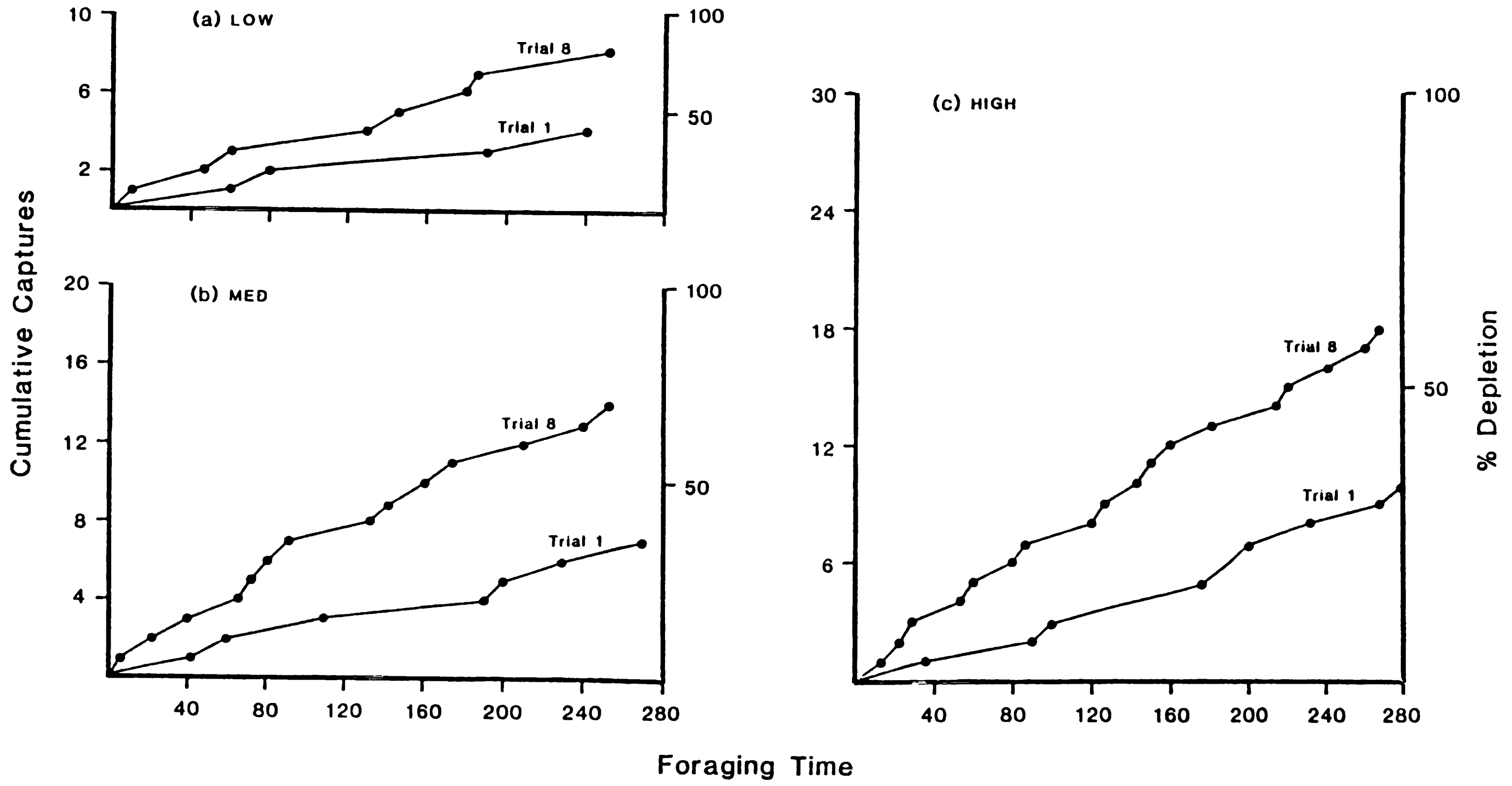

(a) LOW
(b) MED
(c) HIGH
Trial 8
Trial 1
Cumulative Captures
% Depletion
Foraging Time
10
6
2
20
16
12
8
4
30
24
18
12
6
100
50
40
80
120
160
200
240
280

Figure 2.4

Table 2.2. Analysis of Variance of mean seconds per capture for bluegills feeding on Daphnia. Model is a split plot design with trials as repeated measures. Data are means using captures up to the 25% prey depletion level in trials. Model: Y = Density + Fish/Density + Trial/Fish + interactions. (* = $P < 0.05$, ** = $P < 0.01$, *** = $P<0.001$).

ANALYSIS OF VARIANCE : Seconds per Capture
PREY TYPE : Daphnia

| SOURCE OF VARIATION | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| AMONG FISH | | | | | |
| Density | 2 | 1904.36 | 952.18 | 5.42 | * |
| Fish/Density | 9 | 1579.93 | 175.55 | 4.57 | ** |
| WITHIN FISH | | | | | |
| Trial | 7 | 845.16 | 120.74 | 3.14 | ** |
| Density*Trial | 14 | 1256.04 | 89.72 | 2.34 | * |
| (Fish/Density)*Trial | 63 | 2419.41 | 38.40 | | |
| TOTAL | 95 | 8004.90 | | | |

Table 2.3. Analysis of Variance of mean seconds per capture for bluegills feeding on nymphs. Model is a split plot design with trials as repeated measures. Data are means using captures up to the 25% prey depletion level in trials. Model: Y = Density + Fish/Density + Trial/Fish. (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

ANALYSIS OF VARIANCE : Seconds per Capture
PREY TYPE : Damselfly Nymphs

| SOURCE OF VARIATION | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| AMONG FISH | | | | | |
| Density | 2 | 2941.73 | 1470.86 | 6.98 | * |
| Fish/Density | 9 | 1895.32 | 210.59 | 0.70 | |
| WITHIN FISH | | | | | |
| Trial | 7 | 5422.56 | 774.65 | 2.58 | * |
| Density*Trial | 14 | 3832.11 | 273.72 | 0.91 | |
| (Fish/Density)*Trial | 63 | 18932.83 | 300.52 | | |
| TOTAL | 95 | 33024.55 | | | |

with *Daphnia* indicates nonparallel responses by fish across trials, i.e. fish learned differently at different *Daphnia* densities. The biological interpretation of this interaction is not obvious readily. However, insight can be gained by looking more closely into the effects of experience on the details of searching and handling.

## II. Changes in Handling Time with Experience

Bluegills' handling times decreased with increased feeding experience (Figure 2.5, Tables 2.4 and 2.5). Because of the significant interaction between density and trial, it is necessary to be careful in interpreting main effects. More specifically, the effects of density for both prey types were attributable to differences in the early trials that disappeared in the later trials (Figure 2.5). During Block I, fish facing high and medium *Daphnia* densities reached minimum handling time by the third trial. All nymph density groups reached minimum handling time by the sixth trial.

The low *Daphnia* density group was somewhat of an anomaly. Handling time declined more slowly across trials for these fish than for the other *Daphnia* groups. When these fish were switched to high density in Block II, handling time decreased to the level of the other density groups within two trials. However, fish that were switched from high density to low density did not show the reciprocal effect, i.e. their handling time on *Daphnia* remained at the low level that it had been when feeding on high density. The lack of any effect for other treatments and the eventual disappearance of differences in handling time between density treatments suggest that group 1 had not reached its minimum

Figure 2.5 Handling time across trials. Each dot is mean for 4 fish in each treatment group. Data for each trial was truncated after the 25% prey depletion level. (a) Daphnia. (b) Nymphs. See Table 2.1 for prey densities for each group. L, M, and H = low, medium and high density repectively.

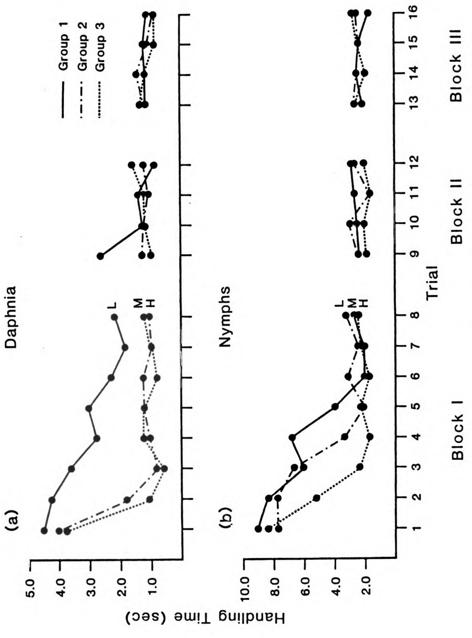

(a)
Daphnia
L
M
H
(b)
Nymphs
L
M
H
Group 1
Group 2
Group 3
Handling Time (sec)
5.0
4.0
3.0
2.0
1.0
10.0
8.0
6.0
4.0
2.0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Trial
Block I
Block II
Block III

Figure 2.5

Table 2.4. Analysis of Variance of handling time per capture for bluegills feeding on *Daphnia*. Model is a split plot design with trials as repeated measures. Data are means using captures within the 25% prey depletion level in trials. Model same as used in Table 2.3. (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

ANALYSIS OF VARIANCE : Handling Time
PREY TYPE : Daphnia

| SOURCE OF VARIATION | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| AMONG FISH | | | | | |
| Density | 2.00 | 357.36 | 178.68 | 28.55 | *** |
| Fish/Density | 9.00 | 56.32 | 6.26 | 7.33 | |
| WITHIN FISH | | | | | |
| Trial | 7.00 | 226.21 | 32.32 | 37.88 | *** |
| Density*Trial | 14.00 | 76.10 | 5.44 | 6.37 | ** |
| Error Within | 63.00 | 53.75 | 0.85 | | |
| TOTAL | 95.00 | 769.74 | | | |

Table 2.5. Analysis of Variance of handling time per capture for bluegills feeding on Nymphs. Model is a split plot design with trials as repeated measures. Data are means using captures within the first 25% prey depletion level in trials. Model same as in Table 2.3. (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

ANALYSIS OF VARIANCE : Handling Time
PREY TYPE : Nymphs (up to 25% depletion level)

| SOURCE OF VARIATION | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| AMONG FISH | | | | | |
| Density | 2.00 | 632.81 | 316.40 | 11.35 | *** |
| Fish/Density | 9.00 | 250.80 | 27.87 | 8.67 | |
| WITHIN FISH | | | | | |
| Trial | 7.00 | 166.03 | 23.72 | 7.38 | *** |
| Density*Trial | 14.00 | 119.46 | 8.53 | 2.66 | * |
| Error Within | 63.00 | 202.46 | 3.21 | | |
| TOTAL | 95.00 | 1371.56 | | | |

handling time on the low density of Daphnia by the last trial of Block I, perhaps because the low prey density did not provide enough motivation. If this was the case, then it can be concluded that, once minimum handling time was attained, handling time was independent of prey density.

Although considerable attention has been given to the role of motivation in fish foraging (see for example Colgan 1973) it is not clear how to measure motivation operationally. One possible expectation is that higher prey densities provide greater motivation for fish and, as such, handling times might be lower at higher prey densities. The lack of differences in handling time between the density treatments in Block II (Figure 2.5) argues against the existence of motivational differences caused by density. However, it is also possible to look at changes in motivation within trials by asking whether handling times increased as prey depleted within trials. Handling time on Daphnia did increase as prey were depleted within trials (Table 2.6) but handling time on nymphs did not. It is not likely that these increases were due to satiation since the total mg of prey eaten by fish at each depletion level was the same for Daphnia and nymph treatments. If motivational levels were directly related to satiation within trials one would expect to see the same increases in handling time for both prey types as prey were depleted. This is not the case (Table 2.6). One explanation is that nymphs, being 4 times larger than Daphnia, provided a bigger payoff per capture and therefore a larger 'motivational incentive' to continue working fast and hard at foraging. This was in spite of the fact that the net capture rates for both prey (in mg/s) were similar (see below).

Table 2.6. Effect of prey depletion within trials on handling time. Data within trials were divided into sequential 25% prey depletion intervals. Data are from Block I (See Table 2.1). ANOVA Model: Y = Trial + Depletion + Fish.

| Prey | Density | F | DF | P |
|---|---|---|---|---|
| Daphnia | 0.25 | 4.09 | 3 | 0.05 |
| | 0.50 | 22.12 | 3 | 0.0001 |
| | 1.00 | 19.40 | 3 | 0.0001 |
| Nymphs | 0.13 | 0.19 | 2 | NS |
| | 0.25 | 0.13 | 2 | NS |
| | 0.35 | 0.52 | 2 | NS |

## Components of Handling Time

The first component of handling time is pursuit. Pursuit distance decreased across trials for all treatment groups with the exception of the low density Daphnia treatment (Tables 2.7 and 2.8). Pursuit times decreased only in the medium and high density Daphnia treatments. Because of the lateral camera view, it was difficult to estimate the distances traveled by fish when they moved toward or away from the camera. This resulted in uneven representation of individual fish within trials for the distance data. In spite of these problems, a significant increasing trend in pursuit velocities was observed for all Daphnia treatments (Spearman rank correlations 0.74 for low, 0.85 for medium and 0.75 for high Daphnia density groups, $p<0.05$). The changes in the nymph treatments were slight.

The time required to position, attack, ingest and pause after successful attacks was combined into what I refer to as 'apprehend time' for analysis. Apprehend time decreased across trials for all treatment groups (Tables 2.7 and 2.8). By the eighth trial, apprehend times were not significantly different between densities within a prey type. Capture success (the proportion of attacks that resulted in successful ingestion) increased for all density treatments. By the eighth trial no Daphnia were missed once attacked and less than 10% of the nymph attacks were unsuccessful.

Table 2.7. Components of handling time for bluegills feeding on Daphnia. Data are means ± 95% confidence intervals pooled for 4 fish in each density group comparing trials 1 and 8 in Block I (up to 25% prey depletion). Times are in seconds, distance in cm and velocity in cm/s. (n = 20, 40, 80 for low, medium and high density respectively).

| COMPONENTS OF HANDLING TIME FOR DAPHNIA | | | | | | |
|---|---|---|---|---|---|---|
| Density | Trial | Pursuit Distance (cm) | Pursuit Time (s) | Pursuit Velocity | Apprehend Time (s) | Capture Success |
| 0.25/1 | 1 | 9.5 | 1.25 ± 0.36 | 7.6 | 3.19 ± 0.28 | 0.95 |
| | 8 | 11.7 | 1.08 ± 0.15 | 10.8 | 1.04 ± 0.15 | 1.00 |
| 0.50/1 | 1 | 8.2 | 1.12 ± 0.34 | 7.3 | 2.88 ± 0.31 | 0.93 |
| | 8 | 6.3 | 0.43 ± 0.09 | 15.0 | 0.80 ± 0.11 | 1.00 |
| 1.00/1 | 1 | 7.7 | 1.01 ± 0.15 | 7.6 | 2.80 ± 0.23 | 0.95 |
| | 8 | 5.2 | 0.48 ± 0.14 | 10.8 | 0.70 ± 0.15 | 1.00 |

Table 2.8. Components of handling time for bluegills feeding on nymphs. Data are means ± 95% confidence intervals pooled for 4 fish in each density group comparing trials 1 and 8 in Block I (up to 25% prey depletion). Times are in seconds, distance in cm and velocity in cm/s. (n = 10, 20 and 30 for low, medium and high density respectively).

| COMPONENTS OF HANDLING TIME FOR NYMPHS | | | | | | |
|---|---|---|---|---|---|---|
| Density | Trial | Pursuit Distance (cm) | Pursuit Time (s) | Pursuit Velocity | Apprehend Time (s) | Capture Success |
| 0.125/1 | 1 | 6.3 | 1.12 ± 0.51 | 5.6 | 7.89 ± 1.55 | 0.81 |
| (low) | 8 | 4.1 | 0.87 ± 0.15 | 4.7 | 1.86 ± 0.54 | 0.90 |
| 0.250/1 | 1 | 5.3 | 0.96 ± 0.12 | 5.5 | 6.73 ± 0.75 | 0.80 |
| (Med) | 8 | 4.6 | 1.05 ± 0.09 | 4.3 | 2.11 ± 0.23 | 0.94 |
| 0.375/1 | 1 | 5.9 | 0.76 ± 0.23 | 7.7 | 7.65 ± 1.23 | 0.68 |
| (High) | 8 | 5.5 | 0.62 ± 0.04 | 8.9 | 2.08 ± 0.35 | 0.92 |

## III. Changes in Searching Time with Experience

Search time up to 25% prey depletion level decreased across trials for each prey density group (Figures 2.6 and 2.7). Naive bluegills (Block I) increased searching efficiency as they gained experience with the prey. The general effect of experience with prey is best illustrated by the fish that faced medium prey density across all trials (group 2 in Figures 2.6 and 2.7). Search time appeared to reach a minimum asymptote by the sixth trial for both prey types and remained at that level for the remaining 10 trials. The decrease in search time was proportionally greater for *Daphnia* than nymphs, decreasing nearly four-fold for *Daphnia* compared to a three-fold decrease for nymphs. Similar decreases in search time across the first block of trials were observed for the other density groups (Figures 2.6 and 2.7, groups 1 and 3).

Search times were affected by manipulations in prey density during Blocks II and III. In treatment Block II (trials 9 through 12 in Table 2.1) fish that had been fed a low density of prey were switched to the high density treatment and fish that had been fed a high density of prey were switched to low density. Search time increased for the fish switched from high to low density and decreased for fish switched from low to high prey density (Figures 2.6 and 2.7, Block II). For *Daphnia*, fish switched from high density to low density started off with high search times in the first 2 trials after the switch. After 4 trials at low density, their search time on *Daphnia* was not different from that for the fish that were at low density through the 8 trials of Block I. Similarly, the search time for the low density group after it was

Figure 2.6 Mean search time on _Daphnia_ across trials for the 4 fish in each treatment group. Data for each trial was truncated after the 25% prey depletion level. See Table 2.1 for prey densities for groups in each block of trials. L, M and H = low, medium and high density respectively.

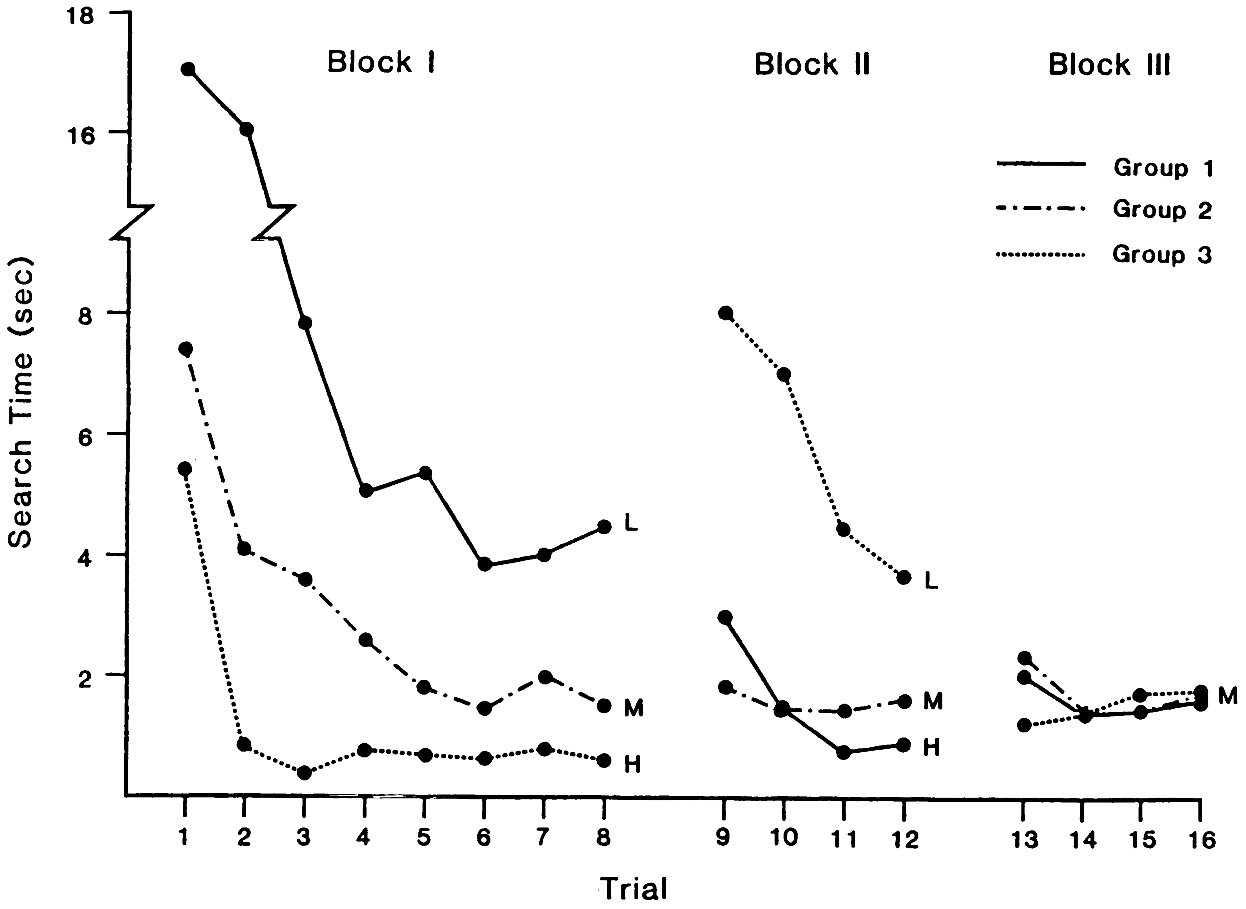

Search Time (sec)
18
16
8
6
4
2
Block I
Block II
Block III
Group 1
Group 2
Group 3
L
M
H
L
M
H
M
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Trial

Figure 2.6

Figure 2.7 Mean search time on nymphs across trials for the 4 fish in each treatment group. Data for each trial was truncated after the 25% prey depletion level. See Table 2.1 for prey densities for groups in each Block. L, M and H = low medium and high density respectively.

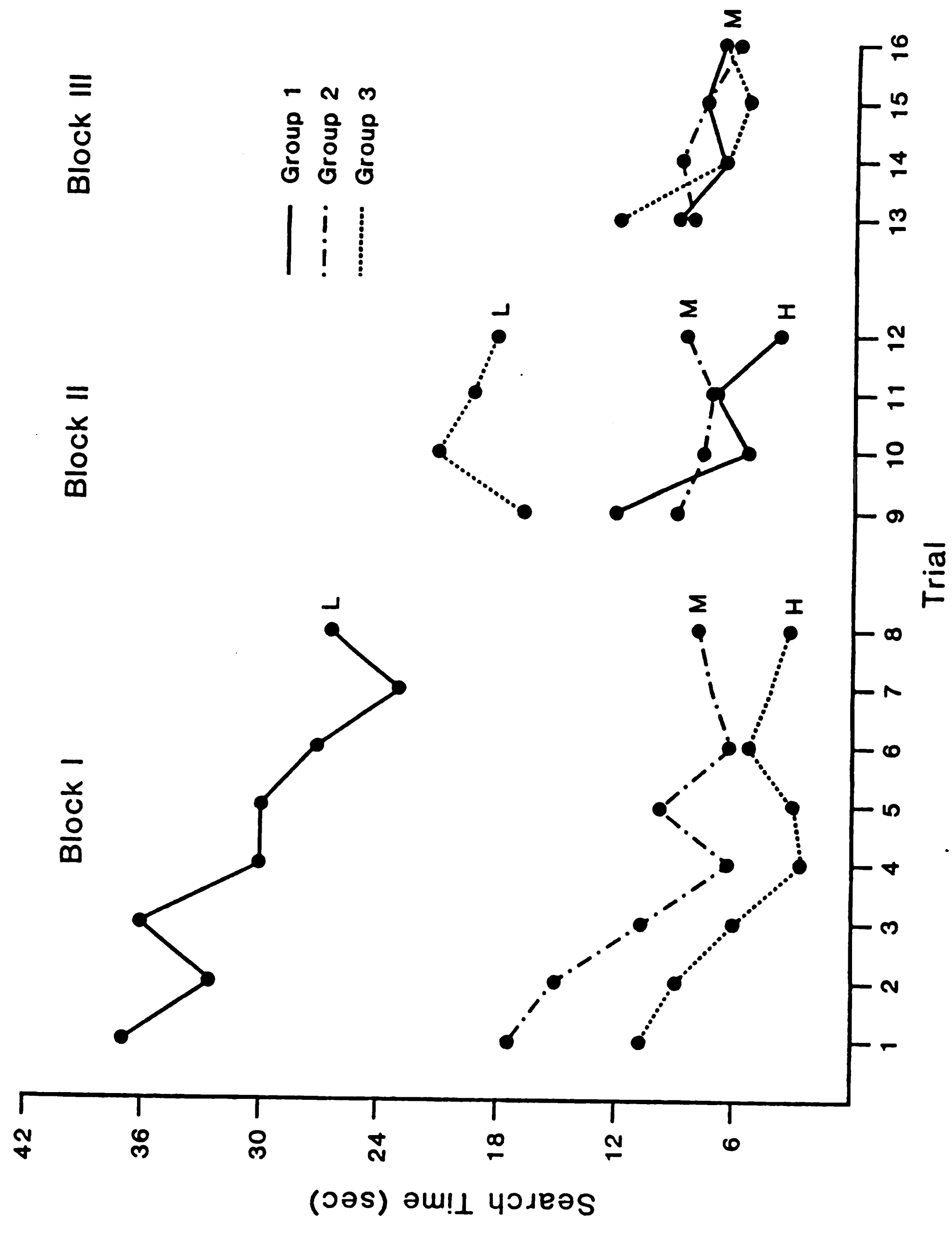

Block I
Block II
Block III
Group 1
Group 2
Group 3
L
M
H
L
M
H
M
Search Time (sec)
42
36
30
24
18
12
6
Trial
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Figure 2.7

switched to high Daphnia density took 3 trials to asymptote to a level equal to that of the fish that had been on high density during Block I. The decreasing trends in search time after density switches indicate that some learning in search time occurred both when density was increased and decreased. Search time on nymphs decreased when density was increased and search time increased when nymph density was decreased (Figure 2.7, Block II, groups 1 and 3 respectively). However, unlike Daphnia, there no strong evidence for trends toward lower search times within Block II after the density switch.

In treatment Block III all fish were switched to medium prey density. By the second trial, search time for the groups that had faced changing densities converged upon the search times for fish that had faced medium density all along (Figures 2.6 and 2.7, Block III). The small changes in density (e.g. high to medium or low to medium) did not require much learning to adjust to the new condition compared to large density changes (e.g. low to high or high to low).

In conclusion, all density groups for both prey types achieved their minimum search time by the 5th trial in Block I (with the exception of the lowest nymph density group). When prey densities were changed, search times increased and/or decreased in the expected direction. Some improvement in search time at the new density occured across trials (i.e. learning) at the new density when the magnitude of the change in prey density was large.

## IV. Components of Searching Time

### Effects of Depletion within Trials

The effects of prey depletion on search time can be investigated by comparisons of the mean search time for sequential 25% depletion intervals within trials. A highly significant interaction between trial and depletion was observed in the *Daphnia* treatments (Tables 2.9, 2.10 and 2.11). This interaction between trial and depletion is seen clearly in Figure 2.8. For fish feeding at low *Daphnia* density, search times actually decreased as prey depleted within the early trials (Figure 2.8a) counter to the general expectation that search time should have increased as prey were depleted. This was due either to learning and/or increased motivation within the first trial. In either case, by the last trial, there was no detectable effect of depletion, i.e. the last prey items taken in the trial were found as quickly as the first prey items.

Search time decreased as prey depleted for fish feeding on medium and high *Daphnia* densities in the early trials (Figures 2.8b and 2.8c). However, by the later trials the trend was reversed; search times began low but increased as prey were depleted within trials. In other words, fish experienced with low prey densities suffered a smaller relative increase in search time with depletion compared to fish experienced with medium and high *Daphnia* density. In fact, the medium and high density treatments actually got worse at dealing with depletion across trials whereas fish at low density got better. Changes in the search paths taken by fish are the most like cause of this difference. This is

Table 2.9. Analysis of Variance of search time per capture for bluegills feeding on 0.25 Daphnia/liter. Model is a split plot design with trials as repeated measures. Data are means using captures within each 25% prey depletion level in trials. Model: Y = Trial + Fish/Trial + Depletion/Fish + interactions. (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

ANALYSIS OF VARIANCE : Search Time per Capture
PREY TYPE : Daphnia
DENSITY : 0.25/liter

| SOURCE OF VARIATION | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| AMONG FISH | | | | | |
| Trial | 7 | 14930.20 | 2132.89 | 3.19 | * |
| Fish/Trial | 28 | 18732.27 | 669.81 | 6.34 | |
| WITHIN FISH | | | | | |
| Depletion | 3 | 936.23 | 312.08 | 2.96 | * |
| Trial*Depletion | 21 | 5053.55 | 240.65 | 2.28 | *** |
| Error Within | 72 | 7595.46 | 105.49 | | |
| TOTAL | 131 | 47247.71 | | | |

Table 2.10. Analysis of Variance of search time per capture for bluegills feeding on 0.5 Daphnia/liter. Model is a split plot design with trials as repeated measures. Model same as in Table 2.9. Data are means using captures within each 25% prey depletion level in trials. (* = P < 0.05, ** = P < 0.01, *** = P < 0.001).

ANALYSIS OF VARIANCE : Search Time per Capture
PREY TYPE : Daphnia
DENSITY : 0.50/liter

| SOURCE OF VARIATION | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| AMONG FISH | | | | | |
| Trial | 7 | 10871.36 | 1553.05 | 2.98 | * |
| Fish/Trial | 28 | 14610.43 | 521.80 | 3.26 | |
| WITHIN FISH | | | | | |
| Depletion | 3 | 1165.70 | 388.57 | 2.42 | * |
| Trial*Depletion | 21 | 10535.72 | 501.70 | 3.13 | *** |
| Error Within | 72 | 11538.98 | 160.26 | | |
| TOTAL | 131 | 48722.19 | | | |

Table 2.11. Analysis of Variance of search time per capture for bluegills feeding on 1.0 Daphnia/liter. Model is a split plot design with trials as repeated measures. Model Data are means using captures within each 25% prey depletion level within trials. Model same as in Table 2.9. (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

ANALYSIS OF VARIANCE : Search Time per Capture
PREY TYPE : Daphnia
DENSITY : 1.00/liter

| SOURCE OF VARIATION | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| AMONG FISH | | | | | |
| Trial | 7 | 8491.74 | 1213.11 | 3.48 | ** |
| Fish/Trial | 28 | 9769.53 | 348.91 | 6.35 | |
| WITHIN FISH | | | | | |
| Depletion | 3 | 498.73 | 166.24 | 3.02 | * |
| Trial*Depletion | 21 | 4118.40 | 196.11 | 3.57 | *** |
| Error Within | 72 | 3956.90 | 54.96 | | |
| TOTAL | 131 | 36835.30 | | | |

Figure 2.8 Mean search time on *Daphnia* (± 95% CI, data pooled for 4 fish in each density group) across trials for each sequential 25% prey depletion interval within the trial. (a) Low density, group 1. (b) Medium density, group 2. (c) High density, group 2.

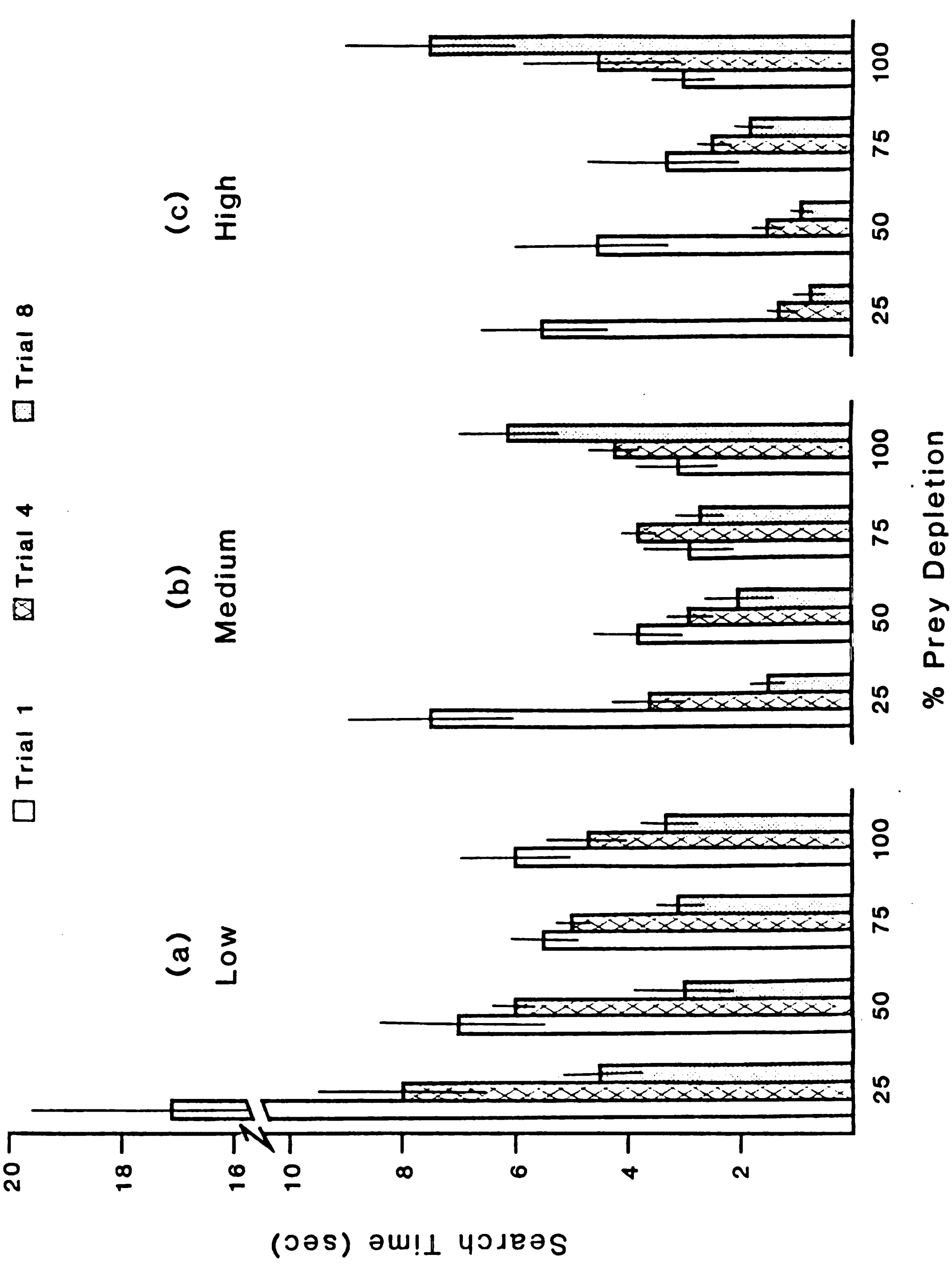

☐ Trial 1
☒ Trial 4
▨ Trial 8
(a) Low
(b) Medium
(c) High
Search Time (sec)
20
18
16
10
8
6
4
2
25
50
75
100
25
50
75
100
25
50
75
100
% Prey Depletion

Figure 2.8

explored in the next section. Unfortunately, nymph densities were seldom depleted beyond the 50% level in these experiments. The fewer total number of captures at each depletion level and the higher variance in search times made it impossible to detect any similar interactions with depletion for the bluegills feeding on nymphs.

## Search Paths

Of all the changes in searching behaviors across trials, the most visually striking were the changes in the directedness of the search paths taken by fish. Figure 2.9 and Figure 2.10 show reconstructions of early and late trials for fish feeding on medium Daphnia and nymph densities. They illustrate the general patterns observed for all fish across trials: (1) a reduction in the number of times they crossed their search path and, (2) a reduction in the number of times they returned to the same location in the arena. The qualitative patterns in the search paths observed suggest strongly that changes in searching path across trials contributed to the overall increase in searching ability. Because prey did not remix in the arena during the experiments, the increased directedness of search paths reduced the effect of depletion on search time by reducing the number of times a forager revisited areas wherein prey were locally depleted.

## Search Velocity

Three factors combined to determine the overall searching velocity for bluegills: (1) the duration of each search hover, (2) the distance moved between hovers and, (3) the swimming speed between hovers.

Figure 2.9 Maps of search paths taken by a bluegill feeding on *Daphnia*. Small dots indicate search hovers. Large dots indicate captures. The fish initiated the trials at the left of the arena. (a) Trial 2. (b) Trial 8.

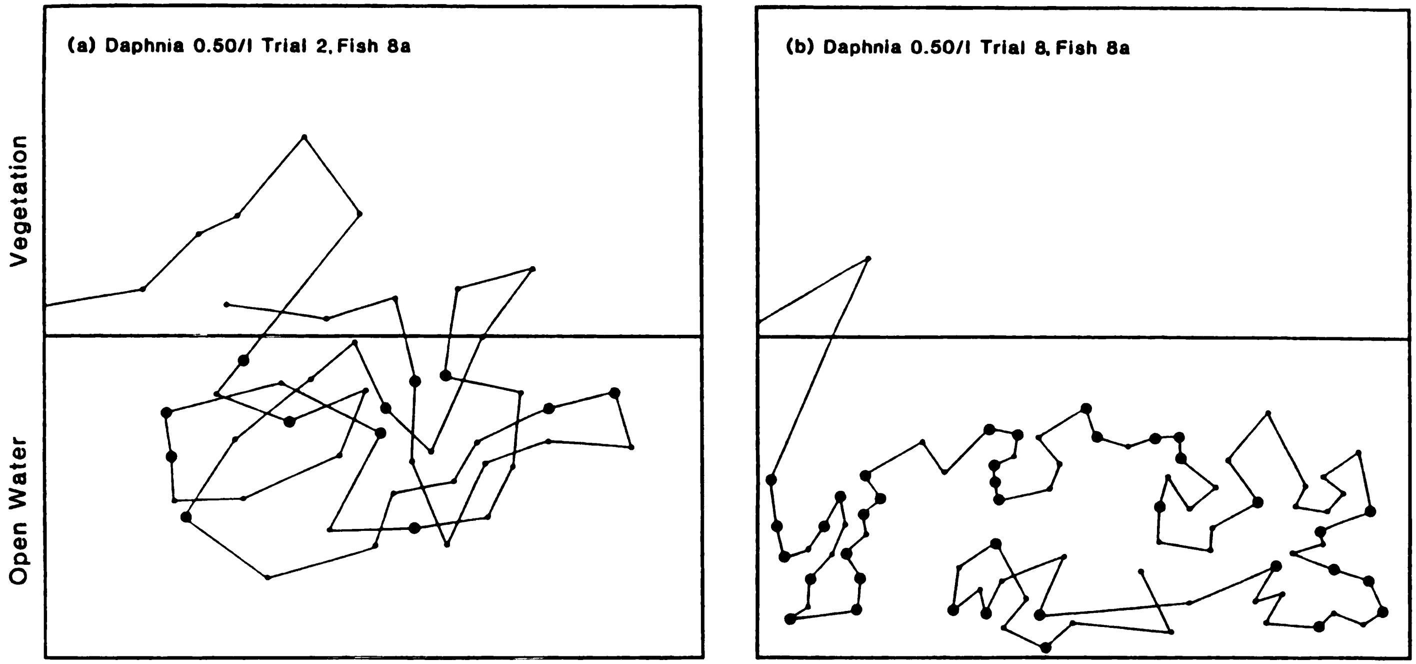
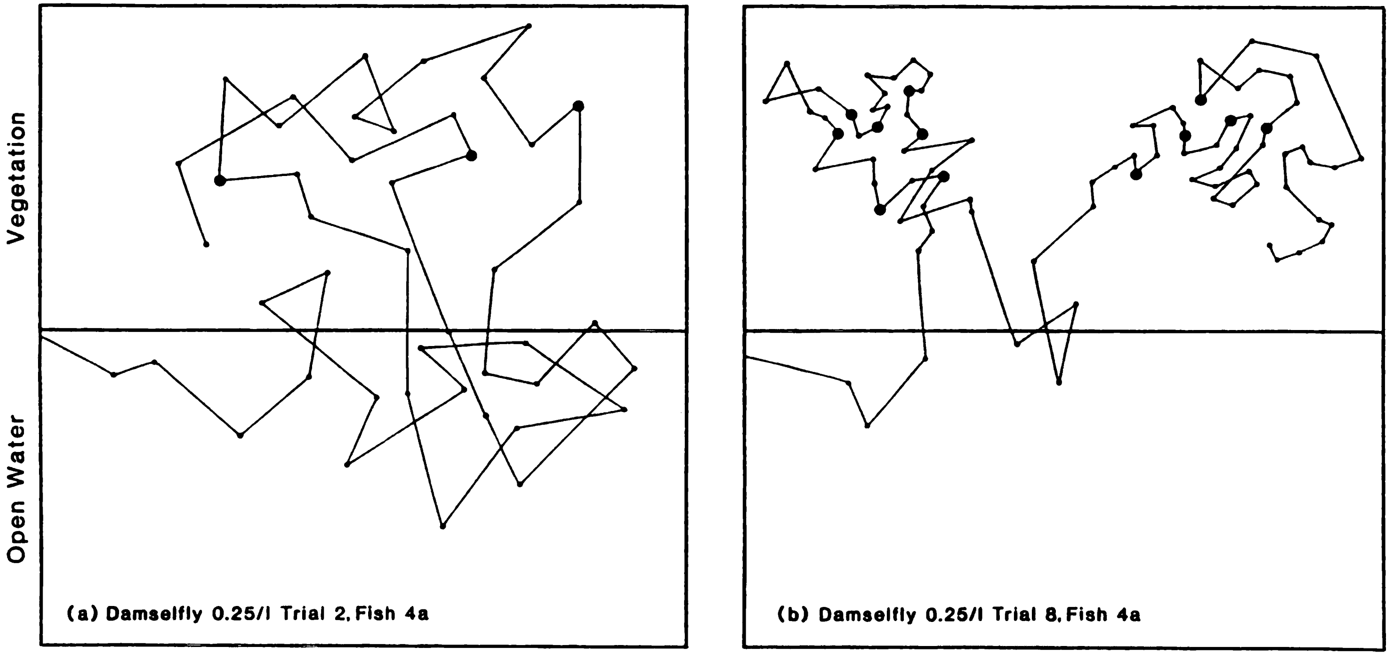

(a) Daphnia 0.50/l Trial 2, Fish 8a
(b) Daphnia 0.50/l Trial 8, Fish 8a
Vegetation
Open Water

Figure 2.9

Figure 2.10 Maps of search paths taken by a bluegill feeding on nymphs. Small dots indicate search hovers. Large dots indicate captures. The fish initiated the trials at the left of the arena. (a) Trial 2. (b) Trial 8.



(a) Damselfly 0.25/l Trial 2, Fish 4a

(b) Damselfly 0.25/l Trial 8, Fish 4a

Figure 2.10

## Time per Search Hover

The analogy between hovers and patches is useful in establishing a context for analyzing the component mechanisms of searching behavior. Search hovers were divided into those that were followed immediately by a prey attack (i.e. capture attempt) and those that were not. If the volume that bluegill search during each hover is considered analagous to a patch (sensu Charnov et. al. 1976) then the duration of each unsuccessful hover is representative of the time that fish were willing to explore the patch before leaving to another (i.e. giving-up-time). Similarly, hovers which terminated with an attack can be viewed as hovers that were interrupted by the detection and pursuit of a prey. Hovers followed by attacks are discussed later in the context of prey detection ability.

The duration of hovers not followed by attacks decreased across trials for the fish in the medium density *Daphnia* and nymph treatments (Figure 2.11, solid lines). The same pattern was observed for the fish in the other treatment groups (Tables 2.12 and 2.13). Interestingly, there was no effect of depletion within trials on hover duration (Table 2.14). All significant changes within individual fish occurred between trials and fish did not appear to adjust hover durations within trials as prey depleted. There was a consistent trend toward lower hover durations with increasing prey density within prey types by the eighth trial (Spearman rank correlations = 1.00, p = 0.05). At medium and high prey density, bluegills hovered longer when searching for nymphs

Figure 2.11 Hover durations (mean seconds per hover ± 1SE, n = 40 for *Daphnia* and n = 20) across trials. Data truncated at the 25% prey depletion level. Dotted line is for hovers followed by attacks on prey. Solid line is for hovers which were not followed by attacks. (a) Medium density *Daphnia* (data pooled for 4 fish). (b) Medium density nymphs (data pooled for 4 fish).

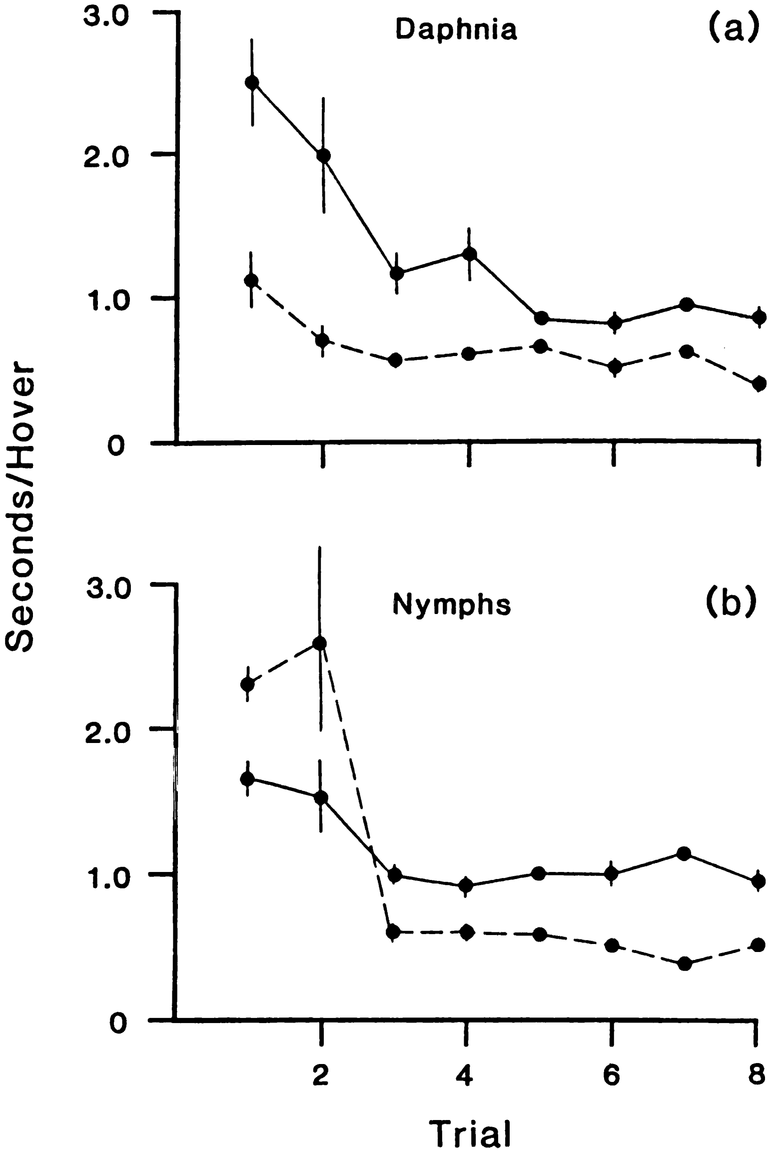

3.0
2.0
1.0
0
Daphnia
(a)
Seconds/Hover
3.0
2.0
1.0
0
Nymphs
(b)
2
4
6
8
Trial

Figure 2.11

Table 2.12. Components of searching time for bluegills searching for Daphnia. Data are means ± 95% confidence intervals for 4 fish in each density group comparing trial 1 and trial 8 in the first block of trials up to 25% prey depletion. (n = 20, 40 and 80 for low, medium and high density respectively). Times are in seconds, distance in cm and velocity in cm/s.

| COMPONENTS OF SEARCHING TIME FOR DAPHNIA | | | | | | | |
|---|---|---|---|---|---|---|---|
| Density | Trial | Sec / Hover (no attack) | Sec / Hover (attack) | Hovers per Attack | Distance / Move | Time / Search Move | Move Velocity |
| 0.25/1 | 1 | 2.19 ± 0.36 | 3.20 ± 0.82 | 4.20 ± 1.12 | 10.5 | 1.96 ± 0.21 | 5.36 |
| (Low) | 8 | 1.20 ± 0.25 | 0.57 ± 0.19 | 1.58 ± 0.49 | 7.5 | 1.03 ± 0.10 | 7.69 |
| 0.50/1 | 1 | 2.53 ± 0.31 | 1.13 ± 0.18 | 2.38 ± 0.88 | 8.0 | 1.20 ± 0.17 | 6.67 |
| (Med) | 8 | 0.88 ± 0.06 | 0.44 ± 0.04 | 0.93 ± 0.19 | 5.5 | 0.52 ± 0.03 | 10.58 |
| 1.00/1 | 1 | 2.60 ± 0.51 | 0.93 ± 0.11 | 1.92 ± 0.30 | 8.5 | 0.90 ± 0.18 | 9.44 |
| (High) | 8 | 0.62 ± 0.11 | 0.47 ± 0.09 | 0.17 ± 0.16 | 5.5 | 0.36 ± 0.08 | 15.28 |

Table 2.13. Components of searching time for bluegills searching for nymphs. Data are means ± 95% confidence intervals for 4 fish in each density group comparing trial 1 and trial 8 in the first block of trials up to 25% prey depletion. (n = 10, 20 and 30 for low, medium and high density respectively). Times are in seconds, distance in cm and velocity in cm/s.

| COMPONENTS OF SEARCHING TIME FOR NYMPHS | | | | | | | |
|---|---|---|---|---|---|---|---|
| Density | Trial | Sec / Hover (no attack) | Sec / Hover (attack) | Hovers per Attack | Distance / Move | Time / Search Move | Move Velocity |
| 0.125/1 | 1 | 2.51 ± 0.19 | 2.88 ± 0.08 | 12.71 ± 3.58 | 8.5 | 2.06 ± 0.85 | 4.13 |
| (Low) | 8 | 1.16 ± 0.21 | 0.86 ± 0.07 | 5.78 ± 1.77 | 4.0 | 1.23 ± 0.30 | 3.25 |
| 0.250/1 | 1 | 1.68 ± 0.07 | 2.03 ± 0.16 | 7.10 ± 2.18 | 9.5 | 0.98 ± 0.09 | 9.69 |
| (Med) | 8 | 0.96 ± 0.03 | 0.50 ± 0.04 | 3.22 ± 0.85 | 3.5 | 0.57 ± 0.07 | 6.14 |
| 0.375/1 | 1 | 1.44 ± 0.10 | 1.90 ± 0.19 | 5.08 ± 1.13 | 8.5 | 1.21 ± 0.18 | 7.02 |
| (High) | 8 | 0.91 ± 0.07 | 0.87 ± 0.07 | 3.87 ± 1.27 | 3.5 | 0.67 ± 0.05 | 5.22 |

Table 2.14. Effect of prey depletion within trials on TIME PER SEARCH HOVER. Data within trials were divided into successive 25% prey depletion intervals. Data are from Block I (See Table 2.1). Model: Y = Trial + Depletion + Fish. Interactions were not significant.

| Prey | Density | F | DF | P |
|---|---|---|---|---|
| Daphnia | 0.25 | 4.27 | 3/7 | 0.05 |
| | 0.50 | 3.09 | 3/7 | NS |
| | 1.00 | 3.40 | 3/7 | NS |
| Nymphs | 0.13 | 2.46 | 2/7 | NS |
| | 0.25 | 1.00 | 2/7 | NS |
| | 0.35 | 4.61 | 2/7 | NS |

compared to Daphnia. The implications of this difference in hover time between prey types are explored further in the discussion.

The time per hover (without attack) decreased for fish switched from low to high Daphnia density (1.20 ± 0.25s on the last trial at low density to 0.68 ± 0.09s by the fourth trial at high density, mean ± 95% C.I.). The time per hover (without attack) increased for fish switched from high to low Daphnia density (0.62 ± 0.11s on the last trial at high denstiy to 1.05 ± 0.13s by the fourth trial at low density, mean ± 95% C.I.). There were no detectable changes in time per hover for nymphs when densities were switched.

## Distance, Time and Velocity of Search Moves

The distance moved between hovers decreased across trials for all fish at all prey densities in Block I (Tables 2.12 and 2.13). Because of the lateral camera view it was often necessary to estimate the distance traveled toward or away from the camera by triangulation. These distance estimates were found to be significantly different from the distances estimated from moves where triangulation was unnecessary. Since there was no reason to expect this difference a priori, the data using triangulation was discarded. The mean distances per search move presented in Table 2.12 and Table 2.13 are only for search moves measured without triangulation. Because of this, not all fish were represented equally in the data on any given trial. Distance moved per hover decreased across trials for all treatment with both prey types (Spearmans rank correlations equal 0.72, 0.81, 0.80 for low, medium and high Daphnia densities respectively; 0.93, 0.89, 0.74 for low, medium and high nymph densities repectively, $p < 0.05$). By the eighth trial mean distance per search move for all nymph treatment groups was less than that for all *Daphnia* treatment groups.

The mean duration of each move between hovers (i.e. time per search move) also decreased across trials for all treatment groups in Block I (Figure 2.12, Tables 2.12 and 2.13). Time per search move in the eighth trial decreased with increasing density for *Daphnia*. Medium and high density nymph treatments were lower than the low density treatment but not different from each other.

The mean distance moved between hovers divided by the mean time per move gives an estimate of the swimming velocity between hovers (move velocity in Tables 2.12 and 2.13). It is interesting to note that mean movement velocity increased for all *Daphnia* densities between the first and eighth trial while it decreased for all nymph densities. Fish moved faster at higher *Daphnia* densities than at the lower densities. There was no clear pattern in move velocity with nymph density in Block I.

Move velocity increased when fish were switched from low to high *Daphnia* density in Block II (7.69 cm/s on the last trial on low density to 14.51 cm/s by the fourth trial on high density). Move velocity decreased for fish switched from high to low *Daphnia* density (15.28 cm/s on the last trial on high density to 9.25 cm/s on the fourth trial on low density). Fish that were switched from low nymph density to high nymph density increased move velocity from 2.25 cm/s to 6.20 cm/s.

Figure 2.12 Durations of search moves across trials (mean ± 1SE, n = 40 for Daphnia, n = 20 for nymphs, data pooled for 4 fish for each prey type). (a) Medium density Daphnia. (b) Medium density nymphs.

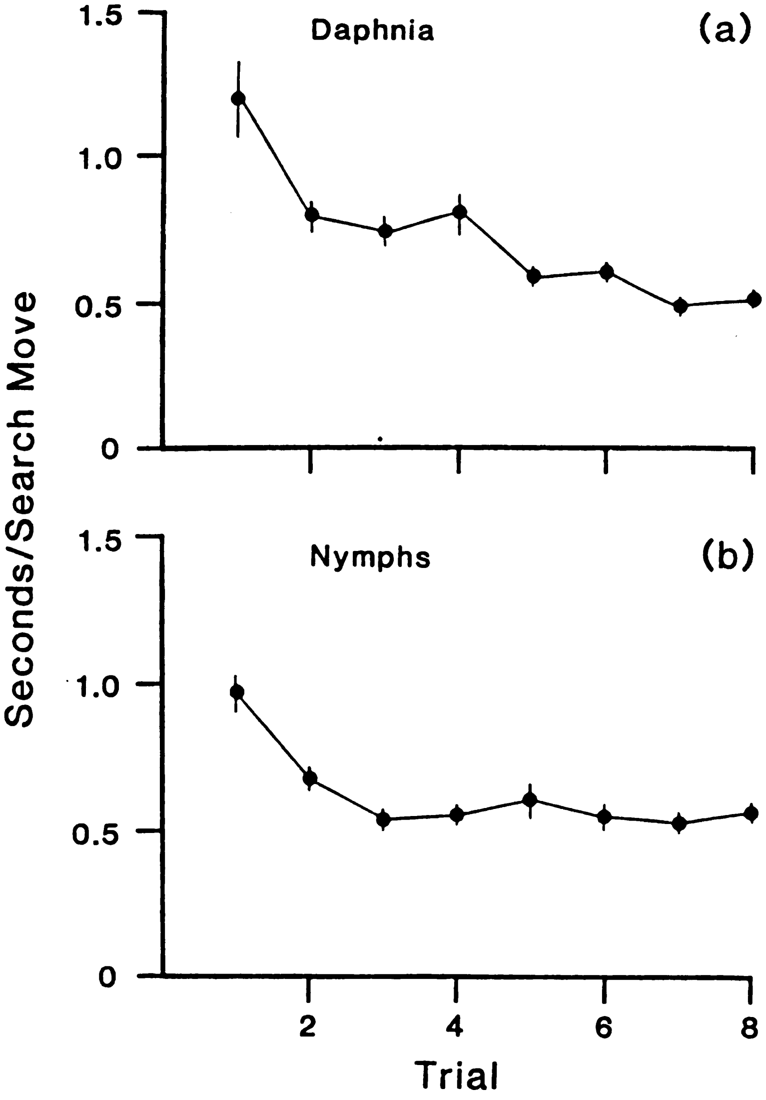

Daphnia
(a)
Nymphs
(b)
Seconds/Search Move
1.5
1.0
0.5
0
1.5
1.0
0.5
0
2
4
6
8
Trial

Figure 2.12

## Detection Probability

Assuming that all prey detected were pursued, the duration of hovers followed by prey attacks was a measure of the time taken to detect a prey on a given hover. This time decreased for all fish in all treatments (Tables 2.12 and 2.13). The comparison of hovers without attacks to those with attacks is instructive. For medium *Daphnia* density, fish continued to hover longer when no prey were detected than the mean hover time required to detect a prey on a given hover for all trials (Figure 2.11a). The same pattern is seen for the high density *Daphnia* treatment (Table 2.12). This contrasts with the other treatment groups. Fish at medium nymph density took significantly longer to detect a prey on a hover than the mean length of hovers that did not result in an attack (Figure 2.11b). Put another way, only the longest hovers resulted in detection of nymphs. However, by the later trials the mean time to detect a prey on a hover dropped below the mean hover duration for all other hovers. This crossover occurred across trials for all nymph treatments and the low *Daphnia* treatment (Tables 2.12 and 2.13).

The large decreases in the time required to detect prey on a hover suggest the formation of search images. However, the crossover of detection time and hover duration indicates that some fish would have increased the number of detected prey in the early trials had they increased the average length of their hovers. There was a strong positive relationship between the mean time per hover and the mean search time per encounter for the early trials. This was the case for both prey types (Table 2.15). Because fish were very poor at detecting

Table 2.15. Regression coefficients and significance for search time in a trial as a function of the time per search hover. Early trials consist of data pooled from trial 1 and 2. Late trials consist of data pooled from trial 7 and 8. (Search time = a * exp (b * time per hover) ).

| PREY | Density | Trial | a | b | $r^2$ |
|---|---|---|---|---|---|
| DAPHNIA | LOW | Early | 7.11 | 0.47 ** | 0.51 |
| | | Late | 2.54 | 0.39 * | 0.54 |
| | MEDIUM | Early | 2.00 | 0.59 ** | 0.35 |
| | | Late | 1.44 | 0.34 * | 0.69 |
| | HIGH | Early | 2.15 | 0.33 * | 0.38 |
| | | Late | 0.92 | 0.16 NS | 0.15 |
| NYMPHS | LOW | Early | 10.76 | 0.52 *** | 0.63 |
| | | Late | 30.80 | -0.35 ** | -0.49 |
| | MEDIUM | Early | 9.86 | 0.30 ** | 0.27 |
| | | Late | 23.90 | -0.65 *** | -0.51 |
| | HIGH | Early | 4.51 | 0.48 ** | 0.30 |
| | | Late | 7.30 | 0.04 NS | 0.19 |

prey in the early trials, search time was lowered if they left hovers relatively quickly and moved to another hover location where a prey might have been more visible.

Daphnia are a relatively non-cryptic prey and by the later trials fish had learned to detect them very quickly in a hover. Therefore, if a Daphnia was not detected right away, the odds were good that no prey item was within the hover area and remaining in the hover longer would have the effect of increasing search time (note positive slopes for regressions in Table 2.15). On the other hand, nymphs were more cryptic than Daphnia and in spite of the fact that bluegills had learned to detect them better by the later trials, the time required to do so was greater than that for Daphnia. As a result, by remaining in hovers longer, fish increased the probability that a nymph would be detected. This would reduce the number of hovers per encounter and the net search time per prey (note the negative slopes for the regressions in Table 2.15).

## DISCUSSION

### Predicting Optimal Hover Duration

This study demonstrates that bluegill sunfish increased their searching and handling efficiency as they gained experience with a given prey type. Generally speaking, bluegill increase encounter rates by searching more slowly for cryptic and/or scarce prey and by searching faster for non-cryptic and/or abundant prey. Likewise, they learn to search in a systematic fashion when prey are cryptic or scarce.

Of the components of searching and handling that change with experience, it is useful to distinguish between components that can be thought of as being under the facultative control of the fish (i.e. search velocity, hover duration and search paths) and those that change more or less as a function of practice (i.e. detection ability and capture techniques). In order to assess the importance of changes in specific components of foraging due to learning, it is necessary to compare these changes to the corresponding changes in net foraging performance.

Hover duration contributes to the realized mean search time in a variety of ways. The optimal hover time (i.e. that which minimizes search time) will depend on the probability that a prey will be detected within a given unit of hover time. This is in turn contingent upon the probability that prey are present within the volume of water searched on a given hover. It is reasonable to assume for the moment that the probability that a prey is present within the search volume of a hover is an asymptotic function of the product of prey density and the volume searched on each hover. Therefore, if we assume that prey are distributed randomly in the habitat, the probability that a prey is present within the volume searched on a given hover is constant for a given density. This assumes that prey remix completely after each capture, there is no prey depletion, and that foragers do not search systematically during the trial.

If at least one prey is present within the hover volume then the longer a fish remains in a hover, the greater the probablity that it will detect a prey during the hover. If a fish chooses a particular maximum duration for hovers ($T_{hov}$) before leaving to another hover, then

$$P(\text{encounter} \mid \text{Thov}) = \int_{0}^{T_{hov}} P(\text{detection} \mid \text{prey present})\, dt \qquad (4)$$

This probability of encountering prey is shown by curve 'P' in Figure 2.13. Defined operationally, 'P' is the inverse of the number of move-hover cycles required per prey encounter. Therefore, if a fish chooses never to hover longer than a particular hover time on a trial ($T_{hov}$), then

$$S = E(m+h) / P \qquad (5)$$

where S is the expected search time for a prey item and E(m+h) is the expected time per move-hover cycle. If every encounter occured exactly at $T_{hov}$, E(m+h) would equal $T_{mov} + T_{hov}$. Since $T_{hov}$ is a maximum hover duration the expected hover time (h) will be less than $T_{hov}$. Therefore, E(m+h) will be an accelerating function of $T_{hov}$, approaching $T_{mov} + T_{hov}$ as an asymptote (Figure 2.13). This consideration is not important unless few hovers occur per encounter and, as such, hovers with encounters occurring prior to $T_{hov}$ would significantly lower E(m+h).

Figure 2.13 shows S as a function of $T_{hov}$ for the case where $P\{\text{prey present}\}$ equals one. Given the assumptions about detection probabilities, there is a $T_{hov}$ that minimizes the expected search time for a prey type. If fish hover for shorter durations the probability of detecting a prey is low and more hovers are necessary per encounter, thereby increasing search time. If fish take a longer time per hover,

Figure 2.13 Schematic illustration of model for determining optimal hover times for a bluegill feeding on conspicuous prey and cryptic prey. $T_{hov}$ = hover time. P = conditional probability of detecting a prey given at least one prey present in the search volume of a hover. E(m+h) = expected time of a move-hover cycle (i.e. $T_{mov}$ + $T_{hov}$). S = search time. 1=conspicuous prey. 2=cryptic prey.

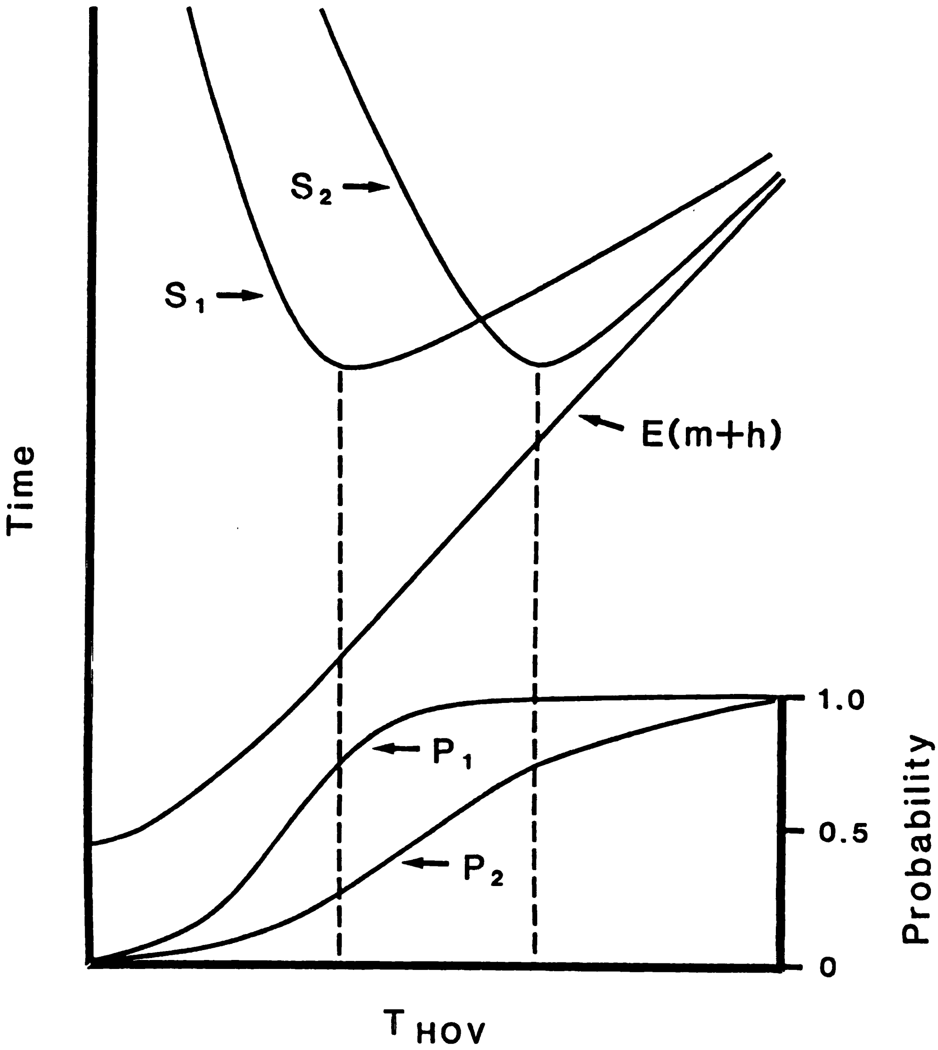


Figure 2.13

the probability of detecting a prey is high but fewer hovers per time reduces the rate that prey enter the search volume, resulting in higher search time. Changes in prey crypticity changed the shape of the 'P' curve in Figure 2.13. Increased crypticity increases the optimal hover time (compare P1 with P2 in Figure 2.13).

Bluegills showed a curvilinear relationship between hover duration and search time in the above experiments. Polynomial regressions (pooling all fish at medium prey densities) showed a significant negative 1st degree coefficient and a significant positive 2nd degree coefficient (Figure 2.14). This results in a parabolic relationship between hover time and search time for nymphs and to a lesser extent for Daphnia. It is interesting to note that search time is minimized at a lower hover time for 'less cryptic' Daphnia compared to the 'more cryptic' nymphs. It is not my intention to argue that these data prove the above model, particularly since all experience levels and effects of individual differences are pooled within the analysis of Figure 2.14. Rather, I present the analysis as support for the general notions that hover time is an important and interpretable behavioral component that contributes to net search time.

Within this framework, it is possible to imagine two ways that learning could decrease search time. The first would be choosing a better hover time by moving along the curves in Figure 2.12. Alternatively, improvements in detection ability such as search image formation (e.g. Dawkins 1971) would change the shape of the 'P' curves. When prey are not distributed randomly within a habitat or if the probability that a prey item occurs within a hover volume is less than one, the problem becomes more complicated. As time passes during a

Figure 2.14 Quadratic polynomial regressions of Search Time with Time per Search Hover. Data pooled for all fish at medium densities of each prey type ($n = 72$ for each regression). For Daphnia : $Y = 2.6 - 1.3 X + 1.2 X^2$ ($r^2 = 0.734$, $p = 0.032$ for 2nd. degree coeff., $p = 0.007$ for 1st. degree coeff.). For Nymphs: $Y = 14.32 - 7.36 X + 2.9 X^2$. ($r^2 = 0.501$. $p = 0.011$ for 2nd. degree coeff. $p = 0.001$ for 1st. degree coeff.).

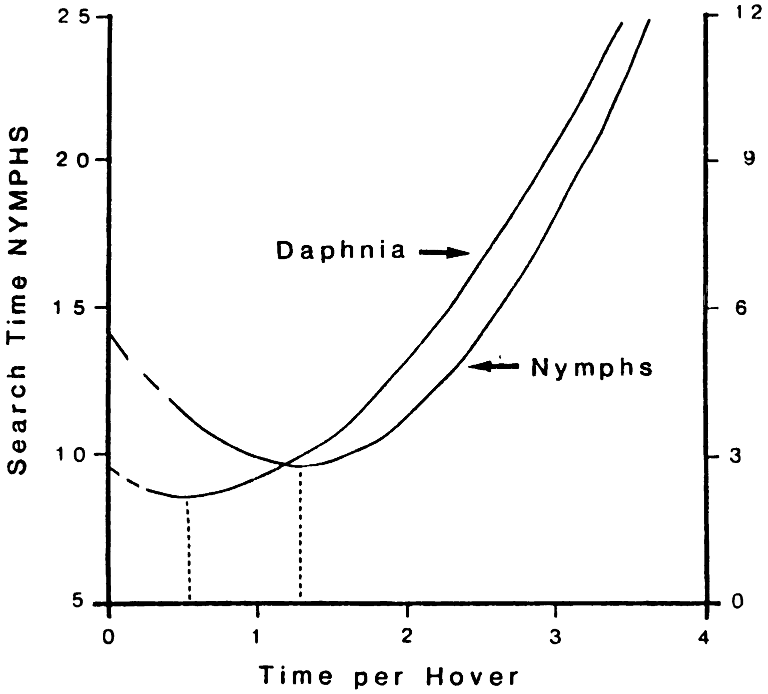

Search Time NYMPHS
25
20
15
10
5
Search Time DAPHNIA
12
9
6
3
0
Daphnia
Nymphs
0
1
2
3
4
Time per Hover

Figure 2.14

hover, a fish would need to compare the probability that a prey item would be detected within the next time unit on the present hover against the same probability if it moved to another hover location. By leaving the current hover prematurely, fish incur a cost, i.e. the travel time between hovers. By remaining in a hover too long fish run the risk of wasting time searching an area with no prey present.

Gendron and Staddon (1983, 1984) developed a similar model to predict the optimal searching rate for foragers that search continuously (In this case, searching rate is analogous to the inverse of hover duration). Their model assumes that the probability of detecting a prey decreases as search rate increases. This appears to be the case for humans (Gendron and Staddon 1984). For example, they showed that when prey were cryptic, increasing search velocity increased encounter rate up to a point, but further increases actually lowered encounter rates due to an inverse relationship between search rate and detection probability. This appears to be the case for bluegills (Figure 2.14). Increasing search rate will increase the rate that prey enter a bluegill's search volume. However, this will not necessarily increase encounter rate. Search time decreased as $T_{hov}$ increased up to a point, then proceeded to increase as $T_{hov}$ rose further.

In order to test these models properly, it is necessary to determine detection probabilities more accurately. This requires manipulations wherein the experimenter knows the availability of prey within the area searched on each hover. Such experiments will allow for proper calculations of how detection probabilities change with experience and allow for the calculation of predicted optimal searching velocities and hover durations.

## Experience and the Other Components of Searching

Decreases in the length of time required to detect a prey during a hover indicate that detection abilities improved with experience. One might expect that bluegills would learn to detect prey at greater distances. This does not appear to be the case. Pursuit distance (i.e., the distance fish travel to capture prey once detected) decreased with experience for all treatments (with the exception of the low density Daphnia treatment). This suggests that bluegills decreased the size of the area that they searched on each hover and, in turn, increased the thoroughness of their search of that area. Although the maximum distance that bluegills detect prey items of particular, sizes has been measured in the laboratory (Wright and O'Brien 1982) it is not clear to what extent search distances are influenced by experience and/or motivational levels. Furthermore, other prey characteristics such as motion, coloration as well as light levels and water clarity will affect the volume that bluegills can successfully search at each hover (Kerfoot 1982, Vinyard and O'Brien 1976).

An alternative explanation for the decrease in pursuit distance with experience is that bluegills saw many prey on each hover and learned to choose the closest prey. This is entirely possible with the medium and high Daphnia treatments since it took an average of less than one hover to detect a Daphnia (Table 2.12).

The fact that the path taken by a forager influences its encounter rate with prey is well documented (e.g. Zach and Falls 1976b, Kohler 1983, Bond 1980, Ollason 1983, Anderson 1983, Smith 1974, Heinrich 1979, Schmidt-Hempfel 1984, Krebs 1973). Describing search paths is not at all straightforward and prediction of optimal search paths is difficult. Gendron and Staddon (1983), generalized from Beukema (1968), define the efficiency of a search path as the ratio of the prey density in the area actually searched by the predator to the overall prey density in the environment. This definition is useful when prey are distributed heterogenously and fish move among discrete patches, searching only with the current patch. However, unless one knows the distance at which the fish can detect a prey, it is not possible to know the volume the fish is searching on a particular hover or the density of prey within the area the fish is searching. Further research in this direction is essential.

Perhaps the most interesting results of this study are the significant foraging differences between individual fish. Individual differences are difficult to quantify and even more difficult to interpret. In any case, their potential importance can not be denied by anyone interested in the evolution of foraging and learning since variance in a trait is one necessary component if natural selection is to influence the trait's distribution (Arnold 1983). The implications of these differences are discussed in greater detail in the Chapter 4.

This study has quantified some of the factors of foraging ability that change with experience and has provided a measuring stick for the next step ... the assessment of how searching and handling abilities are affected by the inclusion of more than one prey type in foragers' diets and whether these changes affect diet choice. This is the subject of the next chapter.

# CHAPTER 3

# HABITAT SWITCHING BY THE BLUEGILL SUNFISH: ALLOCATION AND FORAGING RETURN

## INTRODUCTION

As discussed in Chapter 1, the problem of information aquisition by foragers can be broken down into two components, refered to as learning 'how' and learning 'about' prey. Most models of habitat selection make predictions based upon the foraging rate that a forager can attain by choosing to feed in a particular habitat or patch. Learning 'how' could influence predictions of diet choice by directly influencing the return rates within those habitats (McNair 1982, 1983, Dill 1983, Glasser 1984, Hughes 1979, Shettleworth 1984). However, empirical demonstration of this interaction between learning 'how' and learning 'about' prey is elusive (cf Heinrich 1979).

Chapter 2 demonstrated that learning 'how' to search for and handle prey affects the foraging rates of bluegill sunfish (*Lepomis macrochirus*). This chapter presents the results of an investigation looking a whether bluegills learn 'about' prey and use this information when making decisions about where to forage. Laboratory feeding experiments with bluegills consisted of a series of trials with the density of prey in one habitat held constant while the density in the second habitat was varied across trials.

Previous studies of the effects of learning on prey and habitat choice by foragers have taken two distinct tracks. One track looks at whether actual foraging behaviors fit some sort of learning model or decision rule. The second attempts to determine if foragers' choices maximize food intake and/or optimize some other currency of foraging behavior (see discussion in Staddon (1983)). This chapter deals primarily with the first track by (1) exploring the relationships between foraging returns and past foraging experience within habitats, and (2) by determining the functional relationship between foraging return and habitat choice.

## METHODS

The details of the experimental tanks, habitats, fish and prey types were similar to those described for the experiments in Chapter 2. Sixteen 57mm bluegill sunfish (Lepomis macrochirus) were assigned to one of two treatment groups (8 fish per group, Table 3.1). Each treatment consisted of 6 blocks of eight trials (2 trials per day per fish) with one prey type (prey type 1) held at a constant density through all trials. The density of the second prey type (prey type 2) was varied across the blocks of trials as show in Table 3.1. Density changes of the second prey type were designed to mimic the seasonal pattern of prey abundance in the vegetated and openwater habitats in local lakes (see Mittelbach 1981). Group N-D was fed nymphs in the vegetation at a density of 0.25/l throughout all trials while Daphnia density was changed in the openwater. Group D-N faced a constant Daphnia density of 0.50/l with changing nymph density. Results from single prey feeding experiments in Chapter 2 indicated that experienced bluegills received equivalent return rates when feeding on these densities of the constant

Table 3.1. Prey densities (#/l) used in two prey experiments. (*Daphnia* in open water and nymphs in vegetation). Blocks consist of 8 consecutive trials with the prey densities shown. Density of the first prey type was constant throughout all trials while that of the second was manipulated. Two trials per fish per day, 8 fish per group.

| BLOCK | I | II | III | IV | V | VI |
|---|---|---|---|---|---|---|
| TRIAL | 1-8 | 9-16 | 17-24 | 25-32 | 33-40 | 40-48 |
| GROUP N-D | | | | | | |
| NYMPHS | 0.250 | 0.250 | 0.250 | 0.250 | 0.250 | 0.250 |
| DAPHNIA | 0.000 | 0.125 | 0.250 | 0.500 | 1.000 | 0.250 |
| GROUP D-N | | | | | | |
| DAPHNIA | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 |
| NYMPHS | 0.000 | 0.063 | 0.125 | 0.250 | 0.375 | 0.125 |

prey type (approx. 0.033 mg/s). The density of the second prey type was increased for each block of trials so that by Block IV the expected maximum return rates for each habitat would be equal (determined from the single prey type experiments in Chapter 2). At the beginning of the sixth block, the density of the changing prey type was decreased to the level of the third block to see whether bluegills would switch back to the constant prey type.

Previous experiments showed that capture rates changed as time elapsed within trials due to the dynamic nature of prey depletion (see Chapter 2). As such, in order to compare response measures between trials, it was necessary to decide on an appropriate place to truncate the data within a trial. Four methods were used: (1) truncation after 1 minute of elapsed foraging time in a trial, (2) truncation after a spcified mg of prey had been taken, (3) truncation after a fish visited each habitat 1 time in a trial, and (4) truncation after 25% depletion of either the constant or changing prey type. All analyses were repeated using each of the truncation methods. Results using the first method (one minute of feeding in each trial) are presented in this chapter. No major differences in observed patterns were attributable to the truncation method used.

# RESULTS

## Allocation of Diet

One measure of diet allocation is the percentage by weight of a prey type in the diet (mg of prey type 1 eaten / total mg of prey eaten). As prey densities changed across treatment blocks a great range in the pattern of diet allocation was observed among fish (Figure 3.1). The mean diet allocation to the second prey type on a given trial for all fish climbed gradually across trials. By the last trial in Block IV mean diet allocation had risen to 50% Daphnia for Group N-D (increasing Daphnia density). Recall that in Block IV fish faced prey densities in each habitat that gave equal return rates in single prey type foraging trials. When density was increased again in Block V, diet allocation rose to almost 90% Daphnia for Group N-D (Figure 3.1a). When Daphnia were decreased in Block VI, diet allocation shifted back toward feeding mostly on nymphs. Similarly, Group D-N increased the percentage of nymphs in their diets with inceasing nymph density (Figure 3.1b).

The mean capture rate with the constant prey type decreased as bluegills allocated more of their diet to the changing prey type. Figure 3.2 shows an increase in the mean time per capture for the eight fish in each group as the proportion of the changing prey type in their diet increased. At the same time, capture rates with the changing prey type increased as bluegills gained foraging experience with the new prey type. This interference pattern is highly variable among fish and is explored in detail in Chapter 4.

Figure 3.1 Percentage of the changing prey type (by mg) in diet (mean and range for the 8 fish in each group). (a) Group D-N as nymphs are manipulated. (b) Group N-D as *Daphnia* density manipulated. Density of the second prey type was held constant across blocks. Data for fish on a trial were truncated after 1 minute of foraging time. See Table 3.1 for prey densities. Data for Block I not shown since only one prey type was available.

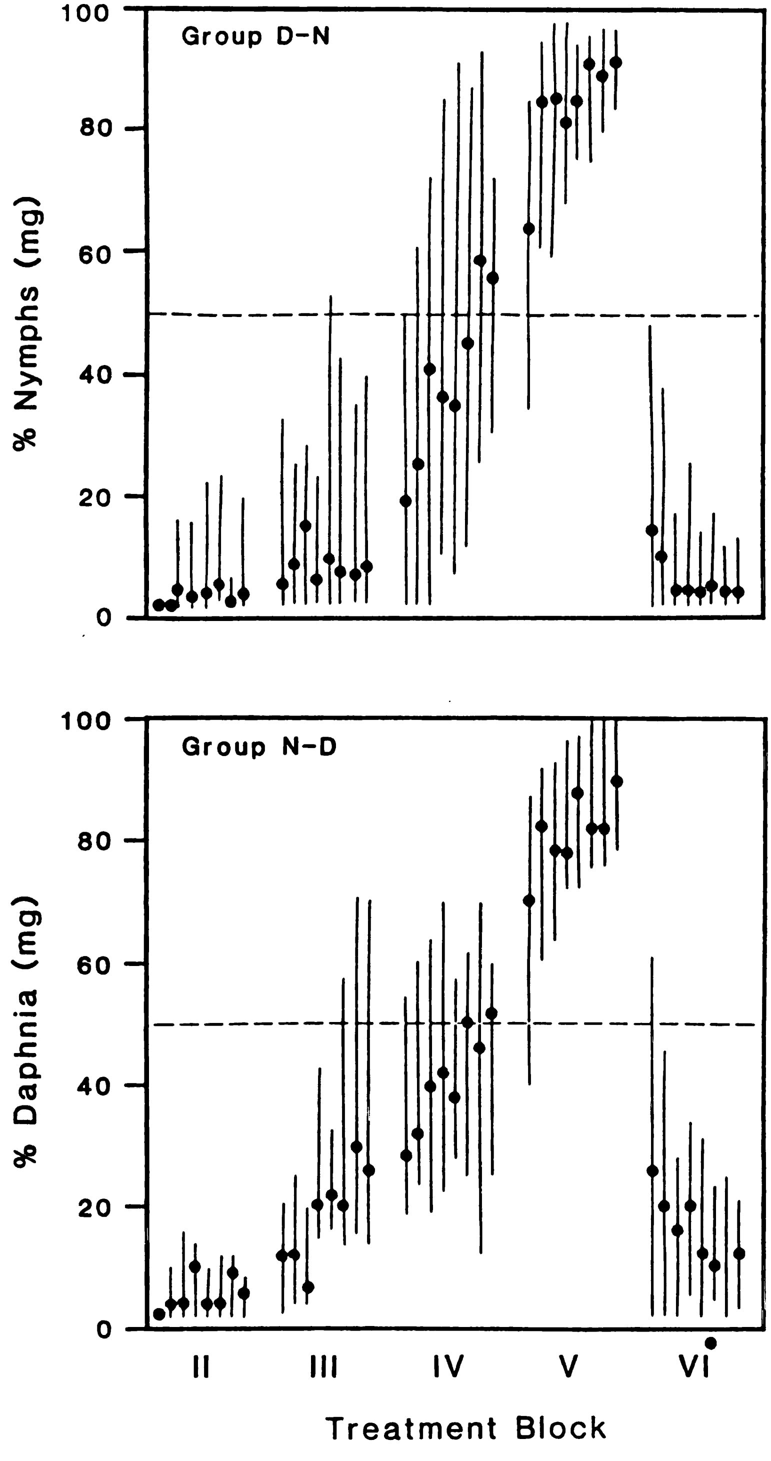

Group D-N
% Nymphs (mg)
100
80
60
40
20
0
Group N-D
% Daphnia (mg)
100
80
60
40
20
0
II
III
IV
V
VI
Treatment Block

Figure 3.1

Figure 3.2 Mean time per capture with the constant prey type on a trial as a function of the proportion of the changing prey type included in the diet. Solid circles represent capture time with nymphs for Group N-D. Open circles represent capture time with *Daphnia* for Group D-N. (N=8 for each group)

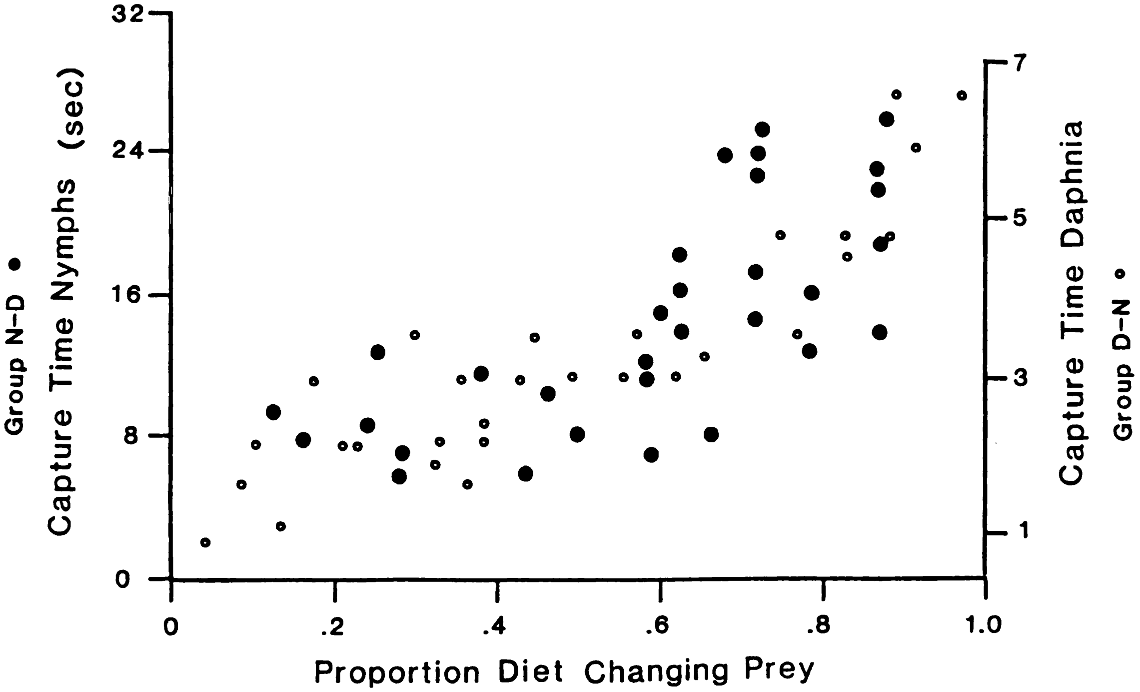

32
24
16
8
0
Group N-D ●
Capture Time Nymphs (sec)
7
5
3
1
Capture Time Daphnia
Group D-N ∘
0
.2
.4
.6
.8
1.0
Proportion Diet Changing Prey

Figure 3.2

## Allocation of Effort

Diet allocation is a function of both the time foragers spend in each habitat and the capture rate in each habitat. Therefore, diet allocation is, in part, an outcome of the decisions about where to allocate foraging effort. One measure of effort allocation is the amount of time that foragers spend searching in a habitat. By excluding the time involved with capture and handling, we are left with the time that fish actually 'choose' to spend in a particular habitat. The assumption here is that fish decide where to search, but handling location is dependent simply upon where prey are encountered (see Chapter 2 for detailed descriptions of the behaviors involved in searching and handling).

For the first trial in Block I (when only one prey type was available), mean searching time was allocated equally in each habitat, although individual scores deviated widlely from the mean (see shaded area in Figure 3.3). By the third trial the mean allocation of searching time approached its lower asymptote. The percentage of searching time allocated to habitats changed across treatment Blocks as densities of the second prey type were varied (Figure 3.3). Searching time in the second habitat showed a significant positive correlation with trials as the density of the second prey type was increased in Block II through Block V (Spearman Rank correlation coefficient ranged from 0.61 to 0.92 for individual fish, n=32 observations per fish with $p<0.01$ in all cases). Both groups were spending over 50% of their searching time in the changing habitat by the end of Block IV.

Figure 3.3 Mean allocation of search time between habitats across trials as prey density in one habitat was held constant and density of the prey type in the other habitat was changed. See Table 3.1 for prey densities used. (a) Proportion of total search time spent in the open water searching for Daphnia for fish in Group N-D (*Daphnia* density changed in each block). (b) Proportion of total search time spent in the vegetation searching for nymphs for fish in Group D-N (Nymph density changed in each block). Shaded area represents the range for the eight fish in each group on each trial.

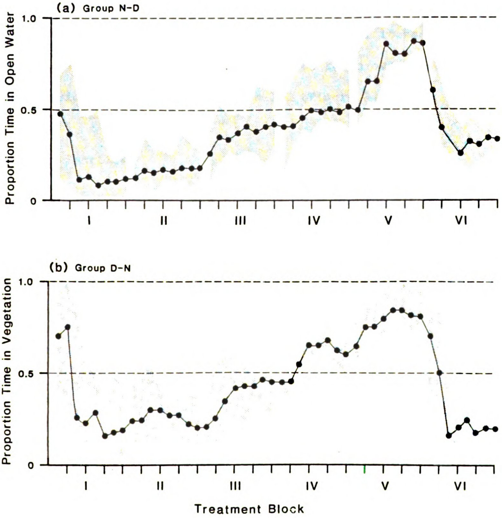

(a) Group N-D
Proportion Time in Open Water
1.0
0.5
0
I
II
III
IV
V
VI
(b) Group D-N
Proportion Time in Vegetation
1.0
0.5
0
I
II
III
IV
V
VI
Treatment Block

Figure 3.3

When the density of the second prey type was decreased back to the densities in Block III, fish immediately shifted their searching efforts back to the first habitat (Figure 3.3, Block VI). Searching effort reached a new asymptote within 3 trials after the density change. Group N-D shifted back to the same mean allocation level it had in Block III (Figure 3.3a). Group D-N, however, shifted to an even lower level than it had previously exhibited in Block III (Figure 3.3b).

## Allocation Function

One possibility that may account for the trends in search time allocation is that fish decided where to forage during a trial as a function of the actual return rates experienced on previous trials. This approach has been modeled in several forms, most involving some form of memory 'window' (e.g. Getty and Krebs 1985, Harley 1981, Cowie and Krebs 1979, Estes 1976). Search time allocation to the openwater on a trial ($P_o(T+1)$) was directly proportional to the relative return rate from the openwater experienced on the previous trial ($R_o(T)$) (Figure 3.4). This approach of allowing the forager a memory window of one past trial upon which to base its allocation represents the simplest way of incorporating memory into a decision model. The regression equation was significant (Table 3.2, model 1), suggesting strongly that search time allocation was dependent upon past foraging rates.

When the relative return in the openwater was low, fish searched primarily in the vegetation and when relative return was high they searched in the openwater. The fit to the data was not as good when relative return rates were in the middle range (i.e. roughly equal

Table 3.2. Summary of regression coefficients and significances for linear search time allocation model. Each subset adds in one additional past trial into the regression. Model: $P_o(T) = a*R_o(T-1) + b*R_o(T-2) + c*R_o(T-3) + \text{intercept}$. Probability levels, *** = 0.001, ** = 0.01, * = 0.05. Significance for variables determined for each variable given effect of other variables in the equation.

| MODEL | VARIABLE | COEFFICIENT | T-STATISTIC | | ADJUSTED R-SQUARED |
|---|---|---|---|---|---|
| 1 | $R_o(T-1)$ | 0.823 | 15.52 | *** | 0.75 |
| | Intercept | 0.097 | | | |
| 2 | $R_o(T-1)$ | 0.503 | 8.31 | *** | 0.81 |
| | $R_o(T-2)$ | 0.402 | 5.21 | *** | |
| | Intercept | 0.057 | | | |
| 3 | $R_o(T-1)$ | 0.430 | 5.92 | *** | 0.85 |
| | $R_o(T-2)$ | 0.289 | 3.94 | ** | |
| | $R_o(T-3)$ | 0.229 | 2.75 | * | |
| | Intercept | 0.035 | | | |

---

SUMMARY STATISTICS FOR LAST MODEL (3 variables in equation)

| | |
|---|---|
| Mallows' CP ................. | 4.000 |
| Squared multiple correlation | 0.847 |
| Residual mean square ........ | 0.012 |
| Standard error of estimate .. | 0.109 |
| F-statistic ................ | 142.73 |
| Numerator d.f. .............. | 3 |
| Denominator d.f. ............ | 77 |
| Significance ................ | 0.0000 |

Biserial residual correlation = 0.502
Durbin-Watson statistic = 0.98

Figure 3.4 Allocation of total search time to the open water on a trial, $P_o(T)$, as a function of the relative return rate in the open water experienced on the previous trial, $R_o(T-1)$. Triangles are for Group D-N, circles are for Group N-D (means for 8 fish in each group). $P_o$ = (search time in vegetation/total time searching during a trial in both habitats combined). $R_o$ = Return rate from the openwater/(return rate from open water + return rate from vegetation). $R_o$ of 0.5 means that realized return rates in the two habitats were identical for the trial. Statistics for the regression line are shown in Table 3.2 (MODEL 1).

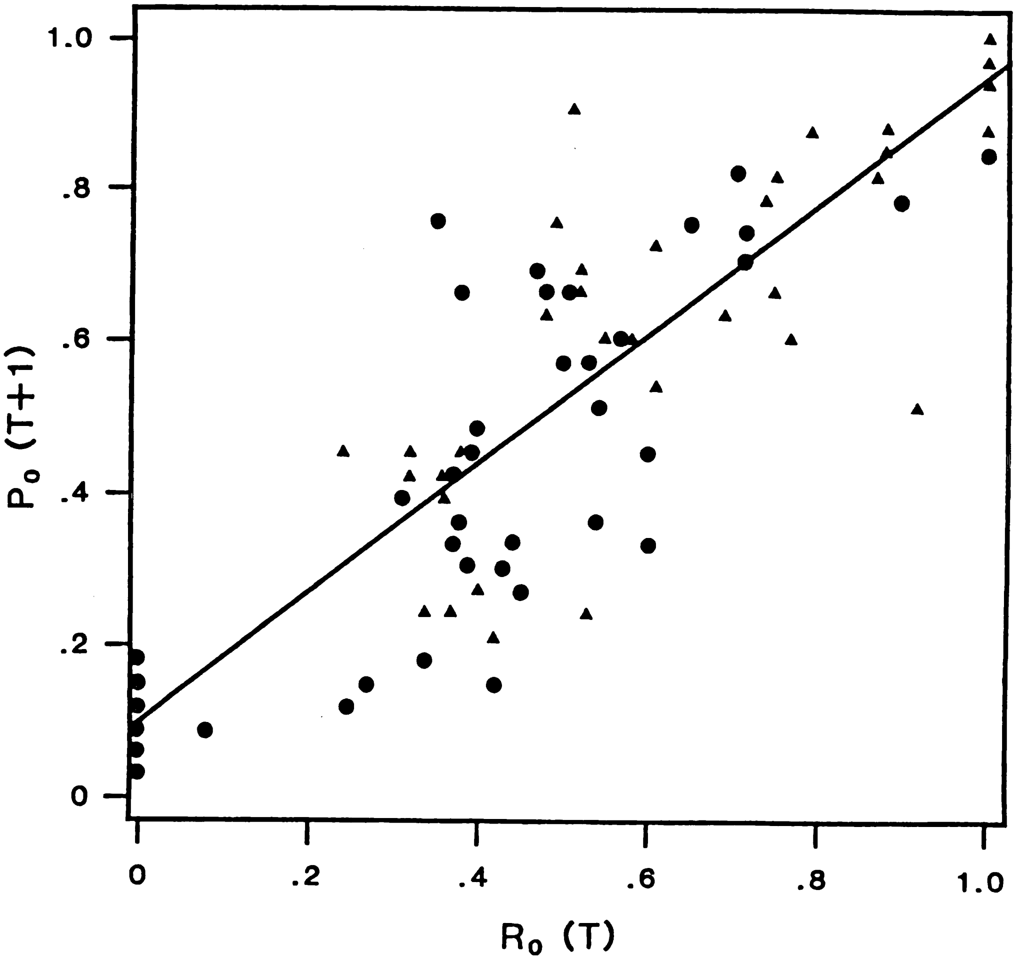


Figure 3.4

return rates in each habitat). There are at least two possible reasons for this: (1) Fish were not very good at determining differences between foraging returns when return rates in habitats were similar (Werner et al. 1981) or, (2) The 'true' allocation function was not linear and may be described more accurately by a polynomial or step function.

With regard to the first possibility, allocation variation when return rates were similar might reflect sampling errors by fish. As such, it would be expected that the variance should decrease as fish gather more information about return rates. One way to explore this possibility is to enlarge fishes' memory windows by 'allowing' fish to consider more past trials in its decision. Using stepwise multiple regression techniques (BMDP manual 1981), the inclusion of each additional past trial into the equation improves the correlation between observed and predicted search time allocation (Table 3.2). The best fit to the data is given by the model that included a memory window of 3 past trials (Figure 3.5a and Table 3.2). Inclusion of any more than 3 past trials did not increase the models fit further. Note also that it took 3 trials for mean searching allocation to reach an asymptote in Block I and Block VI (Figure 3.3).

Although the linear regression memory window model resulted in a good fit to the allocation data, there was still a positive correlation between observed allocation and the residuals from the regression (Figure 3.5b and Table 3.2). This indicates that the form of the allocation function may be nonlinear. Applying a polynomial regression with a 1 trial memory window did not result in a better fit to the data than the 3 trial linear memory window model ($R^2 = 0.83$ for 3rd. order polynomial regression compared to $R^2 = 0.85$ for multiple linear regression).

Figure 3.5 (a) Plot of observed search time allocation against predicted search time allocation for both treatment groups using linear memory window model with 3 past trials. (b) Plot of residuals from the memory window allocation model. See Table 3.2, MODEL 3 for details of the regression model and the analysis of residuals.

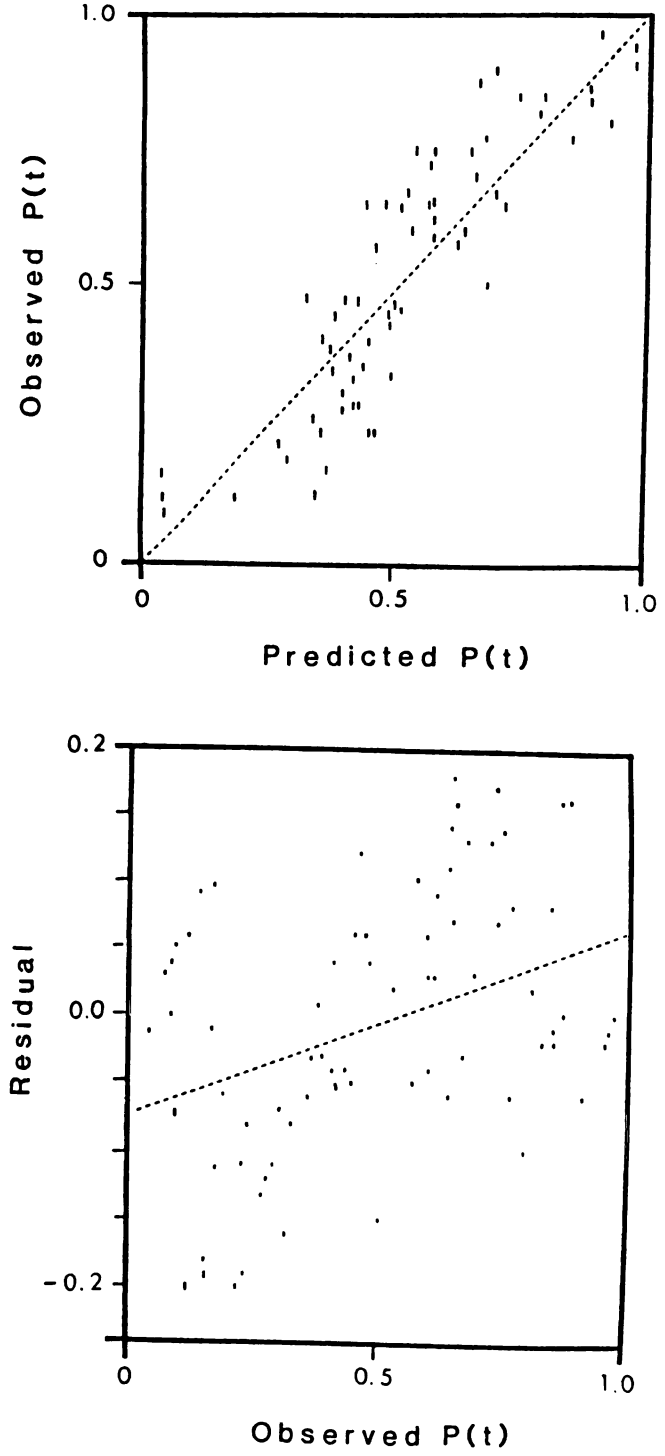

1.0
0.5
0
Observed P(t)
0
0.5
1.0
Predicted P(t)
0.2
0.0
-0.2
Residual
0
0.5
1.0
Observed P(t)

Figure 3.5

# DISCUSSION

The results of these experiments demonstrate three points. First, bluegills changed their diet allocation between habitats in the experimental tanks as prey densities within those habitats changed over time. Secondly, bluegills were not able to forage at their highest efficiency on both prey types at the same time. This is shown by the decrease in capture rate on the first prey type as the second type is included in the diet. Lastly, the allocation of foraging effort among habitats can be shown to be a function of the relative return rates that fish actually received in the habitats. The effects of interference between prey types on capture rate affect diet choice in as much as they change the relative return rate that bluegills receive in the habitats.

Although the data appear to lend strong support to a memory window model, it is very important to recognize that the increased fit of the model to the data by adding in past trials might be expected, given the way that allocation and relative return rates are both correlated with trials. When using multiple regression in analysis of allocation data across time, it is imperative to be careful to control for correlations among independent variables (see Gill 1978a). In the present case, $R_o(T)$ is correlated with $R_o(T-1)$ and, as such, the inclusion of each independent variable into the regression equation is based upon its partial correlation with search time allocation. It is very common to have these sorts of correlations in choice patterns across trials for two reasons. Firstly, choice is often a 'hill climbing' process, i.e., comparing returns from each alternative at each step along the way and changing allocation to the alternatives based upon the perceived differences in return (Staddon 1984 for review). Therefore, these smaller changes in allocation can sum up across trials until exclusive or majority choice is attained (Houston et al. 1982). Secondly, return rates often show correlations across time independent of choice and/or learning due to the seasonal growth and decline in many prey populations (e.g. Mittelbach 1981).

In and of itself, an empirical determination the shape and mathematical form of the allocation function sheds little light on the underlying behavioral mechanisms of choice, memory and learning. It would be more satisfying to have independently derived expectations for the values of the memory coefficients to test against fish behavior. This sort of 'bottom-up' approach of building predictions of complex behavior from its component parts is a characteristic of the psychological approach to the study of foraging. Alternatively, it is possible to establish an independent expectation for the shape of the allocation function from optimal foraging theory and then judge how well habitat selection adheres to the predicted shape. For example, early optimal foraging theory predicts that foragers should switch abruptly to a new habitat when its relative return rises above that of the mean for all habitats (Pyke 1984 for review). This prediction argues for a step function as the most reasonable form for the allocation function based upon first principles of optimization and natural selection. The problems of sampling the environment in order to assess return rates would be expressed as deviations from the step function, perhaps resulting in a sigmoidally shaped allocation function (Krebs et al. 1978).

Psychologists have analogous, but empirically derived prediction for the shape of the allocation function. Probability matching theory predicts that animals allocate time to alternatives in direct proportion to the rates of return from those alternatives (see Staddon (1983) for review). Therefore, the allocation function would be expected to be linear. However, if fish are capable of sensing trends in prey density changes over time (Bitterman 1971), it is likely that the allocation function could deviate from the linear form as well. If prey density is increasing, and fish sense the increase, they may anticipate future return rates and 'over allocate' to the increasing habitat. This would result in the same sort of sigmoid curve described above for the optimal-foraging approach that included sampling errors.

If the primary use of the allocation model is to make predictions about diet and habitat selection of populations then either model will be sufficient in as much as they are statistically indistinguishible in their predictive ability. As long as the predicted behavior is representative of a population's resource utilization then such models can be used to address questions at the levels of population growth and/or community dynamics. On the other hand, if the motivation is to discern the 'true' nature and mechanisms of the allocation decisions, one must perform additional experiments to investigate the mechanisms used by individuals to sample their environment (e.g. Lima 1985) and to allocate their behavior (e.g. Hodges 1985).

This chapter supports the hypothesis that return rates affect foraging allocation on a population level, but the search for the behavioral mechanisms of sampling and allocation requires more detailed scrutiny of what individuals are doing. This is the subject of the last chapter.

# CHAPTER 4

# FORAGING STRATEGIES IN CHANGING ENVIRONMENTS: EXPERIENCE, CAPTURE EFFICIENCY AND INDIVIDUAL DIFFERENCES IN ALLOCATION

## INTRODUCTION

Predators often face prey distributions that vary spatially and temporally on many scales. To monitor the changing availability of prey and to adjust foraging effort appropriately is no small task. Since the development of the first generation of patch selection models (sensu Charnov 1976), one major aim of foraging theory has been to determine the 'appropriate' behavior for foragers to adopt in stochastic environments. The general technique has been to investigate how the inclusion of stochastic variables into the deterministic models changes the behaviors that optimize procurement of the model's currency, usually the rate of energy intake (Caraco et al. 1980, Oaten 1977, Green 1980, Iwasa et al. 1981, see Pyke 1984 for review).

A distinction is often made in the literature between the so called "RISK" models and "INFORMATION" models (Krebs et. al. 1983). RISK models address the problem of foragers choosing between constant and variable prey types (e.g. Caraco et al. 1980). In these models the primary emphasis has been put upon determining whether or not foragers should be 'risk prone' (favor the variable prey type) or be 'risk averse' (favor the constant prey type (for review see Krebs et al. 1983). INFORMATION models are more concerned with how sampling behavior helps foragers to recognize types of patches in the environment; the underlying idea is that sampling improves the estimates of the mean and variance of return rates in the patch types (e.g. Houston et al. 1982, Lima 1984).

Learning about prey distributions is dependent upon sampling. Little attention, however, has been given to the possibility that sampling may change foragers' searching and handling abilities on prey. These changes may affect estimates of return rates in patches and therefore allocation among patches (Dill 1983).

With a few notable exceptions (e.g. Lima 1984, 1985, Real 1981, Caraco 1981, Caraco et al. 1980), the development of the theory of foraging in stochastic environments has far outpaced the accumulation of empirical tests of the models and/or description of how animals actually cope with prey variability. Recent empirical work has emphasised the study of "rules of thumb" that foragers may use to "solve" the complexity of their environment (see Krebs and McCleery 1984 for review, Hodges 1985, Ydenberg 1984). It is thought that foragers may use "rules of thumb" to approximate the optimal solutions of the models without performing complex mathematical computations. The study of "rules of thumb" holds great potential for the study of foraging behavior; not because "rules of thumb" approximate the predictions of foraging models, but rather because some rules might do better under some circumstances than others (Houston et al. 1982, Iwasa et al. 1981). As such, there may be no reason to expect any one rule to be used by an individual all the time, or for that matter, by all individuals in a population at any given time.

The study of how foragers deal with prey variability is important for at least two reasons. First, foraging models must be made more realistic if optimal-foraging theory is to expand as a predictive tool for ecologists (Schluter 1981). Secondly, a better understanding of how foragers modify their behaviors in response to changing prey environments speaks to our growing awareness and questioning of how natural selection operates in changing environments. This second aspect is particularly important when one considers that foraging theory has traditionally ignored the variation among individuals. Variance in foraging behavior is necessary for natural selection to take place (Arnold 1982).

This chapter presents an extended analysis of the data collected from the experiments described in Chapter 3. Bluegill sunfish faced foraging environments with 2 habitats; one constant and the other varying over time. Habitats contained different types of prey, each requiring different searching and handling techniques. My purpose is twofold: (1) To describe how learning the components of capture efficiency (i.e. searching and handling ability) is affected by sampling a second prey type, and (2) To explore whether variation in allocation patterns among individuals can be explained by differences in searching strategies and/or by variation in decision rules used to switch among habitats. The discussion addresses the problems inherent in studing the behavior of individuals and constructing a framework for properly judging the adaptedness of foraging behavior in changing environments.

# METHODS

Details concerning fish, prey, tanks and experimental procedures for this study are described Chapter 3. Eight fish were placed into each of two treatment groups. Daphnia and nymphs were available simultaneously in their respective openwater and vegetation habitats. Each treatment consisted of six blocks of eight trials (2 trials per day per fish) with one prey type held at a constant density through all trials. The density of the second prey type was increased across the blocks of trials (Table 4.1). Each fish faced two 5min. feeding trials per day. During trials, hover search, move search, location, pursuit and handling were recorded in timed sequence on a MORE (tm) electronic event recorder (See Chapter 2 for detailed descriptions of searching and handling behaviors). Analyses were performed using two methods for truncating the data within trials. The first truncation method involved stopping the analysis after a given amount of prey depletion within trials. The second method truncated the data after a given amount of feeding time in each trial. Unless stated otherwise, mean searching and handling times presented here were calculated using data from the first 25% depletion level of each prey type within trials and allocation data were calculated using the first 1 minute of foraging time in trials. Unless otherwise noted, no qualitative differences in the patterns of analyses were attributable to the truncation method used.

Table 4.1. Prey densities (#/l) used in two prey experiments (*Daphnia* in openwater and nymphs in vegetation). Blocks consisted of 8 consecutive trials with the prey densities shown. Density of the first prey type was constant throughout all trials while that of the second was manipulated. Two trials per fish per day, 8 fish per group.

| BLOCK | I | II | III | IV | V | VI |
|---|---|---|---|---|---|---|
| TRIAL | 1-8 | 9-16 | 17-24 | 25-32 | 33-40 | 40-48 |
| GROUP N-D | | | | | | |
| NYMPHS | 0.250 | 0.250 | 0.250 | 0.250 | 0.250 | 0.250 |
| DAPHNIA | 0.000 | 0.125 | 0.250 | 0.500 | 1.000 | 0.250 |
| GROUP D-N | | | | | | |
| DAPHNIA | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 | 0.500 |
| NYMPHS | 0.000 | 0.063 | 0.125 | 0.250 | 0.375 | 0.125 |

## RESULTS

### I. Effects of Diet Allocation on Searching and Handling

The mean diet allocation to the variable habitat increased as the prey density in the second habitat was increased (see Chapter 3, Figure 3.1). However, this gradual increase (averaged for all fish) did not accurately represent the behavior of individual fish. Individuals exhibited abrupt changes in allocation and switched at different prey densities (examples in Figure 4.1). Because searching and handling ability change as a function of experience with prey (Chapter 2 and Chapter 3), it is necessary to control for the extent to which individual fish had switched to the new prey type.

Three distinct phases of switching were recognizable within individual fish. In the first or 'preswitch' phase, fish focused their foraging effort on the constant prey type. In the second or 'switch' phase, fish increased the percentage of the changing prey type in the diet across trials. The switch phase was considered to be the block wherein a fish first crossed over the 50 percent diet allocation to the changing prey type. Generally, the switch phase was detected easily in the data and could be assigned to a single treatment block. For example, in Figure 4.1a fish 3N switched from nymphs to *Daphnia* during Block III, while fish 4N switched in Block V. Similar patterns were observed for fish switching from *Daphnia* to nymphs (Figure 4.1b). Sometimes fish appeared to begin to switch in one block and completed the shift in the next (Figure 4.1b, fish 10D Blocks IV and V). In the final or 'postswitch' phase, fish focused primarily on the variable prey type.

Figure 4.1 Percentage (by mg) of the changing prey type in the diet across trials. (a) Percentage of _Daphnia_ in diet for 2 fish in Group N-D (increasing _Daphnia_ density and constant Nymph density across Blocks, see Table 4.1 for prey densities). Data for each trial was truncated after 1min. elapsed time in trials. (b) Percentage of Nymphs (by mg) in the diet for 2 fish in Group D-N (constant Nymph density and increasing Daphnia density). Data for each trial was trunctated after 1min. feeding time in trials.

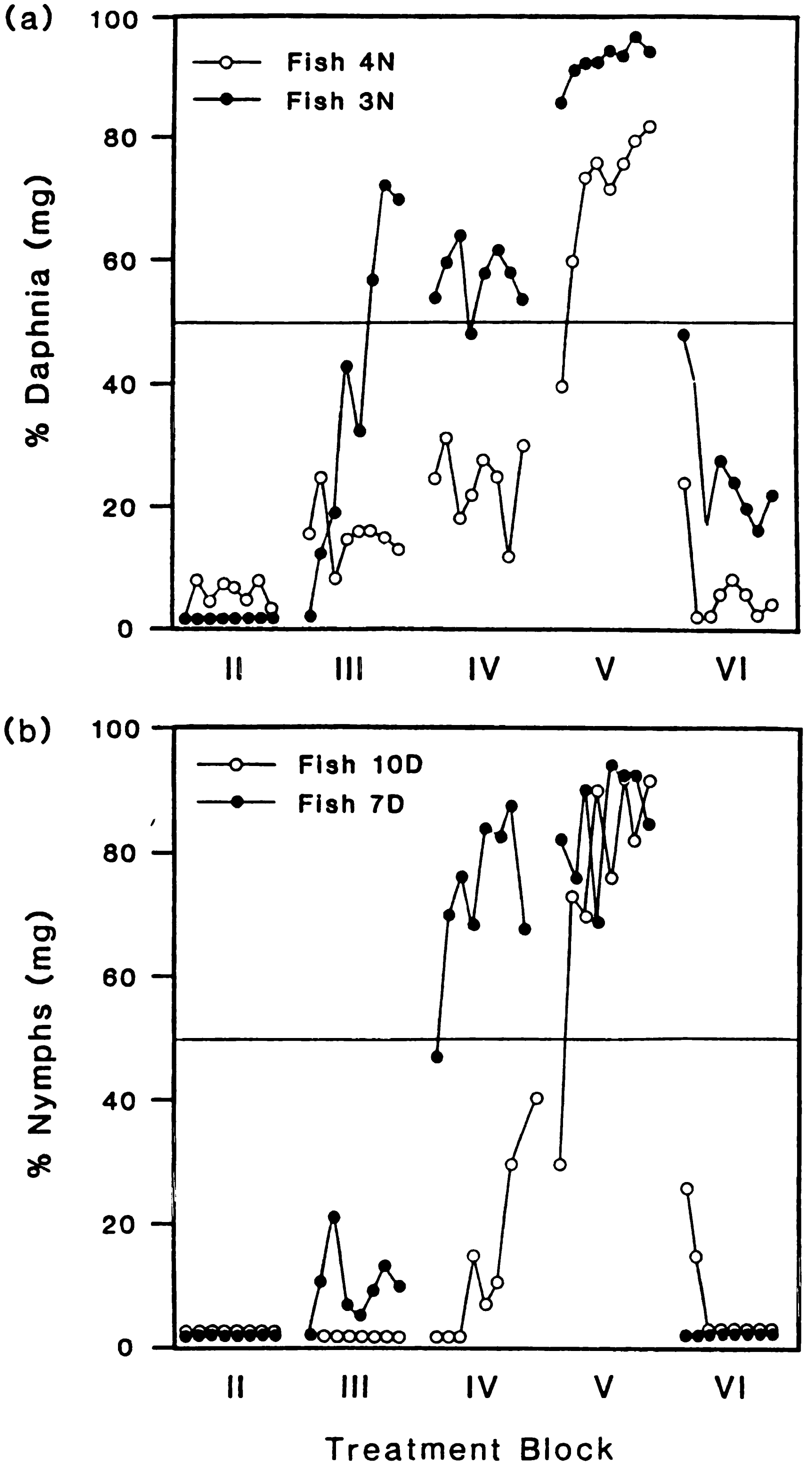

(a)
Fish 4N
Fish 3N
% Daphnia (mg)
0
20
40
60
80
100
II
III
IV
V
VI
(b)
Fish 10D
Fish 7D
% Nymphs (mg)
0
20
40
60
80
100
II
III
IV
V
VI
Treatment Block

Figure 4.1

## Allocation, Handling and Searching Ability

Decreases in handling and searching times that occured across trials within set prey densities (i.e. within a treatment block) reflect learning in capture ability. Likewise, increases in handling or searching time reflect a loss of ability, perhaps attributable to interference due to the inclusion of the second prey type. We can separate these two effects (learning and interference) and look at them for both the constant and changing prey type.

## Learning in Handling

Handling times on the constant prey type decreased during treatment Block I (one prey type available) in a manner similar to the single prey experiments described in Chapter 3. Handling time on the changing prey type also improved as fish accumulated experience feeding on the prey type (Table 4.2, example in Figure 4.2). Fish that switched from nymphs to *Daphnia* (Group N-D) showed significant decreases in handling times on *Daphnia* while they were still feeding primarily on nymphs (Preswitch phase in Table 4.2, example in Figure 4.2a). Fish switching to nymphs (Group D-N) did not show improvement in their ability to handle nymphs until nymphs became a major part of the diet during the switch phase (Table 4.2, example in Figure 4.2b). Nymphs are more difficult to capture than *Daphnia* and are more likely to escape from inexperienced fish. For the group switching to nymphs (Group D-N), the decreases in handling times on nymphs were attributable to reductions in the number of nymphs that escaped the first attack (32 percent escaping preswitch

Table 4.2. Percent changes in HANDLING TIMES on prey occuring between the first and eighth trials of each phase of switching. (Data are means for 8 fish in each group. * = change significantly different from 0 at $p < 0.05$). First and second prey types are constant and changing types respectively.

| | | PHASE OF SWITCHING | | |
|---|---|---|---|---|
| | | Preswitch | Switch | Postswitch |
| Group N-D | Nymphs | -0.18 | +0.27 * | +0.29 * |
| | Daphnia | -0.63 * | +0.05 | -0.29 * |
| Group D-N | Daphnia | -0.05 | +0.30 * | +0.17 * |
| | Nymphs | +0.06 | -0.18 * | -0.32 * |

Figure 4.2 Handling time (mean ± 95% CI) on manipulated prey type across trials during block when greatest amount of learning occured. (a) Handling time on *Daphnia*, fish 1N, Block II. (b) Handling time on nymphs, fish 10D, Block IV. Data truncated at 25% depletion level of manipulated prey type.

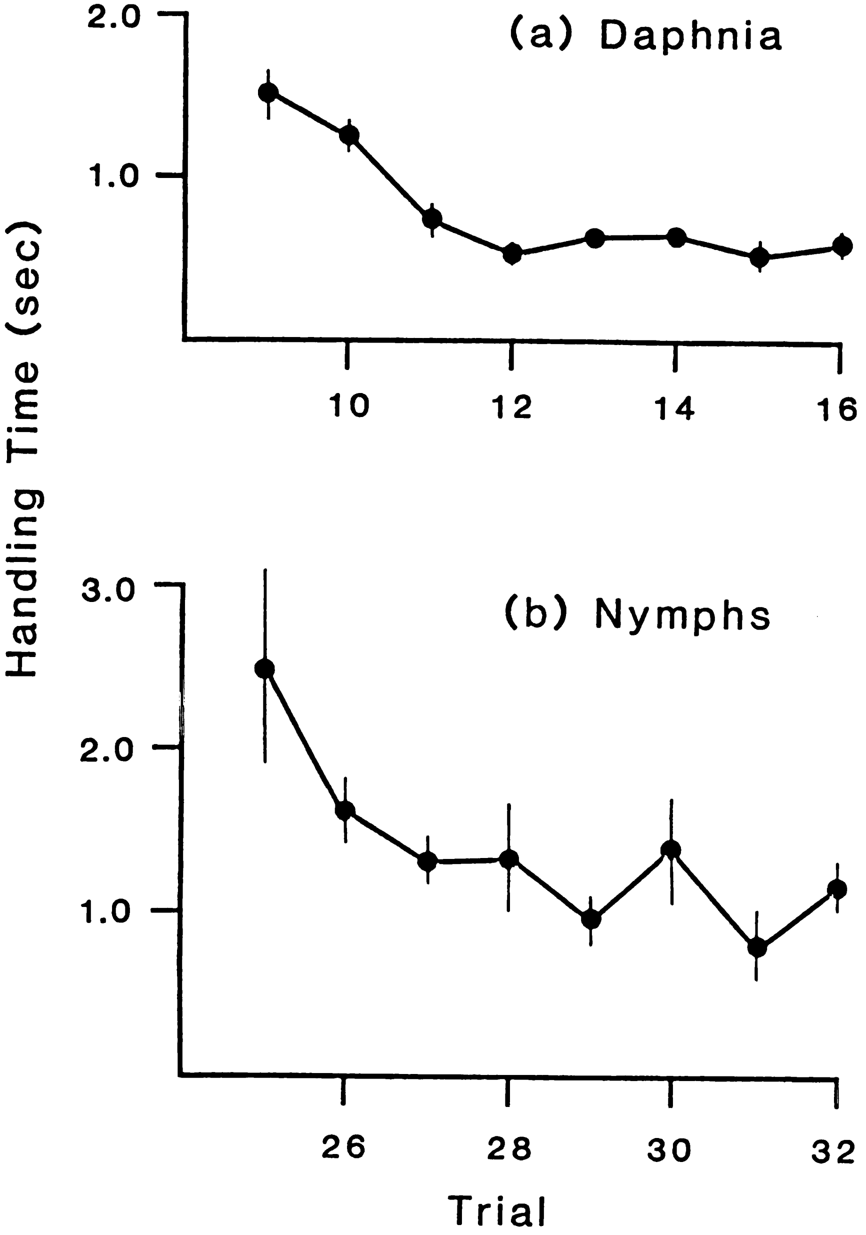

(a) Daphnia
2.0
1.0
10
12
14
16
Handling Time (sec)
(b) Nymphs
3.0
2.0
1.0
26
28
30
32
Trial

Figure 4.2

Figure 4.3 Handling time on constant prey type during switch phase, plotted against diet allocation to manipulated prey type. Handling time truncated at 25% prey depletion level. Percent diet truncated after 2 minutes of foraging time in trial. (a) Handling time on nymphs against % *Daphnia*. Fish 3N. $Y = 1.89 + 0.0195X$, $r^2 = 0.502$. (b) Handling time on *Daphnia* against % Nymphs for fish 5D. $Y = 0.40 + 0.006X$.

r2 = 0.956.

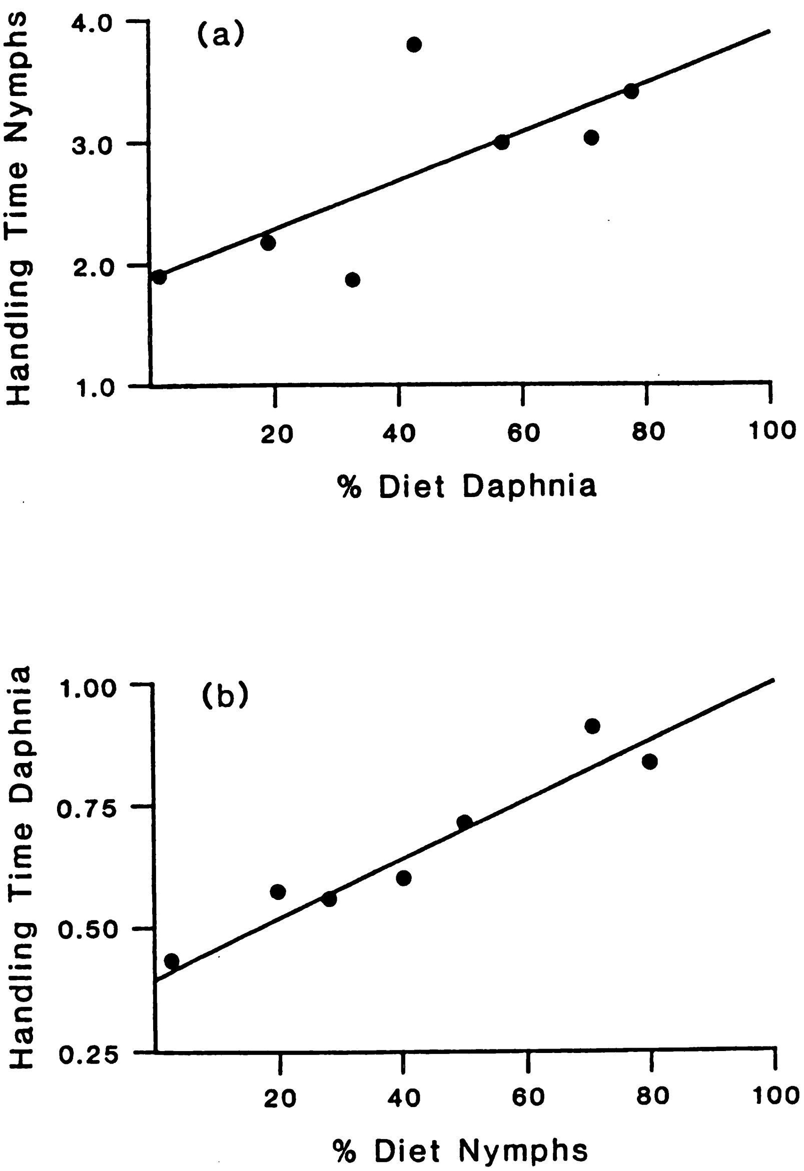

(a)
Handling Time Nymphs
4.0
3.0
2.0
1.0
20
40
60
80
100
% Diet Daphnia
(b)
Handling Time Daphnia
1.00
0.75
0.50
0.25
20
40
60
80
100
% Diet Nymphs

Figure 4.3

down to 7 percent escaping postswitch). Improved handling ability on Daphnia was due largely to decreases in the time required resume searching after successful captures (presumably swallowing time).

## Interference in Handling

Handling times for the constant prey type increased during the switch phase and postswitch phase as fish included greater percentages of the second prey type in their diet (Table 4.2, examples in Figure 4.3). Increased handling time on nymphs was due in part to an increase in the number of missed attacks and/or prey escapes (5 percent of all attacks preswitch to 24 percent postswitch). It is not as easy to identify one specific component of handling time most responsible for the increased handling time on Daphnia. The number of missed attacks on Daphnia was never significantly different from zero in any phase. Eighty-five percent of the increase in handling time for Daphnia appears to be due to increases in the time required to manipulate and swallow Daphnia once within the mouth. The internal manipulations required to swallow Daphnia require special modulations of the muscles controling the pharyngial mill. Lauder (personal communication) showed that bluegills contract these muscles in different patterns depending upon the prey type being eaten (see also Liem 1979). It is not known to what extent these muscle modulations are subject to learning and/or interference. In any case, general handling abilities for Daphnia and nymphs were mutually exclusive and fish did not maintain maximum handling proficiency on both prey types simultaneously.

## Learning in Searching

All bluegills in both treatment groups improved their searching abilities on the constant prey type during Block I. The patterns of improvement were similar to those described in single prey experiments (See Figures 2.6 and 2.7 in Chapter 2).

Although fish included the changing prey type in their diets as early as Block II, significant improvement in searching ability on the changing prey did not occur until the switch phase (Table 4.3, examples in Figure 4.4). Search time on *Daphnia* decreased 29 percent during the switch phase for the group that switched to *Daphnia* (Table 4.3, Group D-N). Search time on nymphs decreased 53 percent during the switch phase for the group that switched to nymphs (Group D-N, Table 4.3).

## Interference in Searching

Switching to the changing prey type affected searching ability on the constant type (Table 4.3). Across the switch phase, the average effect (data pooled for all fish within each treatment group) was nearly a doubling of the net capture rate (mg/sec) on the prey fish switched to and a corresponding decrease of nearly 50 percent in capture rates on the prey type fish switched from. Note that prey densities were the same across trials within each phase, therefore the changes in searching are independent of changes in prey density. The pattern and magnitude of this effect varied among individual fish. Fish that switched from nymphs to *Daphnia* experienced an increase in search time for nymphs as they included a greater percentage of *Daphnia* in their diet (Table 4.3,

Table 4.3. Percent changes in SEARCHING TIMES on prey occuring between the first and eighth trials of each phase of switching. (Data are means for 8 fish in each group. * = change significantly different from 0 at $p < 0.05$). First and second prey types are constant and changing repectively.

| | | PHASE OF SWITCHING | | |
|---|---|---|---|---|
| | | Preswitch | Switch | Postswitch |
| Group N-D | Nymphs | -0.06 | +0.33 * | -0.21 * |
| | Daphnia | -0.40 * | -0.29 * | -0.15 * |
| Group D-N | Daphnia | -0.11 | +0.41 * | +0.42 * |
| | Nymphs | +0.07 | -0.53 * | -0.34 * |

Figure 4.4 Search time (mean ± 95% CI) on manipulated prey type across trials during block when greatest amount of learning occured. (a) Search time on *Daphnia*, fish 1N, Block III. (b) Search time on nymphs, fish 7D, Block IV. Data truncated at 25% depletion level of manipulated prey type.

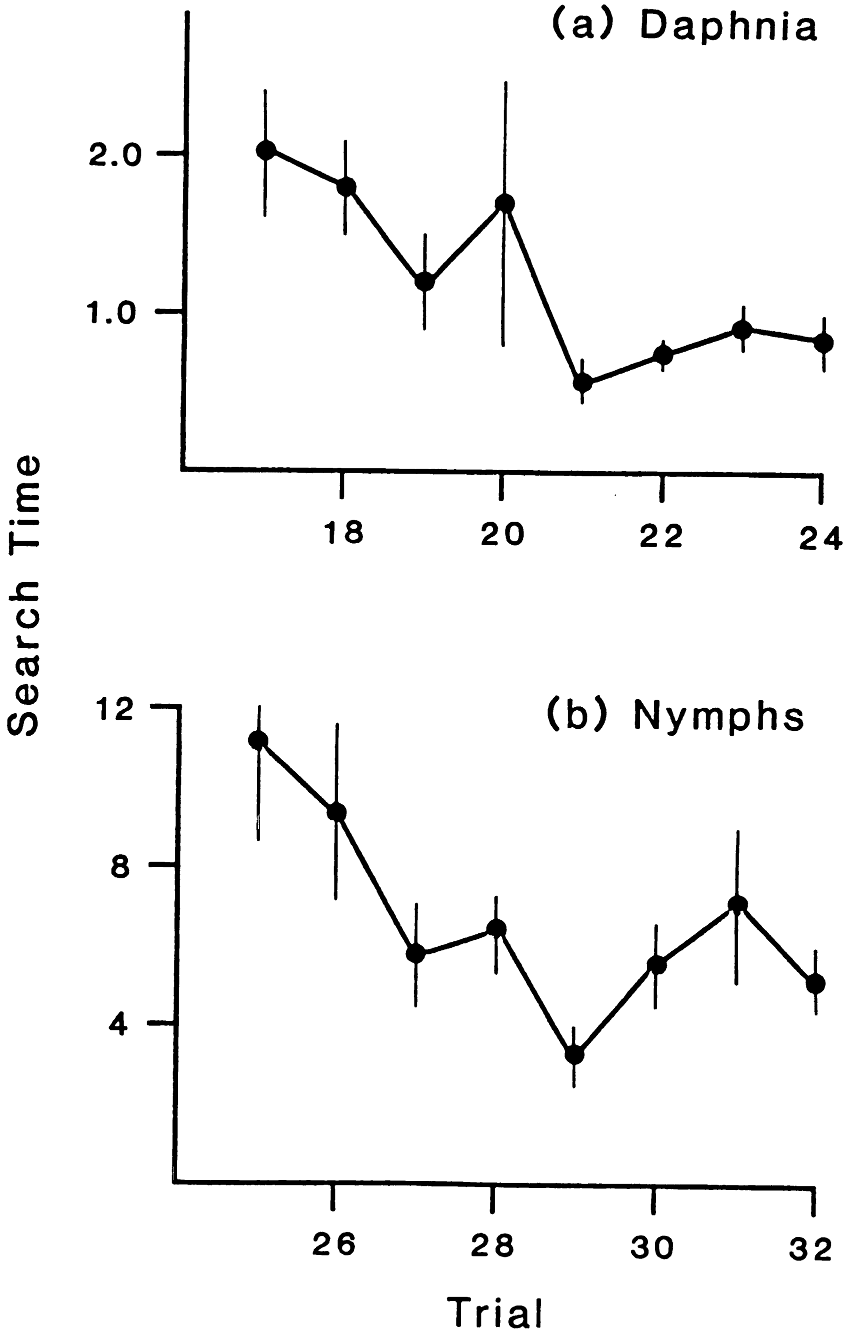

(a) Daphnia
2.0
1.0
18
20
22
24
Search Time
(b) Nymphs
12
8
4
26
28
30
32
Trial

Figure 4.4

Figure 4.5 Search time on constant prey type during switch phase, against diet allocation to manipulated prey type. Search time truncated at 25% prey depletion level. % Diet truncated after 1 minute of foraging time in trial. (a) Search time on nymphs against % *Daphnia*. Solid line, fish 3N (early switcher) $Y = 5.02 + 0.310X$, $r^2 = 0.82$. Dashed line, fish 4N (late switcher) $Y = -2.56 + 0.18X$, $r^2 = 0.53$. (b) Search time on *Daphnia* against % Nymphs. Solid line, fish 14D (early switcher), $Y = 0.86 + 0.016X$. $r^2 = 0.58$. Dashed line, fish 22D, $Y = 1.02 + 0.00015X$, $r^2 = 0.003$ (NS).

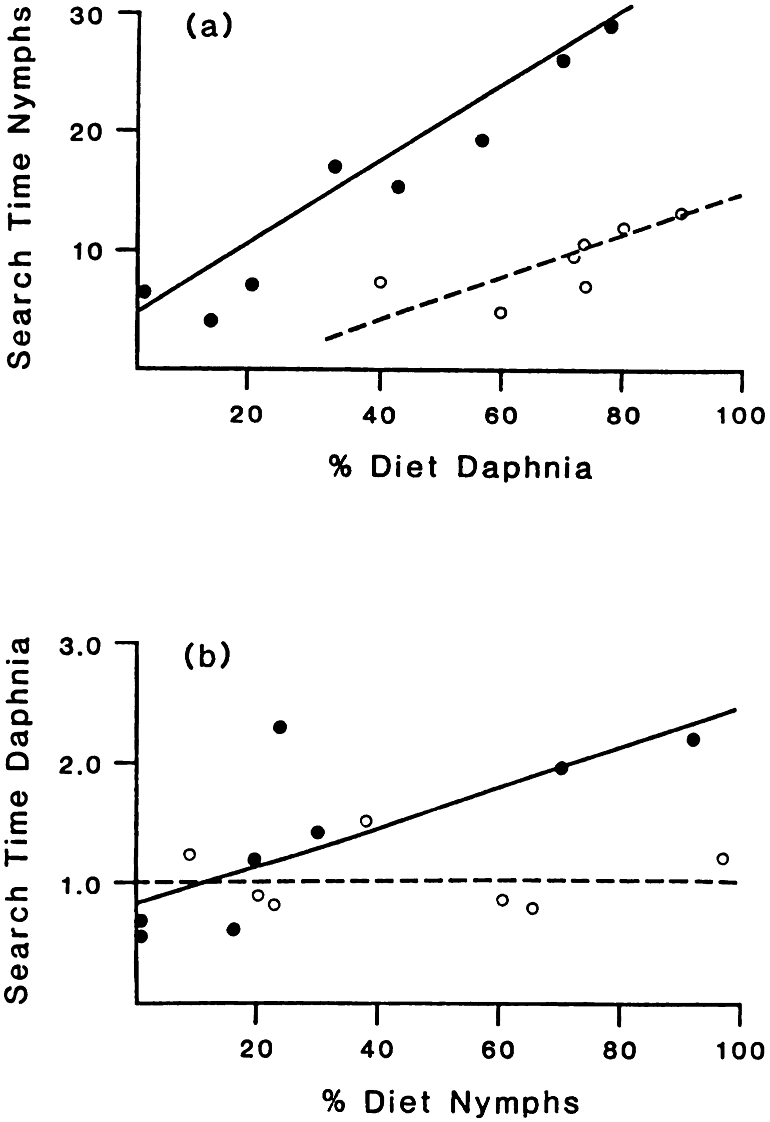

(a)
Search Time Nymphs
30
20
10
20
40
60
80
100
% Diet Daphnia
(b)
Search Time Daphnia
3.0
2.0
1.0
20
40
60
80
100
% Diet Nymphs

Figure 4.5

examples in Figure 4.5). However, some fish showed less of an increase than others (Figure 4.5a). A similar pattern was observed for fish that switched from Daphnia to nymphs (Table 4.3, Group D-N). Search times on Daphnia increased for some fish as they switched to nymphs but other fish showed little or no loss of searching ability on Daphnia (Figure 4.5b).

Inclusion of the second prey type interfered with searching ability on the first prey type. This interference is most likely the result of conflicting searching techniques and/or search images specific to each prey type. A result opposite to the general trend was the decrease in search time on nymphs during the postswitch phase for the fish that had switched to Daphnia (Group N-D in Table 4.3). In order to understand interference (or the lack of it) it is necessary to scrutinize the individual components of searching (see Chapter 2) and the differences among individual fish.

## II. Individual Differences in Searching and Handling Techniques

Individual fish were categorized by the treatment block of their switch phase and entered into a discriminant cluster analysis (PSTAT Version 80, 1984). The analysis confirmed the categorization of most fish into one of two 'types' (98.5 percent for Group N-D and 84.4 percent for Group D-N) and was highly significant (Mahalanobis D2 = 266.88 p = 0.0000 for Group N-D (constant nymphs), D2 = 56.71 p = 0.0000 for Group D-N (constant Daphnia)). Thirty one percent (N=5) of the fish switched early (at lower densities of the changing prey) while 63 percent (N=10) switched later (at higher densities of the changing prey). The remaining 6 percent (N=1) were not classifiable as either type. It is not my intention to argue that there are two distinct switching types among bluegills. If more fish had been used in the experiments the discriminant analysis may well have shown a more continuous distribution of types. However, the fact that two statistically distinguishable types of fish existed within each treatment group raised the possibility that other differences existed between the switching types in addition to the timing of the habitat switch.

By using the results of the discriminant analysis to categorize individual fish as either 'early' or 'late' switching types, it was possible to test directly for differences between switching types in analyses. No differences in minimum handling times between switching types were observed ($p = 0.37$ for nymphs, $p = 0.14$ for Daphnia, two-sided student's T-test). Significant differences in search time and components of search time were however observed between switching types (Table 4.4, split plot ANOVA with trials as repeated measures (Gill 1978b)). Switching types differed in search times for both prey types. Switching types also hovered different durations while searching for prey and moved at different rates between hovers while searching for the constant prey type but not for the changing prey type.

Although ANOVA analyses establish the existence of significant effects, they give little information about the directionality, time course or dynamic nature of the differences between switching types. The results from Chapter 2 suggested that hover duration and time spent moving between hovers were important in determining searching ability. Since measures of the distance moved between hovers are not available,

Table 4.4. Summary of P values for differences in searching parameters between switching TYPES (Group N-D = constant nymph density, Group D-N = constant *Daphnia* density). Model: Y = Block + Type + Fish/Type + Trial/Block + (interaction terms) + error. Data for analysis were truncated at the 25% depletion level of the prey type.

| DEPENDENT VARIABLE | Group N-D | Group D-N |
|---|---|---|
| Search Time Nymphs | 0.0001 | 0.0052 |
| Time per Hover | 0.0001 | 0.0068 |
| Time per Move | 0.0030 | 0.2426 |
| Search Time Daphnia | 0.0066 | 0.0001 |
| Time per Hover | 0.0036 | 0.0039 |
| Time per Move | 0.1379 | 0.0026 |

it is difficult to interpret changes in move time. For example, a decrease in the amount of time to move between hovers could have been the result of either increased swimming speed while moving the same distance or of moving a shorter distance at the same speed. It is my intention to explore the changes in move time with experience in future experiments. For the purposes of this chapter, I focus only on the role of hover duration.

## Hover Time on the Constant Prey

Hover times on the constant prey changed between the preswitch and switch phases. Hover times while searching for nymphs decreased for both early and late switchers in the group that switched from nymphs to Daphnia (Group N-D, Figure 4.6). The time per hover while searching for Daphnia increased for both switching types among fish that switched from Daphnia to nymphs (Group D-N, Figure 4.7). Although both switching types changed hover times, the late switchers did not change their hover times on the constant prey as much as the early switchers. During the switch phase the late switchers did not suffer as great an increase in search time as the early switchers.

Hover times on nymphs decreased further as fish in group N-D continued to switch onto Daphnia (switch to postswitch in Figure 4.6). Hover times on nymphs for the early switchers decreased more than for the late switchers in the postswitch phase Figure 4.6).

Hover times on Daphnia did not continue to increase as fish switched further onto nymphs (Figure 4.7). After switching to nymphs, hover times on Daphnia decreased compared to the switch phase but not down to the

Figure 4.6 Mean search time on nymphs for early switchers (solid circles) and late switchers (open circles) in group N-D, against mean hover time on nymphs (means ± 95% CI) for the 3 switch phases. B = Preswitch phase. S = Switch phase. A = Postswitch phase. Data pooled for fish within each switch type (N=24 for early, N=40 for Late).

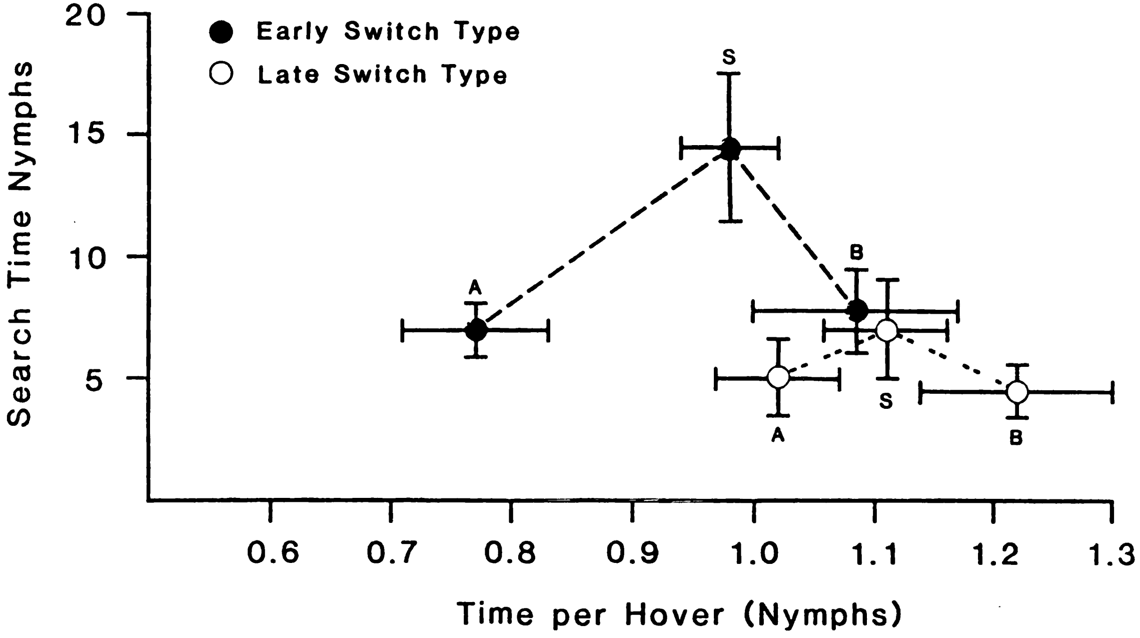

20
15
10
5
Search Time Nymphs
● Early Switch Type
○ Late Switch Type
S
A
B
A
S
B
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
Time per Hover (Nymphs)

Figure 4.6

Figure 4.7 Mean search time on Daphnia for early switchers (solid circles) and late switchers (open circles) in group D-N, against mean hover time on Daphnia (means ± 95% CI) for the 3 switch phases. B = Preswitch phase. S = Switch phase. A = Postswitch phase. Data pooled for fish within each switch type (N=32 for early, N = 24 for late).

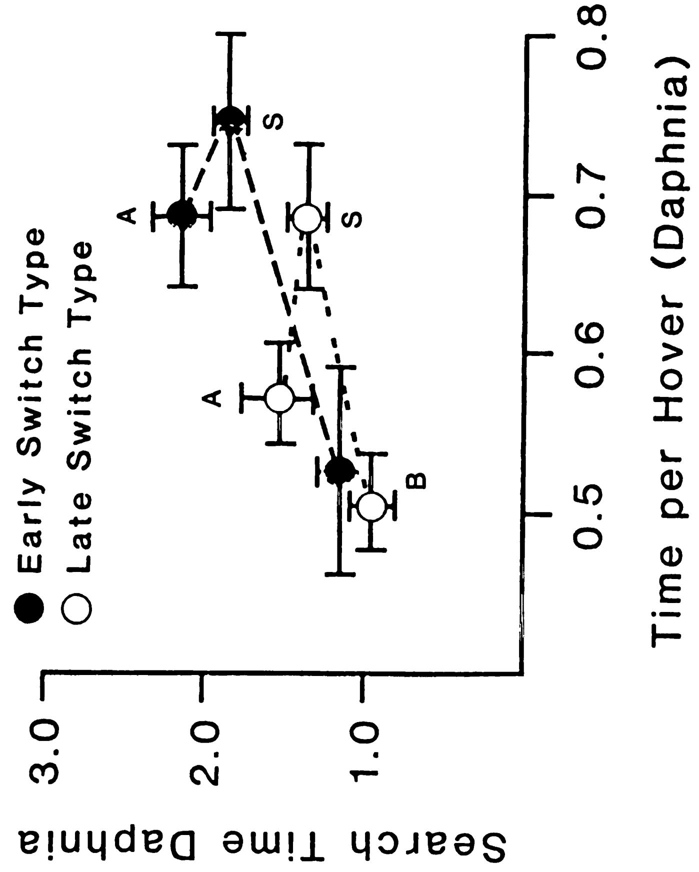

Search Time Daphnia
3.0
2.0
1.0
Time per Hover (Daphnia)
0.5
0.6
0.7
0.8
● Early Switch Type
○ Late Switch Type
A
S
A
S
B

Figure 4.7

level of the preswitch phase (Figure 4.7), and early switchers continued to hover longer while searching for Daphnia than the late switchers.

In the case of group N-D, search times for nymphs decreased after fish switched to Daphnia, even though hover times continued to decrease (Figure 4.6, Group N-D in Table 4.3). This was most likely due to the interaction between the physical disturbances caused by bluegills while foraging in the vegetation and the tendency for nymphs to stop moving when they sensed disturbances nearby. Although no data were taken on nymph movements in these experiments, my impressions and data from other experiments with mayfly nymphs (Charnov et al. 1976) suggest that nymphs decreased their activity within seconds after a nearby disturbance (such as a bluegill swimming past or attacking another nymph). As such, when fish first entered the vegetation there was a good chance that some of the nymphs were moving around on the vegetation and were thus more susceptible to being detected by the fish. After initial disturbances of either a capture or a number of searching movements by the fish, the number of moving nymphs decreased markedly. Nymphs would usually resume movements within 20 to 40 seconds after fish left the vegetation. The early switchers visited the vegetation less often and for shorter durations during the postswitch phase (see Table 4.6 and Section III of the results). It is likely that during the short visits to the vegetation fish detected moving prey soon after entering the vegetation then left without searching for the now motionless nymphs.

Search times for Daphnia did not change between the switch and postswitch phase for either switching type in Group D-N (Figure 4.7). Hover times decreased for the late switchers only. Compared to the late switchers, th early switchers showed greater increases in hover time and search time on Daphnia in the postswitch phase. The most likely reason for the increased search time was the breakdown of the systematic search paths used by bluegills when feeding on Daphnia (see Chapter 3, Figure 3.8). During the switch and postswitch phases, bluegills often returned from feeding on nymphs in the vegetation and began searching for Daphnia in an area of the openwater that had already been searched and depleted of prey. This increased the net search times for Daphnia.

### Hover Times on the Changing Prey

Because they switched at different times, early and late switchers had different amounts of experience on the changing prey in any given trial during most of the experiment. However, by Block V all fish had switched and attained their asymptotic searching efficiency on the changing prey. Hover times in Block V are summarized in Table 4.5. Early switchers used the same hover time on both prey types whereas the late switchers used a long hover time on nymphs and short hover time on Daphnia. This was the case for each treatment group. The hover time used by the early switchers for both prey types was intermediate to those used by the late switchers.

## III. Relationships Between Searching and Allocation

The major point to be made from the above analysis is that searching and handling abilities changed as a function of diet allocation to (i.e. experience with) prey and the inclusion of another prey type. The notion that foragers allocate their foraging effort among habitats in

Table 4.5. Comparison of HOVER TIMES (sec ± 95% CI) between switching types in Block V after switching to the second prey type. Group N-D switched from nymphs to *Daphnia*. Group D-N switched from *Daphnia* to nymphs.

| | SWITCH TYPE | NYMPHS | DAPHNIA |
|---|---|---|---|
| Group N-D | early | 0.79 (0.07) | 0.71 (0.05) |
| | late | 1.01 (0.07) | 0.52 (0.04) |
| Group D-N | early | 0.70 (0.05) | 0.68 (0.04) |
| | late | 0.92 (0.03) | 0.57 (0.03) |

some "energetically logical" relationship to the foraging return rates of the habitats is a fundamental tenet of optimal-foraging theory. It is possible, given the above data on searching and handling times, to ask whether the bluegills moved between the habitats with respect to changes in energetic return rates. Secondly, it is important to explore how quickly behavioral responses occured in order to get a feeling for the time horizon over which bluegills were able to adjust to changing prey conditions.

Because bluegills used both habitats to some extent on most trials, it was possible to study two distinct levels of allocation decisions: (1) "What determined the first habitat in which fish began searching on a trial?" and, (2) "What determined when fish moved between habitats during trials?". For simplicity, I only refer to fish that faced constant nymphs and increasing Daphnia (Group N-D). (Data for the other treatment were similar and will be presented in another paper within the context of differences between switching onto a cryptic vs. non-cryptic prey type.)

## Initial Habitat Choice

One possible hypothesis concerning initial habitat choice in trials is that fish began in the habitat in which they had experienced the higher average return rate on the previous trial. This is similar to theories of probability matching in psychology (Bitterman and Mackintosh 1969). The general idea is that fish compare the return rates experienced within habitats on trials and then, through learning about the differences between habitats, come to choose the more profitable alternative (Bitterman 1975 for review).

Figure 4.8 Probability of starting in the open water on a trial as a function of the relative return rate experienced in the open water on the last trial. Points along the X axis represent midpoint of interval. Y axis represents probability for the interval. Data are pooled for fish within switch types. Probability calculated as Proportion of trials intitiated in the open water following a trial with a given relative return rate.

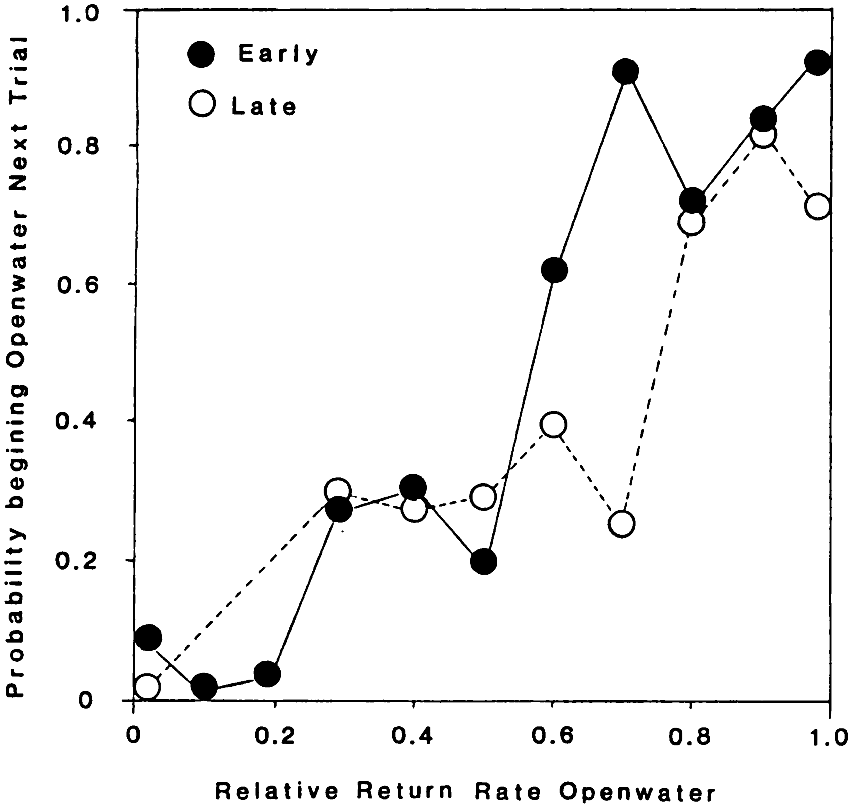

1.0
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1.0
● Early
○ Late
Probability begining Openwater Next Trial
Relative Return Rate Openwater

Figure 4.8

The probability that fish began searching in the open water on any given trial was proportional to the relative return rate in the open water on the previous trial (Figure 4.8, data pooled for all fish in a switching type for each 0.1 interval in relative return rate). Because the data were pooled for the fish within each switching type, it was not possible to test for the significance of pairwise comparisons between types at a given relative return rate. However, other comparisons were possible. Recall that Daphnia were increasing across trials, so across trials in the experiments fish generally moved from left to right in Figure 4.8. The fact that early switchers switched earlier to the openwater is mirrored by the more rapid increase in their probability curve in Figure 4.8 (solid circles). A rapid jump toward favoring the openwater over the vegetation occurred just above the 0.5 relative return level. Though the late switchers showed a qualitatively similar pattern, they did not show such a jump toward the openwater until their relative return in the openwater passed 0.7 (Figure 4.8, open circles).

As mentioned earlier, fish of both switch types moved back and forth between habitats within trials and, as such, had ample opportunity to "discover" the increasing prey type. Therefore, it does not appear likely that differences in initial habitat choice could have accounted for the larger differences in diet allocation that distinguished the early from late switching type. The allocation to a habitat within trials is more likely a function of the initial habitat choice combined with the persistence of foragers in remaining within a habitat during a trial.

## Searching Persistence Within Habitats

Trials consisted of sequences of visits to habitats and, given the way data were collected, individual searching and handling acts could be ordered temporally within a particular visit to a habitat. This allowed for detailed analysis of the foraging events immediately preceding moves between habitats during trials. I report this analysis, first for the constant habitat, then for the changing habitat. During the following presentation it is important to keep in mind the distinction between "switch phases" which refer to allocation patterns across blocks of trials and "switches (or moves) between habitats" which refer to fish moving back and forth between habitats within trials.

## Leaving the Vegetation (Constant Nymph Density)

One measure of searching persistence in vegetation was the number of search hovers taken preceding a move to the openwater since the last nymph capture. These data, summarized for each switching type, are presented in Table 4.6. The number times early switchers hovered prior to leaving a visit to the vegetation (HovL) was always less than the number taken by the late switchers during any particular phase of switching and overall (Table 4.6). The early switchers always hovered fewer times before leaving the vegetation (HovL) than the mean number of hovers required to locate and attack a nymph during the visit (HovA). Conversely, for late switchers HovL was significantly greater than HovA during the switch phase and roughly equal to HovA during the switch and postswitch phases. The early switchers required more hovers in order to locate a nymph than did the late switchers.

Table 4.6. Search time on NYMPHS (Search), unsuccessful search time before leaving VEGETATION (GUT), number of hovers per attack on Nymphs (HovA), number of unsuccessful hovers taken before leaving vegetation (HovL), and number of visits to vegetation during a trial (Visits) across the 3 phases of switching. Mean ± 95% CI of trials in each phase for fish of each type in Group N-D (Constant Nymph Density, n = 24 for Early type, n = 40 for Late type in each phase). Arrows indicate direction of significant differences.

EARLY SWITCH TYPE

| SWITCH PHASE | Search | | GUT | HovA | | HovL | Visits |
|---|---|---|---|---|---|---|---|
| Preswitch | 8.62 (1.55) | | 7.07 (2.25) | 7.41 (0.96) | > | 3.65 (0.42) | 5.3 (1.42) |
| Switch | 14.50 (3.14) | > | 7.78 (1.55) | 14.11 (1.78) | > | 3.41 (0.68) | 13.0 (2.52) |
| Postswitch | 7.18 (0.95) | > | 2.73 (0.02) | 9.38 (1.32) | > | 1.90 (0.71) | 2.7 (1.06) |

LATE SWITCH TYPE

| SWITCH PHASE | Search | | GUT | HovA | | HovL | Visits |
|---|---|---|---|---|---|---|---|
| Preswitch | 4.58 (1.00) | < | 14.51 (3.70) | 4.07 (0.30) | < | 9.38 (0.89) | 1.6 (1.09) |
| Switch | 7.20 (1.82) | | 10.06 (2.44) | 6.82 (0.95) | | 5.56 (0.54) | 9.6 (0.57) |
| Postswitch | 5.23 (1.71) | < | 10.73 (1.93) | 5.39 (0.67) | | 5.71 (0.43) | 3.4 (1.1 ) |

A second measure of searching persistence on a visit was the amount of unsuccessful searching time spent in the vegetation following the last nymph capture and immediately preceding a move to the openwater. This is often refered to as 'Giving-Up-Time' (or GUT in Table 4.6). Early switchers left the vegetation sooner after a nymph capture than did the late switchers. Furthermore, Giving-Up-Time for early switchers was less than the mean search time required per nymph encounter during visits whereas Giving-Up-Time for late switchers was greater than their mean search time for nymphs (compare SEARCH and GUT in Table 4.6).

### Leaving the Openwater (Variable *Daphnia* Density)

Comparisons of searching persistence in the openwater between early and late switchers is summarized in Table 4.7. During the preswitch and switch phases, the early switchers persisted in the openwater only as long as their mean search time on *Daphnia* (or alternatively, the mean number of hovers required per *Daphnia* encounter, HovA). However, by the postswitch phase they persisted longer than their mean search time and HovA for *Daphnia* (Table 4.7). The late switchers persisted longer in the openwater than mean HovA or mean search time for *Daphnia*.

### Allocation Patterns and Searching Persistence

The overall allocation to a habitat is determined by the combination of the probability of initial habitat choice and the searching persistence within habitats. For example, allocation to the initially chosen habitat would be high if persistence there is high relative to

Table 4.7. Search time on DAPHNIA (SEARCH), unsuccessful search time before leaving openwater (GUT), number of hovers per attack on DAPHNIA (HovA), number of unsuccessful hovers taken before leaving open water (HovL), and number of visits to open water during a trial (Visits) across the 3 phases of switching. Mean ± 95% CI of trials in each phase for fish of each type in Group N-D (Daphnia changing, constant Nymph Density, n = 24 for Early type, n = 40 for Late type in each phase). Arrows indicate the directon of significant differences.

EARLY SWITCH TYPE

| SWITCH PHASE | Search | GUT | HovA | HovL | Visits |
|---|---|---|---|---|---|
| Preswitch | 3.21 (0.51) | 2.57 (1.50) | 2.12 (0.43) | 1.88 (0.23) | 5.3 (1.42) |
| Switch | 1.85 (0.32) | 2.58 (1.15) | 1.40 (0.61) | 1.76 (0.26) | 13.0 (2.52) |
| Postswitch | 1.29 (0.09) | < 2.39 (1.25) | 0.68 (0.27) | < 2.04 (0.17) | 2.7 (1.06) |

LATE SWITCH TYPE

| SWITCH PHASE | Search | GUT | HovA | HovL | Visits |
|---|---|---|---|---|---|
| Preswitch | 4.08 (0.90) | < 7.80 (0.92) | 2.03 (0.34) | < 5.46 (1.08) | 1.6 (1.09) |
| Switch | 1.29 (0.39) | < 4.01 (0.78) | 1.86 (0.75) | < 3.38 (0.79) | 9.6 (0.57) |
| Postswitch | 0.94 (0.14) | < 2.93 (0.67) | 0.54 (0.31) | < 1.91 (0.20) | 3.4 (1.10) |

the expected search time per prey; due to the low chance that fish would ever leave the initially chosen habitat. However, as persistence decreases relative to expected search time, the probability that fish will move to the other habitat during the trial increases. As such, net allocation for the trial now becomes a combined function of persistence in both habitats. If persistence is low relative to search time then fish would be expected to move between habitats frequently during trials.

This process is illustrated in Table 4.8. Early and late switchers both had a high probability of beginning a trial in the vegetation during the preswitch phase. Operationally, net persistence in a habitat can be measured as the difference between Giving-Up-Time and the mean search time for a habitat. A positve net persistence shows that fish remained in the habitat longer after the last capture than the mean search time per prey during the visit. Likewise, a negative net persistence shows that fish remained in the habitat for a shorter time after the last capture of visits than the mean search time per prey during visits. Early switchers were less persistent in both the vegetation and open water than the late switchers. This was reflected in the greater number of visits and higher percentage of the diet taken from the openwater for the early switchers compared to the late switchers. The late switchers' high net persistence in the vegetation combined with the high initial choice of the vegetetation resulted in few visits to the openwater and a lower percentage of their diet from prey there compared to the early switchers. The small number of visits to the openwater by late switchers offset their high net persistence in the openwater with respect to any effect on diet allocation during trials.

Table 4.8. Comparisons of the probability initially choosing the open water habitat and net searching persistence in both habitats with the number of visits to and percentage of diet from the open water. Percent Initial Open Water = # choosing openwater/total initiations. Persistence Vegetation = GUT in veg.- Mean Searching Time on Nymphs. Persistence Open Water = GUT in open - Mean Searching Time on *Daphnia*. Visits = # of Visits to open water in a Trial. % Allocation Open Water = mg *Daphnia* captured/total mg captured in trial.

EARLY SWITCHERS

| Phase | % Initial Open Water | Persistence Vegetation | Persistence Open Water | Visits | % Allocation Open Water |
|---|---|---|---|---|---|
| Preswitch | 8 | -1.55 | -0.64 | 5.3 | 27 |
| Switch | 47 | -6.72 | 0.73 | 13.0 | 59 |
| Postswitch | 78 | -3.45 | 1.10 | 2.7 | 83 |

LATE SWITCHERS

| Phase | % Initial Open Water | Persistence Vegetation | Persistence Open Water | Visits | % Allocation Open Water |
|---|---|---|---|---|---|
| Preswitch | 3 | 9.93 | 3.72 | 1.6 | 10 |
| Switch | 52 | 2.86 | 2.72 | 9.6 | 49 |
| Postswitch | 91 | 5.50 | 1.45 | 3.4 | 88 |

Initial choice and net searching persistence in the vegetation decreased for both early and late switchers during the switch phase. As expected, the number of visits and diet allocation to the openwater increased.

By the postswitch phase, both the early and late switchers had a net positive persistence in the openwater. Since both types had a high probability of beginning trials in the openwater, both switching types received a high percentage of their diet from the openwater. This is inspite of the fact that net persistence in the vegetation was negative for the early switchers but still positive for the late switchers.

## Persistence and Energetic Return

Although the above analyses suggest that bluegill allocation patterns were produced through the combination of persistence and initial habitat choice, it does not tell us anything about why persistence in habitats changed as prey densities were manipulated. Many authors have suggested that foragers should adjust their persistence in habitats as a function of the return rates they experienced in the habitats (see McNair (1982) for review and clarification of the various forms of the hypotheses).

It is possible to compare the mean return rates of visits across phases with the corresponding mean persistence (Giving-Up-Time) at the end of the visits (Figure 4.9). Although mean return rates on Daphnia increased across phases, they did not increase equally for early and late switchers. Return rates on Daphnia for late switchers were less than those for early switchers during the preswitch phase (B in Figure

Figure 4.9 Mean Giving-up-Time (GUT) on Daphnia for trials in each switching phase against mean return rate (mg/s) realized in the open water. Solid circles = Early switch type. Open circles = Late switch type. B = Preswitch, S = Switch and A = Postswitch phases. (N = 24 for early switchers, N = 40 for late switchers).

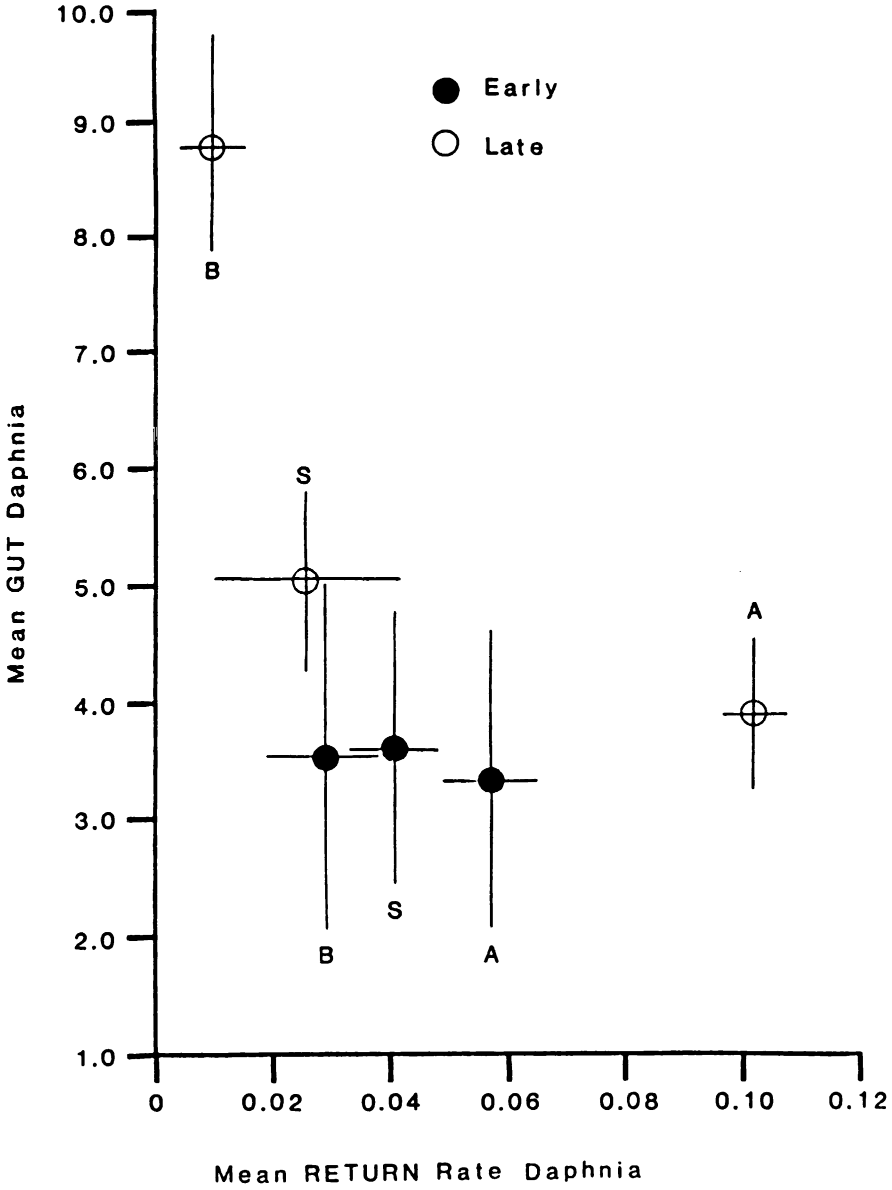

10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
Mean GUT Daphnia
0
0.02
0.04
0.06
0.08
0.10
0.12
Mean RETURN Rate Daphnia
● Early
○ Late
B
S
A
B
S
A

Figure 4.9

4.9), but increased and surpassed those for the early switchers by the postswitch phase (A in Figure 4.9). Concurrent with the late switchers' increase in mean return rate for visits was a corresponding decrease in mean Giving-Up-Time for visits (open circles in Figure 4.9). In contrast for the early switchers, mean Giving-Up-Time did not change as return rates of visits increased (solid circles in Figure 4.9).

Similar analyses to those described in the last paragraph were performed using each individual visit during the entire duration of trials wherein at least one prey was captured (Figure 4.10 and Table 4.9). Note that those visits without captures were excluded since they, by definition, had no return rate. Return rate for each visit was calculated as the total mg of prey taken during the visit divided by the total duration of the visit excluding Giving-Up-Time. Therefore, return rate for each point in Figure 4.10 is independent of Giving-Up-Time. Giving-Up-Time for visits decreased as the return rates of visits increased (Table 4.9, Figure 4.10), with the exception of the early switchers in the open water (Figure 4.10b). Slopes for the regression lines were the same for both switching types in the vegetation (constant habitat, Figure 4.10c and 4.10d, Table 4.9) but different between types in the openwater (changing habitat, Figure 4.10a and 4.10b, Table 4.9). The non-significant slope for early switchers in the openwater (Figure 4.10b) indicates that they used the same Giving-Up-Time in the openwater independent of return rates. Examination of this difference in Giving-Up-Time between the early and late switching types is pursued in the discussion.

Since the return rates used in Figure 4.10 and Table 4.9 included all levels of prey depletion within trials as well as changes due to

Table 4.9. Regression equations and tests for equality of slopes for the relationship between GUT of a visit to a habitat and the return rate during that visit. Regressions correspond to Figures 10a, 10b, 10c, 10d respectively. Regressions were calculated using individual visits with at least one prey capture.

REGRESSION EQUATIONS

Model : Log(GUT) = Intercept + Slope * Return Rate.

| Switch type | Prey | Intercept | Slope | Significance |
|---|---|---|---|---|
| Late | Daphnia | 0.78 | - 5.72 | 0.000 |
| Early | Daphnia | 0.70 | 0.61 | 0.753 |
| Late | Nymphs | 0.99 | - 3.45 | 0.019 |
| Early | Nymphs | 1.09 | -11.50 | 0.016 |

TEST FOR EQUALITY OF SLOPES

1. Late vs Early switchers on DAPHNIA ... DF = 1
F = 11.92
P = 0.0353

2. Late vs Early Switchers on NYMPHS .... DF = 1
F = 1.84
p = 0.1743

Figure 4.10 Plots and regression lines for the relationship between the GUT of a visit and the return rate during the visit (not adjusted for the GUT). Data are shown for Group N-D (increasing *Daphnia* and constant Nymphs). (a) Late switchers on *Daphnia* in openwater. (b) Early switcher on Daphnia in openwater. (c) Later switchers on Nymphs in vegetation. (d) Early switchers on Nymphs in vegetation. Regression equations and tests of significance are presented in Table 4.9.

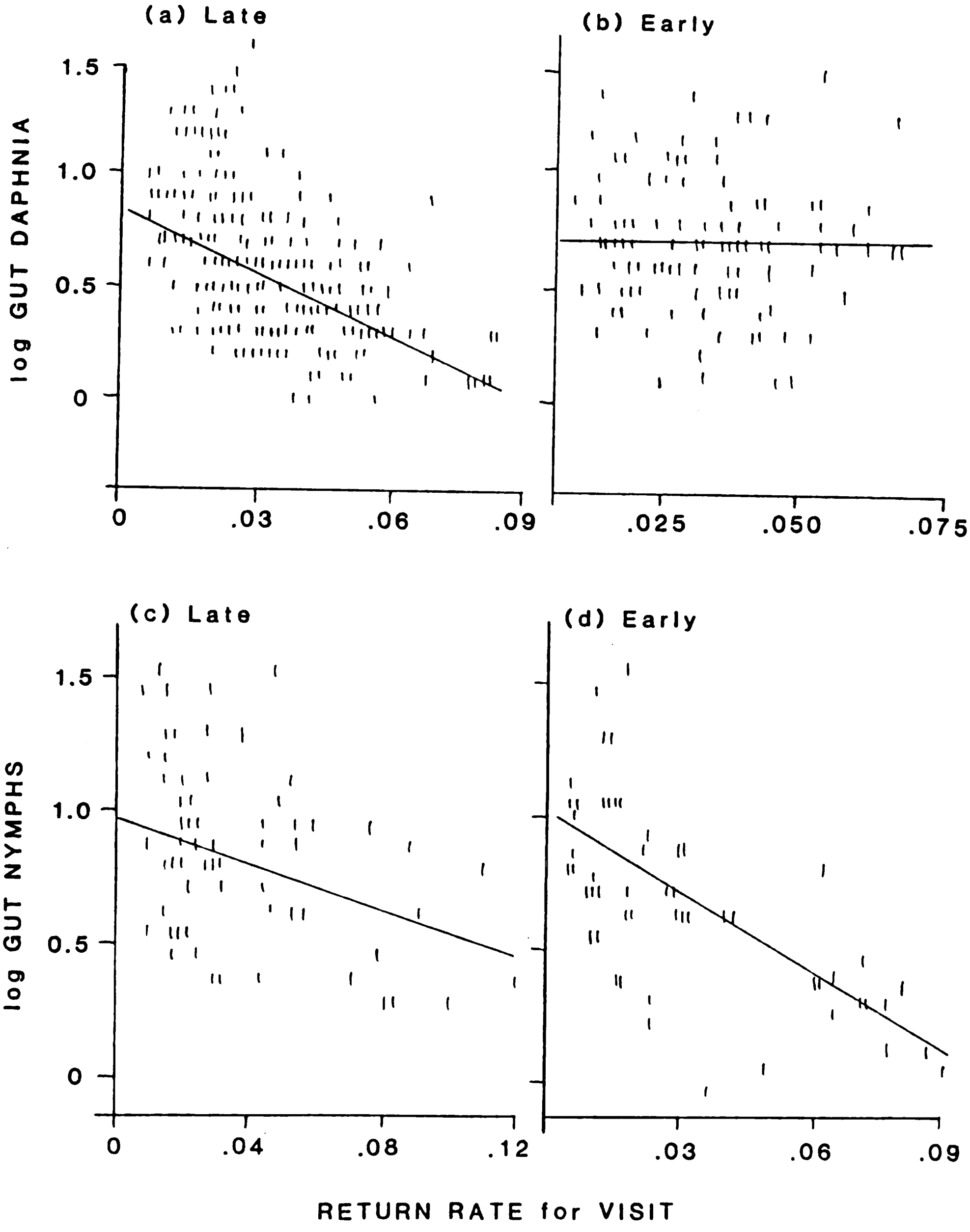

(a) Late
(b) Early
(c) Late
(d) Early
log GUT DAPHNIA
log GUT NYMPHS
1.5
1.0
0.5
0
0
.03
.06
.09
.025
.050
.075
0
.04
.08
.12
.03
.06
.09
RETURN RATE for VISIT

Figure 4.10

learning and density changes between trials, it demonstrates that bluegills were capable of modifying their Giving-Up-Time on a very short time scale within trials as well as making adjustments on the longer term between trials.

## IV. Switching Types and Total Return Rate

It is interesting to ask which, if either, switching type performed better with respect to net total energetic intake rate. Total return rate for a trial was calculated as the total accumulated mg of both prey types captured during the first 2min of a trial divided by 2min. This measure of return rate included the Giving-Up-Time and time spent moving among habitats, not included in previous measures of return rates calculated for the separate habitats. During the first block of trials when only one prey type was available (nymphs in the vegetation) total return rate climbed to an asymptote by the the fourth trial (Figure 4.11). Early and late switch types did not differ in return rate on any trial during Block I.

In Block II (when Daphnia was introduced at very low density in open water) early switchers began to include a low percentage of Daphnia in their diet. Because of the low return rate from Daphnia and the interference effect of including Daphnia on searching abilility on nymphs, the total return rate of the early switchers fell significantly below that of the late switchers for the last four trials of Block II (Figure 4.11). Daphnia density was increased in Block III and the early switchers switched to taking more than 50 percent of their diet from the Daphia. The total return rate for early switchers started below that of

Figure 4.11 Total return rate in trials (Total mg captured in trial/120sec.) across trials for early and late switching types in group N-D (increaing _Daphnia_). See Table 4.1 for prey densities in each Treatment Block. Early switchers = solid circles (N=3). Late switchers = Open circles (N=5).

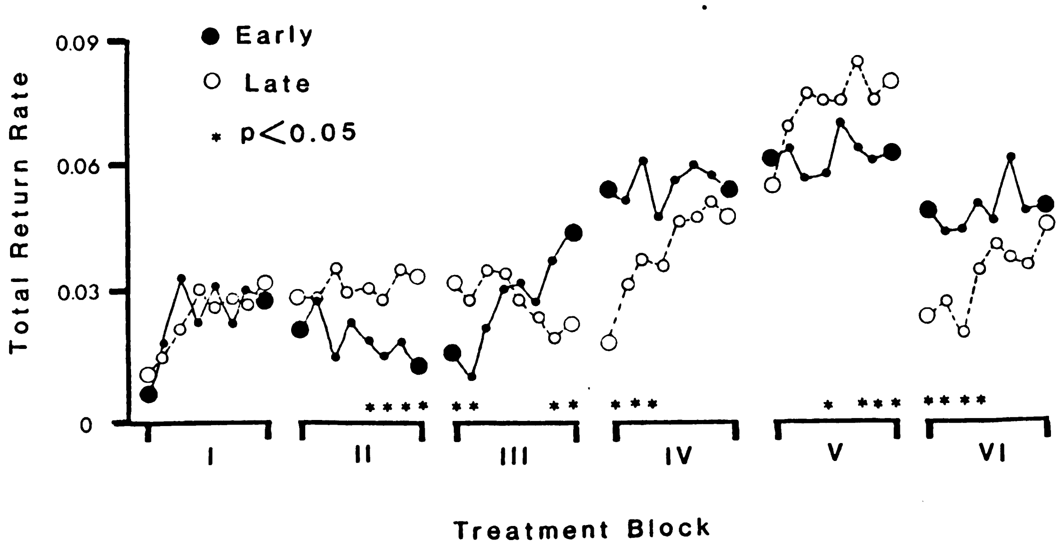

● Early
○ Late
* p<0.05
Total Return Rate
0.09
0.06
0.03
0
I
II
III
IV
V
VI
* * * *
* *
* *
* * *
*
* * *
* * * *
Treatment Block

Figure 4.11

the late switchers but surpassed the late switchers by the last two trials of Block III. Total return for the late switchers dropped during Block III, due in most part to the interference effect of Daphnia on their searching ability on nymphs (see section I above). The early switchers had a significantly higher return rate for the first 3 trials of Block IV, but the late switchers eventually reached an equivalent level as they switched out onto the Daphnia in the openwater.

When Daphnia were increased again in Block V, the late switchers surpassed the early switchers (Figure 4.11), due in great part to the higher percentage of time they spent foraging in the openwater. However, when Daphnia density was dropped suddenly in Block VI, return rates for the early switchers did not fall as much as for the late switchers. It took four trials at the new densities for the late switchers to reach the same return rate as the early switchers.

Overall, the early switchers had a higher total return rate than the late switchers on nine trials, whereas the late switchers did significantly better on ten trials (Figure 4.11). Actual calculation of the net difference in payoff between types for the entire experiment involves integrating the differences in return across all trials. However, it is obvious that the result of this calculation would be a direct experimental artifact of the number of trials in each treatment block. Assessment of costs and benefits for each switching type is left for the discussion.

# DISCUSSION

## Optimal Searching Technique

Experience with prey can influence search times in two distinct ways (see discussion to Chapter 2). Detection ability can improve by the formation of specific search images for prey types (Tinbergen 1960). Search time can also be reduced through the modulation of searching techniques that increase the rate of prey encounters independently of improvements in detection ability (Smith 1974b, see Gendron, ms. for review). A good deal of confusion has surrounded the use of the term 'search image' (Lawrence and Allen 1983) and controversy exists over whether search images are formed gradually with experience (e.g. Dawkins 1971) or formed quickly after only several encounters with a prey (e.g. McNair 1981). The empirical evidence in the literature suggests that search images are formed gradually, but there is a good deal of variability in the rate of formation (Gendron ms.). Bluegills modulate searching techniques and form specific search images. However, it is not operationally possible to separate out their relative contributions to improved searching ability in the above data.

Assuming that prey types differed only in relative crypticity, the probability of detecting non-cryptic prey is greater than that for cryptic prey (compare "P" curves in Chapter 2, Figure 2.12). When feeding on each prey type separately, the hover time that minimizes the expected search time for the cryptic prey type is greater than that for conspicuous prey. Given this framework, the optimal hover strategy for bluegills in these experiments was to use short hover times on Daphnia and long hover times on nymphs.

However, in order to determine the hover duration that maximizes the foraging rate on both prey types simultaneously, one must first consider how the spatial distribution of the prey restricts the available set of searching strategies. For example, if prey types are homogeneously mixed within a habitat or if foragers are unable to recognize distinct prey types, they might adopt one searching strategy and feed on both prey types as they are encountered. A forager using this strategy would be expected to exhibit random run lengths on prey types. Alternatively, foragers could adopt distinct hover times for each prey type which minimize the search time for each type independently. This technique would be useful only if foragers are able to make runs on prey types longer than random by focusing attention on one prey type at a time (e.g. by forming specific search images). Although this latter strategy might appear to be better, additional costs are incurred if time is required to adjust searching techniques when switching between prey types. The advantages of adopting a 'two hover time' technique are more apparent when prey types are distributed heterogenously among habitat types or patches. By focusing foraging effort on one habitat at a time, foragers might cue on habitat types and adopt different searching techniques for the prey in each habitat.

The experiments in this chapter involved distinct prey types in distinct habitats. As such, it was expected that bluegills would use the "two hover time" technique. However, when feeding on both prey types, the early switchers used a single hover time for both nymphs and *Daphnia*, whereas the late switchers used a long hover time for nymphs and a short hover time for *Daphnia*. At first glance, it appeared that the early switchers were "suboptimal" compared to the models predictions. This appearance illustrates the dangers of judging the optimality of dynamic behaviors with models developed for static conditions. In fact, using another time horizon the early switchers actually increased their total performance above that of the late switchers (e.g. Block IV in Figure 4.11). These results make it obvious that predictions of optimal hover duration in changing environments (or more generally, optimal searching strategies) must consider the larger picture of allocation and switching behavior.

## Optimal Sampling

Differences in persistence between early and late switchers were not as pronounced when using the time horizon of individual visits as opposed to entire blocks of trials (see Figure 4.10 and Table 4.9). Given only visits wherein prey were actually captured, both types exhibited similar relationships between persistence and return rates of visits to the non-changing habitat but different relationships with visits to the changing habitat. This raises the possiblity that early and late switchers used the same rules for searching persistence when conditions were constant, but differed in how they dealt with "new" prey and/or changing prey abundances. However, when faced with similar prey densities in habitats, early and late switchers did not use the same persistence when switching between habitats (Tables 4.7-4.9, Figure 4.9). In general, early switchers gave up searching in a habitat sooner after successful captures than late switchers. As a result, the early switchers moved between habitats more frequently. If visits reflected sampling, then one might attribute the "earlier" switch to better estimates of prey availability in the changing habitats.

It is not possible to discern whether the number of visits was simply an emergent property of persistence rules combinied with searching ability within habitats or whether visits reflected actual decisions by bluegills to sample other habitats. In either case, the net result for the early switch type was a lower return in each habitat separately compared to the late switchers, but an increased propensity to include a second prey type in their diet.

Including Daphnia in the diet when it was at low density reduced total return rates (Block II in Figure 4.10) due both to spending time in a "suboptimal" habitat and interference in searching and handling abilities on nymphs (Tables 4.2 and 4.3). However, by including the second prey in their diet in Block II, the early switchers received a "head-start" in learning the searching and handling techniques for Daphnia. When Daphnia density increased further, this "head-start", combined with spending more time in the openwater, resulted in a rapid increase in total return rate for the early switchers (Figure 4.10, Block III). At the same time, the late switchers were just beginning to include Daphnia in their diet and realized a decrease in total return. Because the late switchers were better at searching for Daphnia (Table 4.7), they eventually reached a higher total return rate than the early switchers (Figure 4.10, Block V).

Early studies of sampling used the simplest situation where naive foragers were allowed to feed in an environment with two types of patches characterized by different prey densities (constant over trials). The idea of these experiments was to see how long it took foragers to "choose" the best patches and to chart how sampling among patches changed with experience. Krebs et al. found that when great tits (Parus major) were faced with two patches of unknown density, birds began by sampling both patches in roughly equal proportions before focusing on the patches with the highest prey density. Using averaged behavior for all birds in the experiment, they showed that tits adjusted the length of time spent sampling as a function of the length of the foraging trials. This conformed with the qualitative predictions from their optimality analysis. Unfortunately, Krebs et al. (1978) did not present the data for the individual birds in their experiments. Apparently there was a great deal of inter-individual variation in responses with some birds showing gradual changes in patch choice (reported in Shettleworth (1984) as pers. comm. from J. R. Krebs).

The advantages of paying close attention to individual behavior is illustrated nicely by the experiments of Smith and Sweatman (1974). Titmice in an aviary were presented with a spatial distribution of patches of different prey density. Across trials, the birds increased the amount of searching effort allocated to the higher density patches. However, the degree of "focus" varied among individuals with some birds spending significantly more time sampling the less profitable patches. When Smith and Sweatman rearranged the distribution of prey densities in patches, the birds with the highest amount of sampling were the first birds to focus their foraging effort in the "new" profitable patches. This study by Smith and Sweatman suggest an adaptive element to the variation among individuals. A potential trade-off may exist between the conflicting demands of sampling in a variable environment and the exploitation of the most profitable resources. Calculation of the costs and benefits of sampling requires a realistic representation of how environments change in nature. Predictions for the optimal amount of sampling generally increasing with increased variability (Houston et al. 1982). Choosing the appropriate currency and time horizon for integration is of paramount importance in the formulation of a model. Ideally, a prediction should maximize reproductive output over an organism's entire lifetime (e.g. Gilliam 1982). However, for the purposes of looking at energetic return and short-term behavioral adaptations in foraging, it is simpler to identify the time scale and spatial scale of the changes in prey abundances.

In addition to specifying a relevent time horizon for integrating performance, one must consider the trade-off between time spent sampling and the loss of searching and handling efficiency on prey. As such, sampling incurs costs in two ways: (1) by reducing the amount of time spent in the most profitable patches, and (2) by reducing the ability to accumulate prey captures within habitats. If prey densities are changing within habitats and if sampling increases the probability of identifying and switching to a "new" most profitable patch, then it may be advantagous to sacrifice on the short term (Houston et al. 1982, Orians 1981).

## Natural Selection and Allocation Rules

It is surprising that the early switching bluegills continued to sample the openwater in spite of the fact that doing so decreased their total return rate (Block II in Figure 4.3). Similarly, it is difficult to imagine that they "hedged their bets" in light of the possibility that the future might be different. Given that foraging behaviors are subject to selection pressures in much the same manner as morphological traits, I find it more plausible that the switching "types" reflect a compromise between the conflicting demands of sampling and searching efficiency in changing environments and limits on individuals abilities to adjust their behaviors.

The development of a framework for assessing the importance of learning and individual differences in foraging behaviors (IDFBs) can take several tracks, each dependent upon how one wishes to use the predictions of foraging theory. IDFBs are ofen attributed to foragers' responses to stochasticity inherent in the environment. Such approaches have generally assumed the existence of a single optimal behavior and that deviations from it are suboptimal. Other approaches have included IDFBs as constraints in the optimization process (e.g. Houston and MacNamara 1985). In many ways, animal foraging has emerged as the premier showcase for application of optimality theory to the study of behavior. However, the main utility of optimal-foraging analysis is not its ability to pinpoint exact behaviors, but rather its ability to establish predictions against which deviations can be measured and studied (Werner and Mittelbach 1981, Maynard-Smith 1978).

In this light, it is possible to explore for patterns in IDFBs with an eye towards an ultimate explanation and/or functional reason for individual variability. It is not at all straightforward how to formulate criteria for judging the "best" foraging stategy in a changing environment. For example, the choice of the relevant currency and time horizon for integrating performance greatly affects outcomes (Inoue 1983, Houston et al. 1982).

It is necessary to recognize that foraging and allocation behaviors are often organized in a hierarchical fashion with complex behaviors often being the product of other 'less complex' component behaviors. In such systems, any variation in a higher level behavior (such as foraging allocation) could arise from variation in lower level components (such as hover durations). When analyzing any one component, one must not forget that it functions as part of a larger system and, as such, the influence of natural selection on the trait might not be direct and/or obvious. The results of the experiments presented in this paper can be used to illustrate some important factors that must be considered. For example, it may be necessary to consider the advantages and disadvantages of being different within the social context of foraging. If individuals make optimal decisions to maximize their foraging rate, they must not only be sensitive to the prey density within patches but also be able to assess the behavior and density of other individual foragers. One potential consequence of the lack of IDFBs is that foragers may tend to aggregate in the same high profitability patches. Resource depression could occur and competition among foragers would serve to decrease individual foraging rates. As such, the fitness of any foraging type that may exist will depend on the frequency of other types in the population of competitors. Both Milinski (1979, with sticklebacks) and Godin and Keenleyside (1984, with cichlids) observed differences among individual fish in the frequency of moving between food patches. Godin and Keenleyside found that the high frequency 'switchers' had a lower foraging rate than the 'stayers'. Godin and Keenleyside do suggest that the switchers may do better in variable environments.

The vast number of variables and calculations required for determining the single "best" strategy in a truly stochastic environment are staggering. Furthermore, the cost of developing and maintaining the necessary cognitive abilities could far outweigh the benefits of increased foraging ability (see Johnston (1983) for an extended discussion and review). The alternative is that individuals use short cuts or "rules of thumb" to approximate the optimal solution. However, no single rule of thumb can be best for all situations in changing environments. As such, all individuals might either possess the same rule that does best averaged over some time horizon, or alternatively, individuals could possess different rules that do best under various conditions. Foraging research has not recognized and/or addressed the potential for adaptive individuality in foraging behaviors.

It is relatively straightforward to show through computer simulations that different variants perform better in some environments than others. Simulations designed to mimic the experiments in this chapter were performed with one habitat type held constant and the other varied as a cosine function across trials (Figure 4.12a, Clark and Ehlinger, in press). Each habitat had the same harmonic mean prey density averaged over the course of the simulation. By varying the frequency and amplitude of prey in the second habitat and integrating return rate across trials, it was possible to plot how the difference in performance between late and early switchers changed with increasing variability in prey densities. Late switchers did best when prey densities remained relatively constant over time (Section 1 of Figure 4.12b). When the frequency of prey changes was increased, the early switchers did progressively better due to their ability to spend more time on the second prey type while it was at a high density and switch back to the constant prey when the second prey type declined. When the

Figure 4.12 Schematic presentation of simulated performance for late and early switchers in variable environments. (a) Prey density changes across trials. Density of prey 1 was held constant while the density of prey 2 was varied across trials as a cosine function (Ampl = amplitude, Freq = frequency). (b) Difference in total return rate (integrated across trials) for the late and early switchers with increasing frequency and amplitude of changes in density of prey type 2.

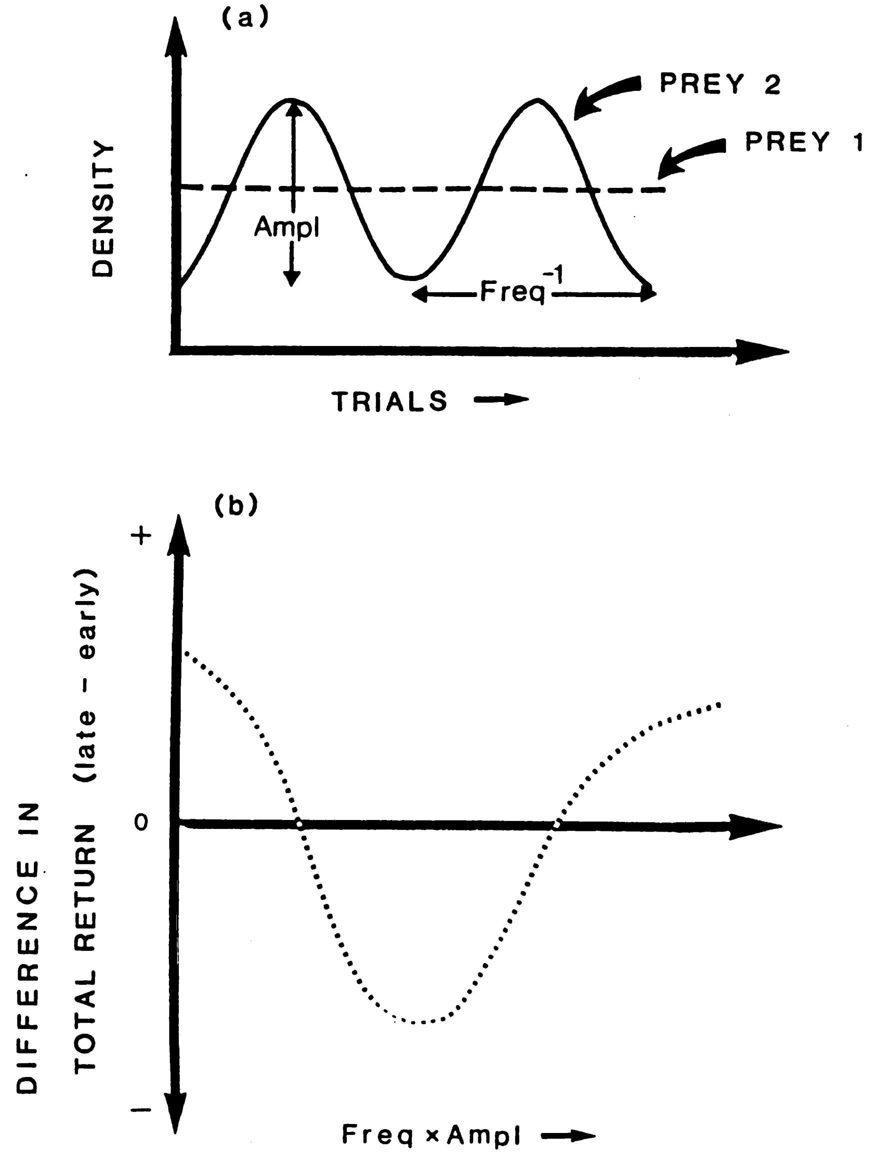

(a)
PREY 2
PREY 1
DENSITY
Ampl
Freq$^{-1}$
TRIALS
(b)
+
0
−
DIFFERENCE IN
TOTAL RETURN (late - early)
Freq × Ampl

Figure 4.12

amplitude of prey changes was large enough, the late switchers would also switch to the second habitat but they would also take longer to switch back to the other habitat when the density decreased. This resulted in the late switchers doing progressively worse than the early switchers (Section 2 of Figure 4.12b). However, when the frequency of prey changes increased beyond a point, the late switchers decreased their switching to the second habitat and their decline in return rate reached an asymptote (Section 3 of Figure 4.12b).

If differences in return rates translate into differences in reproductive output and fitness, then the late type should predominate in environments (e.g. lakes) that are characterized by particularly stable or slowly changing prey distributions (Section 1 in Figure 12b). Similarly, the early type should do best in environments with moderately variable prey abundances (Section 2 in Figure 12b). If the environment itself changes in variability from year to year, it is easy to imagine the types existing in various proportions. If the trait is continuous rather than discrete (e.g. a continuous range of switching types from early to late) then environmental variation could produce a distribution of switching phenotypes, each doing best in different years. As an extreme case, alternating years of variable and constant prey conditions could produce a bimodal distribution with early types favored in some years and late types favored in others.

Simply demonstrating selective potential is not sufficient to claim that natural selection can operate on the traits; one must also establish the genetic basis for the differences. A comprehensive framework for studying IDFBs requires a thorough investigation of alternative explanations for observed differences (Clark and Ehlinger, in press). As a start, IDFBs must be distinguished from transient differences such as "random walks" in behaviors (e.g. Slater 1981). As such, IDFBs must be shown to be stable across replication and time. In conjunction with demonstrating stability, it is necessary to distinguish between phenotypic and genotypic IDFBs. For example, observed IDFBs might arise from differences in experiences during ontogeny, particularly if sensitive phases in development influence adult behavior (Immelmann and Suomi 1981, e.g. food imprinting: Arnold 1978, Burghart 1971). The crucial test is whether a heritable trait is attributable to genetic variation.

## CONCLUSIONS AND IMPLICATIONS FOR FURTHER STUDY

The data presented in this chapter show that individual bluegills used different foraging strategies in dealing with multiple prey types. The late switchers used distinct hover times in each habitat whereas the early switching types adopted a single intermediate hover time and used it in both habitat types. Differences in searching technique corresponded with variation in searching persistence within habitats. Persistence together with bluegills' tendency to begin trials in the habitat that provided the higher return rate on the previous trial can account for allocation patterns of the switching types.

Although the manipulations of the experiments were meant to mimic the seasonal changes in prey abundance between the openwater and vegetation, identifying the constraints imposed by the spatial scale of the experimental arena is always a concern when generalizing the results of laboratory studies to field situations. The distances between habitats in the arena were more analagous to microhabitat separations within the litoral regions of local lakes and/or to the interface between the vegetation and openwater habitats. In this respect, I anticipate the results of these experiments will apply most directly to bluegills foraging among microhabitats where fish move quickly between habitat types (e.g. Werner et al. 1981). The same general processes may apply to the larger scale of chosing between the openwater and vegetated habitats of lakes. However, the greater volume and spatial separation of habitats will reduce the importance of searching persistence within habitats and increase the importance of initial habitat choice for any given feeding period.

Determining whether the switching types reflect a process of natural selection will involve pinpointing the origins of the individual differences. By raising bluegill larvae of known parentage in controlled laboratory environments it should be possible to sort out experiential and genetic contributions to IDFBs. Preliminary experiments (Ehlinger, unpublished) suggest that larval bluegills develop prey-specific capture techniques and show preferences for familiar prey types. The types of prey available and variability in prey abundances early in the development of foraging behaviors might influence adult searching techniques. Once the origins of IDFB's are identified it will be possible to make specific predictions about the distributions of IDFBs in lakes that differ historically in the variability of prey and/or habitat types.

The development of foraging theory must include a greater emphasis on individual behavior and variation among individuals.

Optimal-foraging theory is based on the assumptions that foraging return contributes to fitness and that fitness is maximized by natural selection. The lack of attention paid to the variation in fitness among individuals in a particular environment and/or changes in the fitness of individual phenotypes across ranges of environments indicates that we are ignoring the premises upon which the theories are based.

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