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The role of early experience in the development of specialized and diverse preferences for foraging techniques by white-footed mice (*Peromyscus leucopus*)

Fulk, Keith Randal, Ph.D.

The University of North Carolina at Greensboro, 1989

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The Role of Early Experience in the Development of Specialized and Diverse Preferences for Foraging Techniques by White-Footed Mice (<u>Peromyscus leucopus</u>)

by

Randal Fulk

A Dissertation submitted to the Faculty of the Graduate School at The University of North Carolina at Greensboro in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy

> Greensboro 1989

> > Approved by

Dissertatio

APPROVAL PAGE

This dissertation has been approved by the following committee of the Faculty of the Graduate School at the University of North Carolina at Greensboro.

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June 27, 1989 Date of Final Oral Examination

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Fulk, Keith Randal, Ph.D. The Role of Early Experience in the Development of Specialized and Diverse Preferences for Foraging Techniques by White-Footed Mice (<u>Peromyscus</u> <u>leucopus</u>). (1989) Directed by Dr. Timothy D. Johnston. 131 pp.

Investigations of foraging behavior (within the Neo-Darwinian framework of Optimal Foraging Theory) have focused on the economic choices made by adult animals. Little research has been directed toward the development of these choice strategies. The objectives of the present study were to provide an evolutionary framework for individual diversity in foraging behavior, and to asses the roles of practice with a difficult foraging technique, the opportunity to compare techniques, and food scarcity on the development of preferences for foraging techniques by white-footed mice (Peromyscus leucopus). Each of the 4 experiment used a different regimen of juvenile experience with 3 foraging tasks, and tested adult efficiency and diversity of preference. Experiment 1 provided baseline efficiency and diversity for task naive mice. Experiment 2 established that practice with a difficult task did not increase preference for the task compared to task-naive mice. Experiment 3 tested the affect of the opportunity to compare the techniques by giving one group (Stable) simultaneous access to the tasks, one group (DF) access to a single randomly fluctuating task daily, and a third group (AF) access to a single, randomly fluctuating task every other day. Experiment 3 indicated that simultaneous experience and daily fluctuations in tasks promoted

specialization, and that every-other-day fluctuations promoted preference diversity. Experiment 4 compared a group with every-other-day access to a randomly fluctuating task and supplemental feeding on the days when no task was presented (AF-SUP) to the AF group in Experiment 3. Experiment 4 indicated that food scarcity promoted preference diversity independently of everyother-day exposure to the tasks. These experiments were a test of the basic assumption of OFT that natural selection for optimal genotypes determines adult foraging, and demonstrates the necessity of a developmental analysis of foraging choices.

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TABLE OF CONTENTS

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Page			
APPROVAL PAGE i			
ACKNOWLEDGMENTS ii			
LIST OF FIGURES			
CHAPTER			
I. INTRODUCTION AND BACKGROUND			
Generalists and Specialists Development and Evolution Proximate and Ultimate Causes Adaptive Behavior I Genotype and Phenotype I Inheritance as a Process An Ecological View of Generalists Contrasting Approaches to Foraging The Concept of Species-Typical Generalist Foraging Local Adaptations Factors Affecting the Perception of Similarity Among Foraging Techniques			
Compare Foraging Techniques			
II. METHODS AND RESULTS 5			
General Methods			
Diversity of Preference			
Preference			
the Diversity of Preference			
Scarcity			
III. GENERAL DISCUSSION			
REFERENCES			

LIST OF FIGURES

1.	A model of evolutionary change incorporating cytoplasmic, physiological, genetic, and environmental changes as interactants in developmental processes that result in evolution	25
2.	Mean Remove Efficiencies of the Naive Group for Hang (REH), Lift (REL), and Slide (RES)	72
3.	Mean Remove Efficiency and Mean Number of Seeds Taken Over the 15 Days of Preference Testing by the Naive Group	74
4.	Mean Remove efficiency of RH for Hang (REH), Lift (REL), and Slide RES)	79
5.	Mean Total efficiency for RH for Hang (REH), Lift (REL), and Slide (TES)	80
6.	Mean Remove efficiency of RH for Hang (REH), Lift (REL), and Slide (RES) are presented in the left panel, and mean number of seeds taken over the 15 days of preference testing for Hang (NUMH), Lift (NUML), and Slide (NUMS) are in the right panel	83
7.	Mean daily H' based on the number of seeds taken from all of the tasks for Stable (S), Day Fluctuating (DF), and Alt Fluctuating (AF)	89
8.	Mean daily H' based on the number of seeds taken from all the tasks for Stable (S), Day Fluctuating (DF), Alt Fluctuating (AF), and Naive (N)	92
9.	Mean daily H' based on the number of seeds taken from all the tasks for Stable (S), Day Fluctuating (DF), Alt Fluctuating Supplemented (AF-Sup), and Alt Fluctuating (AF)	96
10.	. The relationship between Remove efficiency and the number of seeds taken of the 15 days of preference testing for Stable (S), Day Fluctuating (DF), Naive (N), and Alt Fluctuating (AF) 1	14

Chapter I

Introduction and Background

The choices made by foraging animals, and the environmental conditions that affect those choices have been the focus of a great deal of research in recent years (R. Gray, 1987). Optimal foraging theory (OFT) (Charnov, 1976; Krebs, 1978; Pyke, Pulliam & Charnov, 1977) has provided a theoretical base for much of this work. As a result, we now have a great deal of information about the choices made by adult animals during foraging. We know relatively little, however, about the development of those choices.

The dominance of OFT in the foraging literature may have impeded developmental investigations of foraging because the theory assumes a knowledgeable, experienced forager (Stevens & Krebs, 1986), and because it was developed within a neo-Darwinian framework that assumes natural selection to be the principle cause of behavior. The assumption of a knowledgeable forager focuses attention on adult, experienced animals, and inhibits asking questions about how foraging experience is acquired, and/or how this experience effects optimal choice. The neo-Darwinian framework, from which OFT was derived, also inhibits asking developmental questions about foraging. Optimality is adaptive, and optimal foraging behaviors are assumed to be adaptations. In the neo-Darwinian tradition, adaptations are due to natural selection; animals exhibit optimal foraging because they have been selected to do so. This approach, however, leaves a very important question unanswered. Since natural selection can only act on existing phenotypes, what is the origin of the phenotypes? A complete analysis of foraging must include not only investigations of adult behavior, but also investigations of the development of adult patterns (Baylis & Halpin, 1982; Hailman, 1977; Jamison, 1986).

The purpose of this dissertation is to show why a developmental analysis of foraging is necessary, and to use a developmental analysis to shed light on the origins and evolution of the diverse foraging patterns of a generalist forager. This work does not directly test hypotheses based on OFT, but it does test the basic assumption of OFT that adult foraging is guided by the economics of foraging as expressed by maximazation of net gain. In order to choose optimally among several alternatives, an animal must identify the highest-valued alternative. The effect of early experience on an animal's subjective perception of the values of various foraging techniques is an important consideration in determining optimal choice and foraging the subjective value of various foraging techniques, and in

the development of diverse preferences is empirically addressed in this work.

Generalists and Specialists

Generalist and Specialist foragers are labels often used to characterize species-typical foraging patterns; these terms, however, have a variety of meanings. Most commonly, eating a broader range or greater variety of prey types defines a generalist. A second, and nonindependant definition of a generalist is the use of a wide variety of foraging behaviors; and a third definition concerns the relative ability of generalists and specialists to extract energy from food (Schoener, 1971). All of these definitions involve distinctions among species, and a continuum from generalist to specialist can be constructed based on the relative diversity of feeding behaviors of various species (L. Gray, 1979; Klopfer, 1973; MacArthur, 1972). Generalists have been described as Jacks of all trades (Klopfer, 1973), and behave as if the foods they eat are very similar (L. Gray, unpublished). The optimal choice of generalists is not to specialize, but to distribute their preferences among a variety of alternatives. The diverse preferences of generalists are often ascribed to natural selection for "generalist" genetic programs (e.g. Drummond & Burghardt, 1983), but

individual experience has also been shown to play a role in foraging diversity (L. Gray, 1979, 1981; Gray & Tardif, 1979). The roles of individual experience and the development of foraging diversity in the evolution of generalists is the focus of this chapter.

Development and Evolution

The modern neo-Darwinian synthesis is the predominant evolutionary theory among biologists (Eldredge, 1985), and as such, it has affected the ways generalists and specialists have been described and investigated. Two aspects of the modern synthesis, and the strict separation of proximate and ultimate causes, and "population thinking" focus attention on the role of natural selection in evolution. Population thinking takes a variety of forms in evolutionary theory. Darwin introduced population thinking in his focus on the natural variation that exists in species to counter the typological views of species that prevailed at the time. The typological view saw species as unchanging, and attributed their form to supernatural creation. The typologists saw species as made up of individual organisms endowed with the "essence" of the species, implying that little variation should exist. The essence, in the form of an humunculus or template, was placed in each individual by a non-natural force. The existence of variation within species that Darwin

documented refuted the logic of typological thinking. Variation should not exist if a template existed that determined individual and species characteristics. For Darwin, competition among varying individuals was a natural phenomenon that shaped the form of species, and competition took place among individuals within a population. Those best able to compete will pass that ability to their offspring, and their form will come to dominate within a species.

The synthesis of Mendalian genetics with Darwinism placed emphasis on genetic variation (alleles) as the source of variations in form. The genetical theory of selection of population genetics describes evolutionary change in the structure of populations in terms of the frequency of alleles or genotypes. An important assumption of population genetics is that characteristics evolve by a fitness-maximizing process in which one allele is selected at the expense of others. Evolution, then, is a maximizing process that produces locally optimal forms based on the fitness of alleles or genotypes. OFT, with its emphasis on selection for maximization of net gain, reflects the logic of population genetics. The view of optimal genotypes that produce optimal foragers comes dangerously close to the typological thinking Darwin reacted against. In its modern form the source of a species' form is natural, not supernatural, but the concept of a species essence is

preserved in the form of genotypes and gene pools. The assumption of maximization of alleles implies inevitability and uniformity of individual characteristics within a species. Uniformity of characteristics is very evident in OFT in its assumption that maximization of net gain underlies foraging behavior in all species, and individuals, regardless of their developmental history. Optimality results from natural selection for optimally efficient genotypes.

The focus on natural selection has been at the expense of development, and development plays only a small role in the modern synthesis (Eldredge, 1985). As a result, investigations of foraging have centered on questions about the role of natural selection in shaping foraging behavior, and the predominance of OFT in the foraging literature reflects the importance of natural selection in the evolutionary theory that underlies it. The lack of developmental studies of foraging behavior, conversely, reflects the lack of attention development receives from the modern synthesis.

Proximate and Ultimate Causes

The small role of development in the modern synthesis, and especially in the theory of population genetics, stems from the strict separation of proximate and ultimate causes. One of the major proponents of the modern

synthesis, Ernst Mayr, in an article titled "Cause and Effect in Biology" (Mayr, 1961, reprinted 1976), states the separation of proximate and ultimate causes very clearly. According to Mayr, proximate cause governs "... the responses of the individual (and its organs) to immediate factors in the environment", while ultimate cause governs "... the evolution of the particular DNA programs of information with which every individual of every species is. endowed" (p. 363). Both proximate and ultimate causes must be investigated in order to have a complete understanding of a phenomenon, but the result of each is distinct. Proximate causes are immediate causes, and affect the development of individual phenotypes. Ultimate causes are historical, and have their effect on the evolution of the genetic information contained in the DNA of every member of a species. The evolution of genetic programs is due to natural selection for the most adaptive programs. The distinction between proximate and ultimate causes can be illustrated as: Proximate -- Developmental -- Individual, and Ultimate -- Selected For -- Population. Proximate causes have their effect on individuals through developmental processes, and ultimate causes have their effect on populations through the action of natural selection.

The strict separation of proximate and ultimate causes places natural selection as the primary cause of

evolutionary change, and relegates development to a supporting role. (Other evolutionary forces besides natural selection have a place in the modern synthesis. For example, genetic drift, polymorphism, sexual selection, and genetic neutrality all are seen as sources of evolutionary change. All of these forces have in common the assumption that evolution occurs through changes in the gene pools of populations or species; this assumption of the genetic base of evolution preserves the proximate ultimate distinction. Parallel arguments to the one presented here could be made for each of the evolutionary forces listed above because each makes the common underlying assumption of genetic primacy in evolution. The focus here will be on natural selection, which remains the predominant source of evolution in the modern synthesis.] From the view of the modern synthesis, development is the means by which genetic programs are played out. The programs have evolved by natural selection, and development merely supports their expression; it plays no direct role in evolution, and only an indirect, supportive, role in the expression of species-typical phenotypes.

Since development occurs in individual organisms, and evolution in populations of organisms, individuals are also unimportant for evolution, except for their contribution to the gene pool of the species. Eldredge (1985) in a review of the major books of Dobzhansky, Mayr, and Simpson states

that these three important figures in the modern synthesis, as well as "evolutionists in general," "tend to see organisms as bystanders in the evolutionary processes" (p.86). Individual organisms can only remain "bystanders" if the separation of proximate and ultimate, development and evolution, remains intact. If, however, development makes significant contributions to the form of phenotypes, then the course of an individual's development is just as important to evolution as is the genetic material it houses.

The strict separation of proximate and ultimate causes is one expression of a group of related dichotomies: phylogeny vs. ontogeny, instinct vs. learning, and nature vs. nurture. The problems created by viewing behavior in this dichotomous manner have been addressed by a number of authors (Gottlieb, 1981; Johnston, 1987; Kuo, 1976; Lehrman, 1953; Oyama, 1985). Lehrman's (1953) critique of Lorenz's dichotomous view of behavior showed, on logical and empirical grounds, that the dichotomous view is untenable. The strict separation of behavior into an ultimate, innate, genetically-caused category, and a proximate, learned, environmentally-caused category gives the false impression that labeling a behavior innate, genetic, or environmental explains it, and that no further developmental investigation is necessary. Lehrman (and others cited above) demonstrated that behavior cannot be

divided into the mutually exclusive categories of innate and acquired. The predeterministic view of genetic programs, and the view of development as an unfolding of those programs does not adequately describe development. Lehrman states, "The interaction out of which the organism develops is <u>not</u> one, as is so often said, between heredity and environment. It is between <u>organism</u> and environment" (p.345, emphasis in original). Development, from this view, is not an unfolding of predetermined, selected-for, genetic programs, but the outcome of a dynamic system made up of coacting elements such as genes, proteins, cells, tissues, organs, experience, and learning. All of the elements are parts of the system, none more or less determined than the others, and development is a product of the coacting system of elements.

In contrast to Mayr's view, Lehrman sees the organism as a critical component of the system that produces a given phenotype. The phenotype, on which selection acts, is the product of a dynamic developmental system, and is not due primarily to inherited genetic programs. The developmental system must now be included as an evolutionary factor. It plays a critical role in the production of phenotypes, and thus in the variability among phenotypes on which natural selection acts.

Johnston and Gottlieb (unpublished) present a model of phenogenesis in which both natural selection and

development produce altered patterns of epigenetic interactions that result in change of the population mean phenotype. In this model, an environmental change produces altered selection pressures, and in turn, a change in the population mean genotype. The change in the population mean genotype alters the pattern of epigenetic interactions of development and produces a change in the population mean phenotype. However, environmental changes can also alter the input to development; thus altering epigenetic interactions and producing a change in the population mean phenotype. This epigenetic model includes both the traditional role of environmental change as altering population mean genotype and its effect on development, as well as environmental inputs to development and their effects on the population mean phenotype. Both natural selection and development contribute to a change in population mean phenotype through their effects on the pattern of epigenetic interactions that produces phenotypes.

A number of authors support the epigenetic view of evolution, pointing out that evolution proceeds through alterations in developmental pathways, and that developmental pathways are the result of epigenesis (de Beer, 1958; R. Gray, 1988; Ho, 1984, 1988; Ho & Saunders, 1979, 1982, 1986; Løvtrup, 1984; Oyama, 1985; Saunders & Ho, 1986). Epigenesis is seen as the primary force in the production of phenotypes and selection acts only to determine their distribution in a population. The primacy of epigenesis for the production of adaptations is clearly stated by Johnston and Gottlieb (1981). They state; "The primary responsibility for supplying adaptations must be assigned to epigenesis: if an adaptation is not supplied by epigenesis, it is not supplied at all" (p. 243).

The epigenetic view sees the phenotype as the product of coacting organismic and environmental elements and not as the product of a set of pre-programmed genetic instructions. Mayr's view of open and closed programs (1974) is a teleonomic description of the control of development. He suggests that a general theory for developmental biology could be found in the execution of these programs during development (Mayr, 1976). Mayr's view is that genetic programs act as goal-directed (i.e. teleonomic), organizing principles for producing adaptive behavior. The concept of programs for producing adaptive behaviors is, however, less straightforward than is implied by Mayr's discussion. Johnston & Turvey (1980) discuss two alternative interpretations for programs for adaptive behavior. The first is a view of development controlled by a set of instructions put into action by some kind of executive component. This is very much the view of the control of birdsong presented by Marler (Marler, 1963; Marler & Sherman, 1983; for an alternative view see

Johnston, 1988). The second interpretation sees the program as embodied in the structure of the system. Development is not guided by a pre-determined set of instructions, but is the outcome of a system of coacting elements. "Program" is used here as an <u>a posteriori</u> description of the operation of the developmental system; not as an <u>a priori</u> set of instructions for determining behavior. From this <u>a posteriori</u> view, programs are descriptions of rules that can be extracted from the operations of dynamic systems. The program does not exist independently of the system, but is a set of rules used to describe the ongoing course of interactions among the system's components that produces a stable outcome. The interaction of the components of a system is the program.

Oyama (1985) discusses the role of information in programs of development. In contrast with the neo-Darwinian view of information as pre-existing and predetermining development, Oyama sees information as inherent in the dynamics of development. The characteristics of a system, elements and their interactions, determine, constrain, and control its functioning. No outside program is required in order for the system to function. Information, in Oyama's sense, guides development in that the information generated in early stages provides the basis for the dynamic interactions of later stages. The program of development

is not a material object (like a genetic program), but a hierarchy of processes that control the sequence in which developmental operations occur.

In the strictest sense there is no program guiding development, because there are no rules contained in a structure that is referred to in the way a carpenter refers to a blueprint to build a house. Rules for development can be deduced from an investigation of the processes of development, but there is no need to infer that the system being observed acts the way it does because it has a structure containing rules that it refers to in initiating changes in operations. Positing genetic carriers of rules is, according to Oyama, just such an inference. She states, "...'rules and decisions' are simply our anthropomorphic descriptions of the events we observe" (Oyama, 1985, p. 62). The regularities we observe in development are multiply determined by the dynamics of the system and are a function of the history of the system. Since the regularities are historical and due to dynamic processes they cannot reside in a component of the system. Regularity "is the <u>result</u> of the operation of the system not its cause" (p. 62, emphasis in original).

Adaptive Behavior

The view of the dynamics of a system as its program brings "adaptive" into a new light. From Mayr's view, and that of the modern synthesis, adaptive behavior results from natural selection for genetic programs. Once the genetic programs have been eliminated, and the program is seen as embedded in development, the source of adaptation changes. Adaptive behaviors are still those that best fit an organism to its environment, but they result from the coaction of the organism and its environment. What is selected for is the outcome of a developmental system, a particular set of organism-environment interactions that produce organisms best able to survive and reproduce.

Seeing natural selection as selection for a particular set of organism-environment interactions is very different from the traditional view of the modern synthesis. The modern synthesis sees natural selection as selection for particular traits produced by genetic programs. But those traits are a description of the outcome of development; that is, the outcome of a particular set of organismenvironment interactions. The environmental events traditionally seen as selection pressures are a part of the organism-environment interactions that determine phenotypes. Relative reproductive success is due to competition among phenotypes, and a phenotype's success in reproducing is due to phenotypic characteristics that develop as a result of organism-environment interactions.

Behaviors that contribute to an animal's ability to obtain its goals (i.e. food, predator escape, breeding) are adaptive, and selection will favor those developmental systems that are best able to reach their goals. The relationship between particular environmental variables and particular behaviors can be expressed in terms of goaldirected behaviors. Johnston & Turvey (1980, following Sommerhoff, 1950) present a model for the analysis of goaldirected systems. A goal is obtained when a given behavior (β) occurs coincident with a given environmental condition They term this the focal condition for adaptation. (**\$**). In other words, adaptation (i.e. goal-directed behavior) is a function of the coincidence of a given behavior pattern and a given environmental condition. Expressed in Sommerhoff's terms; $F(\beta, \phi) = 0$. Adaptive behaviors are here defined in terms of a theory of goal-directedness in which a focal condition that includes behavioral and environmental conditions must be satisfied in order for a goal to be reached. Viewing adaptive behaviors as goaldirected behaviors that involve both an environmental and behavioral component gives an ecological description of adaptations. Natural selection alone is not an adequate explanation of adaptive behavior when adaptation is defined in the ecological, animal-relevant terms above. The

relationship between environmental conditions and behavior remains an important aspect of adaptation, but more importantly, the development of that relationship becomes a critical component in understanding how adaptations arise.

Johnston (1982) provides an example of the development of adaptive behavior. In order for a behavior to be adaptive it must occur in a specific environmental context so that the coincidence of a given environmental condition and a given behavior leads to obtaining a specific goal. For example, suppose the particular environmental condition is a food source, and the particular behavior is the behavioral skill needed to exploit that food resource. Suppose, further, that the behavioral skill develops over a period (T_0 to T_k). Developmental responses to the environment early in the period (T_0) will determine the eventual form of the behavior at the time when the food source is present (T_k) . Two parallel sets of events must There must be a reliable change in the environment occur. so that the environment at T_0 reliably predicts the environment at T_k , and the developmental response of the epigenetic system at T_0 must lead to the appropriate behavior at T_k . This parallel progression of environmental and developmental events can occur if the two are coordinated by an environmental event Y_0 at T_0 . Y_0 may be the same as the later environmental condition to which the foraging behavior is adapted, but it need not be; any event

that is reliably related to the coincidence of environment and behavior would serve to coordinate the two. No causal relationship need exist between the earlier and later environmental events, they need only be correlated, and the developmental response to the earlier event must be part of the epigenetic interactions that lead to an adaptive phenotype when the later event occurs. Development is seen here as a progression of epigenetic interactions, leading from one behavioral state to another through the interaction of organism and environment.

The environmental conditions that serve to coordinate phenotype and environment are termed coenetic variables (Sommerhoff, 1950). Coenetic variables may be external, such as day length, or a complex relationship among internal and external variables (Johnston, 1982). Johnston (1982) cites examples of coenetic variables that are dynamic relationships between perceptual processes and external environmental conditions. He cites Held and Hein's (1963) study of visuo-motor development in kittens as an example of a coenetic variable that involves the dynamic relationship of perceptual and external conditions. Held and Hein show that optical stimulation must be selfproduced in order for visuo-motor coordination to develop normally. In this example the coenetic variable (selfproduced optical stimulation) is jointly defined by environmental and organismic factors.

A complex relationship of internal and external variables may also be important for the development of diverse foraging behavior. One way to produce a diverse forager is to develop a "coarse-grained" perceptual system which focuses on the general features shared by a number of food types. Unpredictable fluctuations in food types could affect an animal's perception of the characteristics of various food types, and result in such a coarse-grained perceptual system. These environmental fluctuations would restrict an animal's experience with each type of food, and so limit the amount of information gained about specific features of the food. Thus only general features of the food would be available to guide foraging. Reliance on the general features would lead to diverse preferences because choices would be made on general features shared by a number of foods, and not on more subtle features that could differentiate them. Diverse foraging behavior would result from the dynamic relationship between environmental variables and organismic variables, and would depend on the local conditions in which development occurs.

Genotype and Phenotype

Placing information in the developmental system rather than in genetic programs tends to blur the distinction between genotype and phenotype, a distinction that is very

important for the modern neo-Darwinian synthesis. Housing information in DNA is important for neo-Darwinism because information is passed from generation to generation, or altered across generations, through inheritance or alteration of gene sequences; i.e. genetic programs. The inherited genotype is seen as inviolate to changes in somatic DNA; that is, Weismann's barrier (Weismann, 1883) is absolute. Somatic DNA changes have no effect on heritability as only germ-line DNA is inherited, and it is protected by Weismann's barrier. From this reasoning, acquired characters (involving somatic DNA changes) are not inherited; only the DNA of gametes is passed to the next generation.

Only inherited information can have an evolutionary impact since evolution is defined as a transgenerational change. From the neo-Darwinian position, only genotypic information is important for evolution as it is the only information passed across generations. The need for a strict separation of a genotype containing inherited programs, and a phenotype which is the playing out of those programs is obvious. The vagaries of phenotypic expression caused by environmental effects are not passed across generations, and the species-form remains stable because unaltered genetic programs are protected from the environmental fluctuations that buffet phenotypes. Geno<u>type</u> can be seen as the species <u>type</u>, or form, determined by DNA sequences.

The strict separation of genotype and phenotype can be attacked on the same logical grounds as the separation of genes and environment, and ontogeny and phylogeny. Once genes take their place as interactants in a dynamic developmental system the species-type cannot reside in the genes alone; instead it becomes the outcome of individual development and interactions among individuals. If the genotype is a set of instructions, and the instructions are embedded in a dynamic system involving nuclear, cytoplasmic, and environmental factors, then the genotype is a metaphor for the system. Any special meaning it had In fact, if the genotype is re-defined as this is lost. dynamic system, it cannot be separated from the phenotype. If the phenotype is taken as the outcome of the dynamic system, it, in turn becomes part of the nuclear, cytoplasmic, and environmental interactants that make up the system. Genotype and phenotype are merged.

Inheritance as a Process

The neo-Darwinian view is that hereditary information pre-exists developmental processes, and that the information is tied to particular entities (genes and chromosomes). Oyama (1985) argues that these entities do not posses any meaningful information outside of the developmental process in which they are embedded. Heredity is not, then, the transmission of packets of information but "... rather the ways in which developmental precesses become available to the next generation" (Oyama, 1988, p.264). The regularity and variability of inheritance is provided by the organized and organizing activity of developmental processes. A broadened view of evolution as a change in developmental processes, not just genetic change, is needed.

The process view of heredity does not recognize the traditional separation of organism and environment. Neither can be defined independently as development is a reciprocal process involving organism and environment. The stability of phenotypes across generations is due to the relative constancy of a wide range of factors in an organism-environment system (R. Gray, 1988). Inheritance would include not only genes but also physical properties of the environment such as temperature, humidity, and photoperiod. Inheritance of maternal cytoplasmic factors has been demonstrated to affect the development of bithorax in <u>Drosophilia</u> (Ho, 1984). Chemical traces from parental foraging are passed on to offspring and affect their flavor preferences (Galef & Henderson, 1972). Foraging techniques can also be inherited (Galef, 1985; Norton-Griffiths, 1968). A change in any of these factors,

genetic or "extra-genetic", would cause a change in population mean phenotype. Evolution, in the broader sense stated earlier, would have occurred.

A convinced neo-Darwinist might argue that extragenetic changes are easily reversed and that they must be ultimately fixed in the genome before they can be a major factor in evolution. However, there is no a priori reason that extra-genetic changes are any more reversible than genetic changes. A genetic change originating from a mutation could be reversed by deletion of the mutation, or a reversal of selection pressure could reverse the effects of genetic change within a population. Extra-genetic change may also persist for long periods. For example, a change from marine to terrestrial environments may persist for millions of years (R. Gray, 1988). While genetic and extra-genetic changes will probably occur together, one cannot be said, a priori, to be more stable or reversible than the other. The persistence of extra-genetic change does, however, free the process view of inheritance and developmentally based views of evolution from demonstrations of violations of Weismann's barrier for their acceptability. Whether or not extra-genetic changes are assimilated into the genome they will have an impact on evolution. If adaptations are seen as the outcome of a dynamic developmental system consisting of genes, cells, tissues, organs, experience, and learning, all of these

coactants must be included in a model of evolution. DNA is part of the system, not playing the executive role of a genotypic program, but as one of a number of coacting elements.

Once genotype and phenotype become part of the same dynamic system, evolutionary models of change in population mean genotype, which in turn, produces a change in population mean phenotype, lose their meaning. A model of evolution must now be drawn in terms of changes in the dynamic system of nuclear, cytoplasmic, and environmental changes; the effects of these changes on development; and the effects of developmental changes on population structure. Such a model is presented in Figure 1.

In the model presented here environmental changes will not only act as selection pressures, but will act directly on the dynamics of development. The ecological circumstances in which animals develop will make a significant contribution to phenotypes, and must be considered in an analysis of species-typical behaviors. An ecological view of foraging behavior is necessary for understanding the development of "specialist" and "generalist" foraging strategies.
Figure 1. A model of evolutionary change incorporating cytoplasmic, physiological, genetic, and environmental changes as interactants in developmental processes that result in evolution.



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An Ecological View of Generalists

An ecological view of foraging is concerned with animal-relevant descriptions of foraging environments and behaviors. In this view, animals are seen as actors (Johnston & Turvey, 1980) who possess certain behavioral skills, termed effectivities (Turvey & Shaw, 1979), that allow them to obtain goals such as finding, capturing, eating, and digesting food. An animal's ability to "act on" its environment depends on properties of both the actor and the environment. The particular environmental properties that support particular effectivities are termed affordances (Gibson, 1977), and an affordance structure can be constructed to describe particular environmental properties in terms of the effectivities of a specific Taken together, effectivities and affordances actor. describe an econiche, and provide an animal-relevant description of the environment (Johnston & Turvey, 1980).

From the ecological view, the econiche is the unit of analysis. The econiche cannot be reduced further (into autonomous animal and environmental properties) without destroying the relationship between animal and environment. The focus of an ecological approach to foraging is on animal/environment interactions that determine adaptable, goal-directed foraging behaviors. General rules can be discerned through comparisons of the foraging behavior of a variety of individuals and species who face similar foraging problems (Gottlieb, 1985; Johnston, 1981). General ecological rules such as, "If competition is high specialize" can apply if a variety of animals facing similar problems solve them in the same way.

The ways in which behavioral skills develop becomes a central issue in an ecological view of foraging. As stated earlier, adaptable behavior requires the coincidence of a set of environmental and organismic conditions at some point in time. This coordination takes place through a series of organism/environment interactions that describes a developmental pathway. The organism/environment interactions of development must be investigated in order to understand the fit between an organism and its environment.

Contrasting Approaches to Foraging

The neo-darwinian base underlying investigations of foraging has resulted in a view of generalists that focuses on species descriptions of diversity. An ecological approach, on the other hand, would focus on organism/environment interactions that produce diverse foraging patterns during development. From the ecological view, species-typical foraging patterns result from common developmental histories, not species-typical programs for foraging plasticity. A contrast is made here between the neo-darwinian view of foraging and an ecological view, and support for an ecological view is provided by descriptions of ecological variables that control diversity.

Traditional, neo-darwinian views of generalist and specialist foragers treat foraging strategies as species properties. These species properties are seen as the result of natural selection for genetic programs for varying degrees of foraging plasticity. From this view, the ability of an animal to achieve its foraging goals is due to a property of the animal, by virtue of species membership. The environment acts as selection pressure for specialized or diverse foraging patterns, but does not figure directly in the development of the patterns. The environment serves as support for the unfolding of genetic programs, but does not contribute directly to the structure of the programs during development.

The diverse foraging patterns of generalists are selected for by the changeable environments in which they live. The neo-darwinian view sees the fluctuating environment of generalists as selecting among phenotypic variation in plasticity to produce generalist foragers. The ability to switch food types is selected for, and the focus is on populations or species.

The usual definitions of generalist and specialist are in terms of relative degrees of foraging diversity among species. A continuum of species from extreme generalists to extreme specialists can be constructed from this species-view of diversity. The species continuum, however, tells us nothing about actual foraging behaviors, and masks the high degree of variability in diversity that can exist within a species.

The labels generalist and specialist imply that species are aggregates of identical individuals, each of which exhibits the species-pattern. Species, however, are aggregates of highly diverse individuals, and only rarely is a behavior pattern found in all members of a species. Kuo (1976) argues that the variability among individuals is so great that "... we can hardly group them into categories and call them species-specific..." (p.18). Labels like "generalist" and "specialist" discount individual variability, and produce a distorted picture of foraging diversity among and within individuals.

Partridge (1976) points up the problems with speciestypical views of foraging patterns. She notes foraging differences among sex and age classes, dominance ranks, and individuals. In the face of this variability in foraging patterns within a species, it is difficult to see which foraging patterns could be called species-typical.

The concept of species-typical

Many species have been described in terms of typical behavior patterns; i.e. monogamous species, polygynous species, generalist foragers, specialist foragers, etc. The labels monogamous and polygynous, and generalist and specialist are descriptions of species-typical mating and foraging strategies.

The related terms species-typical and species-specific both imply that most members of a species exhibit a particular behavior. While species-specific behaviors are restricted to a single species and the same species-typical behaviors can be found in a number of species, both species-specific and species-typical imply that most members of a species exhibit a given behavior. Lorenz (1970) refers to "species-specific instinctive patterns" (p. 76) in describing invariant behavioral characters. Certain aspects of the phenotype are present in all members of a species (except those exposed to "bad rearing"), and may be found only in that species. Tinbergen (1963), commenting on Lorenz's view of behavior patterns as organs, states that "...each animal is endowed with strictly limited, albeit hugely complex, behavior machinery which (if stripped of variations due to differences in environment during ontogeny, and of immediate effects of a

fluctuating environment) is constant throughout a species or population." (p. 414).

A very different view is that of Kuo (1976) who states that the stereotypy of species-specific behavior patterns disappears on close examination of the behavior. He states that behavioral variability among individuals within a species, and also within individuals repeating behavior patterns, is so great that the term species-specific should be abandoned, and replaced with species-typical or speciescharacteristic. The latter terms are less predeterministically loaded, and allow for the view that species-typical behavior results from uniform epigenetic interactions in the development of individual members of a species. Sex and age class differences in foraging behavior illustrate the range of variability that can exist within a species (Partridge & Green, 1985). Consistent individual differences in foraging strategy have also been observed, and in the case of coal tits (Parus ater) have been related to differences in wing and tarsus length (Gustafsson, 1988). Both of these morphological features are part of the epigenetic interactions that determine foraging habitat and technique used by the birds.

Similarity in behavior patterns of individuals within a species would result from similarity of development, that is, in similarity in organism/environment interactions. The species-typical response of Peking (<u>Anas</u> platyrhynchous) ducklings to the maternal call is dependent on the duckling's experience of hearing its own vocalizations (Gottlieb, 1976a). What makes the response ubiquitous among individual ducklings is their common experience. Species-typical, then, refers to the probability of an individual exhibiting a given behavior pattern, and this probability is dependent on the presence or absence of a common developmental history.

Gottlieb (1976b), in a paper on the roles of experience in development, uses "... species-typical in the normative or descriptive sense" (p. 25). Only ducklings who have the common history of hearing themselves vocalize will develop the species-typical response. The importance of a common developmental history for development of species-typical behavior means that species-typical behaviors are not pre-determined, or pre-programmed, but are descriptive of the most common behavior pattern in a population. In practice, species-typical refers to the probability of observing a particular behavior. For a species to be labeled typically monogamous, one would survey a population and calculate the proportion of monogamous versus polygynous matings. If most observations were of monogamous matings, then the species-typical mating pattern would be monogamy. Species-typicality is a statistical expression of the probability of observing a particular behavior, or the proportion of a population

exhibiting a particular behavior. Species-typical behavior does not require a pre-determined, guiding program.

However, the statistical nature of species-typicality creates several problems analogous to sampling error. How does one decide which subset of the population best represents the population or the species as a whole? If one observes only adult males, for example, one may get a very distorted view of the behavior of the species as a A particular behavior pattern can vary widely among whole. individuals, sex classes, age classes and/or dominance classes (Partridge & Green, 1985). Differences in behavior patterns among individuals are reflected in the terms facultative and opportunistic polygamy (Ford, 1983). Trivers (1972) defines a polygamy threshold that is set by environmental conditions (operational sex ratio, synchronization of fertility etc.). The breeding strategies of individuals are determined by these environmental conditions, and will vary with different environments. The term facultative polygamy reflects this variation in mating strategy with variation in environment. To say that a species is typically facultatively polygamous really says that individuals respond to local environmental conditions that determine mating strategies. No single strategy then, is typical of the species, but there are strategies that are typical of individuals in particular environments. The same sort of ecological regularities may

underlie foraging diversity, and ecological rules may describe differences in foraging diversity better than a continuum in species-typical behavior from generalist to specialist.

Generalist Foraging

A task description (Johnston, 1981a) of the foraging problems animals face must be made before questions of how they solve those problems can be addressed. The basic problem is, of course, to obtain sufficient calories, proteins, and minerals to sustain metabolic processes. The problems faced by generalists and specialists in doing this, however, differ. While both generalists and specialists must find and recognize food, the way in which they solve the problem may differ. The fluctuating environments of generalists require that they be able to recognize a wide variety of items as food, or to ignore small, irrelevant differences among foods. The number of items specialists must recognize is smaller, or may require attention to more subtle differences among foods.

Generalists are often called "Jacks of all trades, and masters of none" (L. Gray, 1985), referring to their diverse diets, and relative inefficiencies compared to specialists. Natural selection for "general purpose" foraging techniques would produce individuals who could use a variety of food types that require similar foraging techniques, but efficiency for obtaining a given food would be lowered by the requirement of having to deal with a number of foods.

Evolution of differences in diversity of foraging patterns has been demonstrated for two sub-species of deer mice (Peromyscus maniculatus blandus and P. m. borealis) (L. Gray, 1979). These two sub-species are found in very different habitats. P. m. borealis lives on the northern prairie of North America, a much more variable environment than the southern desert habitat of P. m. blandus. Gray raised each sub-species under identical laboratory conditions, and tested their diversity in approaching a food source (search), acquisition of food (foraging technique), and consumption of food (choice of food type). P. m. borealis was more diverse than P. m. blandus on all three measures. Gray concludes that genetic differences between the two sub-species, resulting from the differing selection pressures of their ancestral environments, accounts for the differences in diversity they exhibit in the laboratory.

Besides genetic differences, differences in experience among individuals in the same species can affect foraging diversity and efficiency. Partridge & Green (1987) exposed one group of jackdaws (<u>Corvus monedula</u>) to experience with a single foraging task, and another group to experience

with three different tasks. Comparisons of efficiencies of the two groups showed a significant difference, with the generalist group less efficient than the specialist. Natural selection for a general-purpose technique of the generalist jackdaws will not explain the difference between the groups, as the birds share a common phylogenetic history. This study indicates that differences in the experience of two groups within the same species can produce a difference in efficiency.

The task description for the two groups in this experiment differed. The specialists had only a single problem to solve, (how to best employ a single technique), while the generalists had a more complex problem, (how to get food using a variety of techniques). The difference in tasks for the groups is the difference in tasks for generalist and specialists in general.

The continuum from generalist to specialist foragers may be better stated in terms of ecological control over foraging patterns than in terms of species differences. Many desert rodents show specializations for foraging microhabitats (Brown & Lieberman, 1973; Price, 1978; Reichman & Oberstein, 1977; Rosenzwig, 1973). Ecological changes in microhabitats have been demonstrated to alter their use by a variety of rodent species. Thompson (1982) provided artificial shelters that in effect reduced the distance between desert shrubs. As a result the foraging

patterns of two desert rodent species (Dipodomys merriami and <u>Perognathus longimembris</u>) were significantly altered. P. longimembris shifted its foraging strategy away from scattered and toward clumped seeds. Price (1978) reduced competition between <u>Dipodomys</u> merriami and six <u>Perognathus</u> species in enclosures, and found that the <u>Perognathus</u> species became more generalized in their use of microhabitats in the absence of D. merriami. The diet diversity of another desert rodent (Dipodomys ordii) may also be affected by competition. The diet diversity of Dipodomys ordii changes with the presence or absence of congeneric competitors. D. ordii in areas with few other Dipodomys species have a more diverse diet than D. ordii in areas where competition is greater (Brown and Lieberman 1973). Diet diversity is, therefore, affected by the ecological conditions imposed by competition on this species. The deer mouse <u>Peromyscus</u> <u>maniculatus</u> responds to population density with increased diet diversity (Van Horne, 1982). Again, the degree of generality of a species is determined by environmental conditions.

The references above to <u>D. ordii</u>, <u>P. maniculatus</u>, and other species are not to specific individuals, but to general characteristics of populations. This use of species-typical language is in reference to what Johnston (1981b) calls the "species-typical individual" (p. 291). This reference is not to a single organism, but to a

composite "individual" that represents the commonly observed characteristics of a species. Individual D. ordii or <u>P. maniculatus</u> may or may not exhibit the dominant or species-typical foraging patterns. Whether they do or not may depend on their individual developmental histories. For example, Burghardt (1967) reports that snapping turtles (<u>Chelydre serpentina</u>) form preferences for the food type they are exposed to when they first begin feeding. This preference is likely due to the particular food type consumed during their first meal (Burghardt & Hess, 1966). The food type that composes the first meal would vary as a function of food availability. Each turtle would have a preference for the food type of its first meal, but as a group (or species) they may appear diverse in their food choices due to individual differences in early experience with different food types comprising the first meal. Fox (1972) reports that dominant wolf cubs (Canis lupus) are more likely than less dominant cubs to kill rats on their first exposure to them, and to attack a moving object. The propensity to attack a moving object and kill prey is affected by social dominance, and would, therefore, vary between dominant and less dominant individuals. Marine iquanas (Amblyhynchus cristatus) use different foraging strategies depending on their body size (Trillmich & Trillmich, 1986). Small iguanas feed exclusively in the intertidal zone, large iguanas in the subtidal zone, and

intermediate size iquanas in both intertidal and subtidal The relationship between body size and feeding zones. strategy is complex, involving the amount of time it takes for an iguana of a given size to warm up after foraging in water, and the effect of early morning and late afternoon tides on available foraging and warming-up time. As a species, marine iguanas show at least three foraging strategies, but individual iguanas show much less diversity. No one strategy could be said to be speciestypical. If both intertidal and subtidal feeding are taken as species-typical, then only intermediate size iquanas would exhibit species-typical foraging techniques. Small size juveniles restricted to intertidal feeding and large adults (mostly males) restricted to subtidal feeding would not be species-typical foragers. Species-typical descriptions of these reptiles would be misleading, and it would be more accurate to describe iguana foraging in terms of ecological factors rather than a species-typical generalization.

A number of studies with, a variety of species, have shown individual specializations in foraging behavior. Specialization for foraging techniques among individuals of avian species has been demonstrated for great tits (Krebs, MacRoberts, & Cullen, 1972; Partridge, 1976a; Partridge & Green, 1985, 1987), herring gulls (McCleery & Sibley, 1986) oystercatchers (Norton-Griffiths, 1967), and wood pigeons

(Murton, 1971). Individual specialization for food type has been demonstrated in zebra finches (Rabinowitch, 1968), and rock doves (Giraldeau & Lefbvre, 1984), of habitat selection in linnets (Gluck, 1984) and pigeons (Brown, 1968). Individual foraging specialization has also been demonstrated for garter snakes (Drummond, 1983), trout (Bryon & Larkin, 1972), bumblebees (Oster & Heinrich, 1976: Heinrich, 1976; Darwin, 1876), seed-harvester ants (Rissing, 1981), housemice, wood mice, bank voles, and short tailed voles (Partridge, 1981), white-footed mice (L. Gray, personal communication), cats (Caro, 1980), and sheep (Arnold & Maller, 1977). While the diet bredth of these species varies considerably, they all show individual specialization for food type, or foraging technique.

The above examples suggest that individuals may or may not exhibit species-typical foraging patterns. Whether they do or not depends on whether or not they share a common developmental history (e.g. exposure to the same food type, similar dominance, similar size). To characterize a species as generalist or specialist tells us very little about how various foraging behaviors are distributed within a species, or about the ecological and experiential factors that determine this distribution. The continuum from generalist to specialist only refers to differences among species, and may hide the potentially wide range of intra-species variability in foraging diversity that could result from ecological determinants of the development of foraging patterns. An investigation of ecological variables is necessary, therefore, in order to understand how diverse patterns of foraging behavior develop, or to put it another way, to look at the origin of the "generalist" phenotype. The continuum from generalist to specialist then, must reflect not just species differences, but the effect of ecological variables on the diversity of foraging behaviors within species.

Local Adaptations

The aim of the analysis of foraging diversity from a neo-darwinian perspective is to investigate species-typical solutions to changes in food supply. The solutions are reached over generations through selection for adaptive patterns. The aim of an ecological analysis is to provide "a set of local principles of adaptation" (Johnston, 1982, p. 135). The task description specifies the nature of the problems an animal has to solve, and the aim of the analysis is to show how development of the solutions takes place. The foci of the two approaches are very different. The neo-darwinian focus is on selection operating in populations; on species-typical solutions. The problems encountered with species-typical descriptions of generalists have already been discussed. The advantage of

the ecological approach is that species-typical descriptions can be made in terms of ecological regularities (affordances), thus maintaining a focus on organism/environment interactions that produce adaptive behavior.

Johnston (1982) uses "local" to refer to the specific solutions a given species arrives at during development. The generality of local adaptations can only be seen through comparisons of species with similar task descriptions. It seems reasonable that local adaptations would also apply to smaller groups than species. If microhabitat differences exist among various groups within a species, then the local adaptations of the groups may differ. For example; in the marine iguana foraging behavior described earlier, three distinct groups are evident, each with a different microhabitat and foraging strategy. The differences among the groups is likely due to different solutions to the common problem of warming up after foraging in cold water. The differences in body size of animals in the three groups, however, provides a different set of organism/environment interactions for the various groups. Each groups reaches a different solution to the problem; a solution that involves different foraging strategies. For marine iguanas, three microhabitats, and three micro-local adaptations can be described.

The ecological approach insures that processes that underlie the correspondence between an animal's behavioral skills and the requirements of its natural environment will be addressed. In this way general principles can be derived from shared relationships between animals and their environment; not from invariant properties of species. Deducing general principles from an ecological approach better describes generalist foraging patterns because of the high degree of intraspecific variability in diversity in generalist species. A continuum from specialist to generalist could be constructed based on guantitative differences in organism/environment relationships. So, for example, a continuum could be constructed based on exposure to fluctuating food sources; with specialists at the low fluctuation end, and generalists at the high end. This continuum has the advantage of scaling individual as well as species differences in diversity, and ties foraging diversity directly to fluctuations in food supply.

The importance of developmental questions in the ecological approach insures that it will provide a more complete understanding of foraging than could be reached from a neo-darwinian approach. Questions about the role of unpredictable experience with food resources in foraging diversity become critical. One way to approach this question is to investigate the effects of unpredictability

on an animal's perception of the value of food items and/or foraging techniques.

Preferences and Perception

Foraging animals have access to environmental information about the location, guality, and work involved in obtaining food. This information is in the form of physical attributes such as color, sound, size, and distance, providing cues that can be used to guide foraging. The physical attributes of food items can be used to discriminate among them. The value of food items (calories per unit handling time or net energy gain) can be associated with the physical attributes of food, and preferences can be formed based on the perception of these cues. An animal's survival depends on appropriate responding to environmental cues, some of which vary continuously from one extreme to another. For example, prey size affects foraging choices in blue gill sunfish (Werner & Hall, 1974) and great tits (Krebs, Erichsen, Webber, & Charnov, 1977). Many desert rodents respond to size cues in choosing seeds, some selecting large seeds (kangaroo rats) and some small seeds (pocket mice) (Brown, Reichman, & Davidson, 1979). The physical continuum of size is an environmental dimension.

The physical continua of environmental dimensions are perceived by the animal as subjective dimensions that can influence foraging choices. Continuously varying environmental cues can be ranked, or ordered, along a subjective dimension, allowing comparisons among them so that perceptual similarities or differences among cues can be established. Subjective ranking of cues is analogous to the psychophysical ranking of tones that differ in loudness, or lights that differ in brightness. The subjective, psychophysical scale of these ranks has a relationship to a physical scale so that changes within a physical dimension are related to changes within a subjective dimension. Changes in sound pressure are perceived as changes in loudness so that the perception of loudness is a function of sound pressure. Lincoln Gray (1985) suggests that animal's preferences for various cues are determined by the perceived similarity among the cues. Cues that are perceived as similar are chosen equally often; i.e. equally preferred. Perceiving similarity requires a comparison of cues and subjective ranking of the cues.

Implicit in this approach is that animals' responses are determined not only by the physical attributes of food but also by the outcome of responding to various cues. Discrimination may be based on the physical attributes of food alone, but preferences must include the outcome of

responding to the cues. Irwin (1958) makes a distinction between discrimination and preference. He states that animals act toward objects based on the "environmental situations" in which the objects are found, and based on the "outcomes" of responding to the objects. Environmental situations are very loosely defined; they may be "sets of 'stimuli'" or any situation that is "describable in the language of science, whether physical, biological or social" (p. 152). An act is any observable "change within the body of an animal." Outcomes are the consequences of acting, such as obtaining food or being praised for a correct answer. Irwin states that "... the objects of preference are never identical to the objects of discrimination. The former are features of the situations that exist before the organism acts" (p. 162). This distinction between discrimination and preference implies that animals may respond to environmental cues in two ways. Perception of differences among cues that vary along a subjective dimension would be sufficient to discriminate the cues, and the underlying dimensions of discrimination could be subjective dimensions of physical differences. The underlying dimensions of preference, however, would be subjective dimensions of the outcomes of responding to these varying cues. Preferences for foods of different sizes (which can be linearly arranged based on the physical property of size) may not increase linearly with size.

Taking small or large foods may be less profitable than taking medium-sized foods. Both small and large sizes could have handling times that make them less profitable than medium-sized foods. If this is true, then the consequences of responding to different sizes are described as a U-shaped, not a linear function. The underlying dimensions of preference are those of outcomes, dimensions such as profitability, efficiency, and palatability. Environmental cues are only "useful" if they can distinguish among objects having different outcomes. The subjective ranking of cues should be based on the different outcomes of responding to those cues.

Preferences for continuously varying cues are often single peaked, so that one value along a subjective dimension will be preferred, and preferences for other values will decrease on either side of the peak (L. Gray, 1985). Single-peaked preference theory (Coombs & Avrunin, 1977) states that the underlying subjective structure determining preference can be derived form an animal's responses. Choices are made by comparison of cues ordered along subjective, and in this case perceptual, dimensions. Optimal foraging theory also predicts single-peaked preferences, and that an animal's foraging preferences should be predictable from environmental conditions (Schoener, 1971). Optimal foraging theory assumes that feeding strategies are subject to natural selection;

optimal foraging strategies enhance survival, thus increasing fitness, and will come to dominate in a population. Fitness is maximized when the net energy gain per unit feeding time is greatest; that is when there is the highest energy gain for the least cost. Ecological factors such as the size, distribution, and caloric content of food items will affect the net energy gain from various food items. In order to forage most profitably, an animal should show a preference for food items with the highest net energy gain. Both the psychological (single-peaked preference) and ecological (optimal foraging) theories of preference see choices as being governed by three equivalent steps: 1) ordering available choices along a dimension, 2) describing the costs and benefits of responding to available choices as a function of the underlying dimension, and 3) solving for optimal or maximal preference (L. Gray, 1985). The equivalence of singlepeaked preference theory and optimal foraging theory makes it possible to identify critical environmental dimensions from subjective dimensions of preference. Forming appropriate preferences is essential for survival; the subjective ranking and the perception of similarity among cues for value is necessary for the formation of preferences. Generalists act as if they perceive little difference among the foods they eat, while specialists act as if large differences exist. Differences between

generalists and specialists may be due to differences in the way each performs the three steps above.

Any factor that affects the ordering of choices, or the costs and benefits of choices, will affect preferences. An animal's experience with various foraging choices could greatly affect its perception of the costs and benefits associated with those choices, and the ordering of choices along a subjective dimension.

Two factors can determine the perception of differences among cues; one is the variability among cues (perceived similarity) and the other is the opportunity to compare the cues. If cues vary, they will be perceived as different, and some will be preferred over others. On the other hand, if cues do not vary, they will be perceived as similar and will be equally preferred. Diverse foraging behavior would result from the perception of similarity among cues associated with various foraging choices.

Perceiving similarity requires ordering cues along a relevant subjective dimension, and ordering cues requires the opportunity to compare various cues. An animal living in a variable environment (which should promote preferences) may fail to develop preferences if it is prevented from making comparisons among the various cues in its environment. Diverse foraging would result from either the perception of similarity among cues (foraging choices)

or from preventing comparisons among differing cues and thus preventing the perception of the differences.

Animals make choices among food types and among foraging techniques. I will focus here on the ways in which experience affects the opportunity to compare various foraging techniques and thus the perception of similarities and differences among them.

Factors affecting the perception of similarity among foraging techniques

Cues that lie in close proximity along a subjective dimension of foraging outcomes are perceived as similar. If foraging animals base their choices on the net energy gain of food, then those foods having equal net energy will be equally chosen. Cues such as size, color, handling time and caloric content can be correlated with the net energy gain of various foraging techniques, and similarity among cues for net energy gain will determine preference.

Net energy gain is determined by the caloric content of food and the energy required to obtain it. If, for example, similar size foods have similar caloric content, and similar handling times, then they will have similar net energy gains. Size would be a reliable predictor of net energy gain, and size differences would be a relevant dimension for distinguishing among foods of different net

energy gain. On the other hand, a single food type may be found in a variety of situations that require different foraging techniques. For example, ripe berries could be found at the ends of small branches, or on the ground. The energetic difference between climbing for a berry and picking it up off the ground would affect the net energy gain from the berry. For foods of equal caloric content, differences in the cost of foraging techniques would affect the value (i.e. net energy gain) of the foods. Factors determining the costs of foraging techniques will affect the perceived similarities of the techniques (and cues associated with those techniques) and, therefore, affect preferences for the techniques.

Quite aside from the energy gain from food, familiarity with a food type has been shown to produce a preference (Burghardt, 1967; Ferrell, 1984; Fuchs & Brughardt, 1971; Galef, 1985; Kuo, 1976; Rabinowitch, 1968). Familiarity with a foraging technique also produces a preference for that technique (Partridge, 1976a). If familiarity is the relevant dimension underlying preference animals should prefer those foraging techniques with which they have had the most experience. The "value" of a foraging technique may depend on the number of times an animal uses a particular technique to successfully obtain food. Preferences should be formed for those techniques that produce the greatest number of successes, and equal PLEASE NOTE:

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techniques. An animal faced with a choice between two techniques could compare the efficiencies of the techniques, and choose the most efficient. Preference would be for the most efficient technique whether it was familiar or not. Practice could also produce diverse preferences by making techniques similarly efficient. Practice with a difficult, inefficient task could increase its efficiency to make it similar to initially easier tasks, and thus promote diversity.

Factors affecting the opportunity to compare foraging techniques

Ranking foraging techniques along an underlying dimension requires that the various techniques be perceived as different and that they be compared with each other to establish their relative ranks. Preventing comparisons among techniques (or cues associated with those techniques) will prevent ranking and thus prevent the formation of preferences. The unpredictable experience with various techniques or cues that fluctuating environments provide may prevent comparisons and result in diverse preference. Fluctuating environments may provide an unpredictable succession of experiences with various cues, requiring comparisons to be made across different events; successive experience is less effective in establishing discrimination

than is simultaneous experience (Mackintosh, 1974; Sutherland & Mackingtosh, 1971). An animal who encounters different cues on different foraging trips would have to rely on successive information to discriminate and rank those cues. If successive foraging trips are separated by a sufficient time interval, comparisons among cues encountered on different trips would be prevented. How long an interval is "sufficient" would depend on the species and individual in question. Kacelnik and Krebs (1985) include a "memory window," representing the memory span of a foraging animal, in their models of optimal foraging. In some optimal foraging models such as the linear operator (Bush & Mosteller, 1955) and relative payoff sum (Harley, 1981) this memory window determines the amount of recent information available to an animal for making choices among patches. The same concept of a memory window can be applied to establishing preferences for foraging techniques. If the time between experiences with different foraging techniques is greater than the memory window, no comparisons among the experiences can be made. Without the opportunity to compare techniques, differences among them could not be established, and specializations would not occur.

Gray and Tardif (1979) show that deermice given access to different food types on different days develop diverse preferences. If the diversity of preference shown by these

mice is due to the lack of opportunity for comparing the food types, then a day's separation would be sufficient to prevent comparisons in deermice. This is not to say that mice have no memory of the previous day's food, but just that the interval between experiences with various foods interferes with making comparisons among the cues associated with the different foods. As stated earlier, preventing comparisons of choices (or cues) will prevent ranking of the choices, and thus produce diverse foraging.

Three factors have been outlined here as important for the development of diversity in preference for foraging techniques:practice with a given technique, the efficiency of that technique, and the opportunity to compare various techniques. The relationship between practice, efficiency, opportunity to compare, and preference is illustrated below.



Starting at the right hand side of the figure above, preference depends on the efficiency of various techniques; presumably the most efficient techniques will be preferred. Efficiency, however, can only determine preference if there is the opportunity to compare among various techniques, and their relative efficiencies determined. Factors other than efficiency (? above) can also contribute to preference. These factors could be food scarcity, palatability of the foods obtained by various techniques, exposure to predators, or other unknown factors. The efficiency of each technique is determined by prior experience with it (practice) which should increase efficiency (assuming that efficiency is not already at its ceiling). Thus, practice will indirectly affect preference because of its effect on the efficiency of various techniques. Efficiency is also affected by the task characteristics, some tasks being "inherently" easier than others. Techniques using motor patterns that are well developed due to an animal's normal activity (foraging or otherwise) should be easier (i.e. more efficient) than those requiring novel patterns. Undesignated factors such as individual morphology, propensity to climb, or "fear" of heights, could also contribute to efficiency differences among tasks.

The experiments reported in Chapter II examined the roles of practice, efficiency (handling time per gram of food), the opportunity to compare the efficiency of

foraging techniques, and food scarcity on the development of preferences in the white-footed mouse (<u>Peromyscus</u> <u>leucopus</u>). The hypotheses tested were that 1) animals will prefer the tasks on which they are most efficient, 2) practice with an inefficient technique will make that technique similar to an already efficient technique, and, therefore equally preferred, 3) the opportunity to compare techniques is necessary in order for preferences to be formed and 4) food scarcity will promote diversity of preferences.

Chapter II

Methods and Results

An animal faced with a variety of foraging tasks can rank order the techniques they require along an underlying dimension (L. Gray, 1985). Choices among the techniques can then be made based on their relative ranks, with the highest ranking techniques being most preferred. Techniques perceived as similar (of equal rank) should be equally preferred. A hierarchy of techniques is only possible when some are perceived as different from others along an underlying dimension such as efficiency or familiarity. Experience that diminishes the perceived difference among techniques should reduce preferences among them, while experience that enhances differences among techniques should promote preferences.

Efficiency is a dimension along which techniques can be ranked, and has been suggested to underlie preferences for foraging techniques (Caro, 1980; Partridge, 1976a,b; Partridge & Green, 1985). Experience that affects the efficiency of a technique should affect its rank in a hierarchy of techniques. Practice with a technique generally increases its efficiency (Partridge & Green, 1985), and should raise its rank in a hierarchy of techniques. Practice with an inefficient technique should raise its efficiency, and make it more similarly efficient to other, already efficient techniques. Diminishing the difference among the efficiencies of techniques should increase their similarity, and make them more equally preferred.

Familiarity alone, independent of efficiency may also be a dimension underlying preference for foraging techniques. Familiarity has been show to produce a preference for food type (Burghardt, 1967; Fuchs & Burghardt, 1971; Ferrell, 1984; Kuo, 1976; Rabinowitch, 1968), and for foraging techniques (Partridge, 1976a). If familiarity is a dimension on which techniques are ranked, then animals should prefer those techniques with which they are most familiar. Early experience with a single task should produce a preference for that task, even if the experience does not increase its efficiency.

Implicit in the idea that animals base preferences on the rank order of techniques is that they have the opportunity to compare the techniques in order to rank them. Unpredictable fluctuations in the circumstances in which food is found may interfere with an animal's ability to order the various techniques required by the different circumstances. Unpredictable access to different food types has been shown to produce diversity of preference for the foods (Gray, 1979; Gray & Tardif, 1980). If fluctuations in access to foraging tasks that require
various techniques prevents ranking of the techniques then it should promote diversity of preference for the tasks just as fluctuations in access to different food types has been shown to produce diversity in preference for the foods.

General Methods

Subjects. All subjects in these experiments were whitefooted mice (Peromyscus leucopus), from the first- to fifth- generation laboratory reared. The breeding stock for the subjects consisted of wild-caught adults trapped in Guilford County North Carolina, and laboratory-reared adults obtained from the Peromyscus Breeding Stock Center, University of South Carolina. Breeding stock were housed in plastic laboratory cages (7.5 X 18 cm), and provided with nesting material, litter (Sanocel Bed-O-Cob), ad lib water and Purina Mouse Chow. Breeding pairs were continuously housed together, and checked daily to establish dates of birth for litters. Litters remained with their parents from birth until weaning (at 21 days old). A standard litter size of four was maintained by culling litters during the first week after birth. Excess mice were culled by either killing (with Halothane gas) or cross-fostering into other litters. In one case an experimental litter was increased from 3 to 4 by crossfostering, all other cross-fostered mice were put into

litters not used in the experiments. Mice were crossfostered into litters of the same age ±1 day. The normal litter size for <u>P</u>. <u>leucopus</u> is 4, and few larger litters were produced; culling was only occasionally necessary. <u>Procedure</u>. All of the experiments consisted of two phases, juvenile and adult. The juvenile phase lasted from weaning (21 days old) until adulthood (50 days old). During the juvenile phase, animals in each experiment were exposed to different feeding regimens (described separately below). As adults all mice were tested for efficiency and preference for foraging techniques using a common procedure (described below).

After weaning, mice were individually housed in large plastic tubs (38.75 X 60 X 35 cm), covered with .0625 cm mesh hardware cloth. The tubs were kept in the colony room where the mice were born. All animals were provided with bedding, nesting material, and ad lib water. The mice were fed exclusively on shelled sunflower seeds. The method for providing seeds differed for each treatment group, and is described for each below. Mice were provided with 50 seeds (2.5 g) each day (except for the Fluctuating group, see below), an amount more than sufficient to maintain them and support growth.

At 50 days all mice were transferred from the tubs into individual plastic laboratory cages (7.5 X 18 cm), and provided with bedding, litter, and water. The mice

remained in the colony room overnight and were then taken into a testing room where they were tested for efficiency and preference. Efficiency and preference testing was conducted in the same way for all mice.

During efficiency and preference testing, individual mice were given access to a wooden foraging arena (30 X 60 X 30 cm), with a glass front to allow observation. The arena had a removeable lid made from a wooden frame covered with hardware cloth. A mouse's home cage could be attached to the arena by a plastic tube (5 cm diameter, 15 cm long). Five foraging arenas were constructed, allowing up to 5 mice to be tested at a time.

Experiment 1: Naive Efficiency and Diversity of Preference

Experiment 1 tested the efficiency of "naive" <u>P</u>. <u>leucopus</u> on each of three foraging tasks (Hang, Lift, and Slide, described below), determined preferences among the tasks, correlations between efficiency and the number and weight of seeds taken from the three tasks, and the diversity of preference among the tasks. Experiment 1 provides a baseline of efficiency and preference for animals without prior experience with the foraging tasks.

Methods and Procedure

Three litters (12 mice) were bred, reared, and housed under the conditions described in the General Methods. During the Juvenile Phase they were provided with ad lib access to sunflower seeds placed in a small plastic cup on the floor of their cage. At 50 days efficiency testing began.

Foraging Tasks

Three foraging tasks were used in this experiment; Hang, Lift, and Slide. In the Hang task animals were required to retrieve seeds hanging below an aerial walkway, 5 cm wide and 60 cm long, suspended 15 cm from the floor of the arena. Fifty 2.75 cm cotter pins were firmly stapled to, and hung beneath the board. A single sunflower seed was attached to the distal end of each cotter pin, and the pins were secured so that a mouse had to hang upside down in order to retrieve the seeds. Steps in the corner of the arena provided access to the walkway, but mice could easily jump from the floor to the suspended board. The Lift task required a mouse to remove a sunflower seed from a 30-mm plastic centrifuge tube with an 8-mm opening covered with a cap. The tubes were split at the rim to allow the cap to be more easily removed. Each tube was glued into a hole drilled into a wooden board with approximately % of the tube extending above the board. Securing the tubes to the board allowed only the caps to be removed, leaving the tube in place. The Slide task required a mouse to slide a plastic cover off a 10-mm hole bored in a piece of wood in order to remove a seed. Each task contained 50 sunflower seeds, each in an individual hole, centrifuge tube, or cotter pin.

The foraging tasks were constructed so that each required a different technique and was analogous to a naturally occurring foraging problem. The Slide task requires the skills a mouse may use to scrape away debris to reach seeds hidden under forest litter. The Hang task mimics the problem of reaching berries hanging from a bush, and the Lift task mimics cracking open seed coats or insect pupae to reach the larvae. Wild <u>P. leucopus</u> are likely to encounter all of these types of foraging problems (Wolff et al, 1985). Pilot data showed that mice will perform these tasks, and that they will form preferences among them.

Efficiency Testing

Measures of each mouse's efficiency for removing seeds from each of the 3 foraging tasks were obtained. For 3 days prior to efficiency testing all mice were given access for 1 hr per day to a foraging arena containing three dummy

foraging tasks. Seeds could be obtained from the tasks from uncovered holes in the Lift and Slide dummies, and lying loose on top of the Hang walkway. The three days provided habituation trials with the arena, but no experience performing the foraging tasks.

Efficiency was measured as the weight in grams of sunflower seeds eaten from each task over the time spent obtaining seeds. Two efficiency measures were calculated; Remove efficiency (RE) and Total efficiency (TE). RE was calculated using the time taken to remove a seed from a task; and TE was calculated using the time to remove and eat a seed. Two efficiency measures were calculated to see whether preferences were based on the efficiency of access to seeds in the 3 tasks (RE), or on a more general measure of differences in nutritional gain among the tasks (TE). The Hang task differed from the other two in that seeds could be partially eaten without removing them; unremoved, partially eaten seeds were included in the calculation of TE, but not in RE. All seeds removed from the tasks, whether eaten or not, were included in the calculation of A silent stopwatch was used for timing. Timing began RE. when a mouse's nose contacted either a centrifuge tube, a plastic cover, or a cotter pin. Timing ended when the mouse stopped eating, or dropped the seed. Mice invariably groom after eating, providing a clear signal for the end of an eating bout. Only instances in which a seed was

successfully removed were included in the efficiency measure. All efficiency testing was done under red light, and each mouse was given access to a single task for 1 hr per day. Testing continued with a single task until a mouse had either taken 10 seeds, had 10 eating bouts on the Hang task, or had 5 trials with a task. Mice were rotated through the three tasks, one at a time, until they had reached criterion on all three tasks. The order of task presentation was counterbalanced across mice within each litter. All mice were given supplemental feeding with approximately 50 seeds every other day in their home cage.

Preference Testing

After efficiency testing was completed, preference testing began. During Preference testing mice were given access to all three tasks simultaneously in the foraging arena. Each mouse was individually tested for 1 hr each day; mice that took only a few seeds were given supplemental feeding in their home cages. Fifty seeds were available from each of the three tasks in the foraging arena, so a mouse could specialize on a single task, or forage diversely and still obtain sufficient food. The measure of preference was based on the number of seeds taken from each task each day, and the weight, in grams, of the seeds. Measures of diversity or specialization were

calculated from the proportions of the number and weight of seeds taken from each of the three tasks each day as described below. The weight of seeds taken was calculated by weighing the 50 seeds before they were loaded into a task, and then subtracting the weight of the seeds remaining at the end of a trial from the pre-trial total weight. Seeds were weighed to the nearest .01 of a gram.

The distribution of responses among the three tasks was analyzed using Shannon's Index of Diversity (Shannon & Weaver, 1964, Gray, 1979); $H' = -\Sigma$ Pi ln Pi, where Pi is the proportion of total daily diet taken from the ith task. H' reaches a maximum when the number or weight of seeds taken from each task is equal; $H'_{max} = 1.10$ for three tasks. If an animal takes seeds from only one task on a given day, H' = 0. Mean H' for the group was calculated by first determining the H' for each trial and each animal (Daily H'), taking the mean of the 15 Daily H's for each animal (Mean Daily H'), and calculating a group mean of the individual Mean Daily H's (Gray, 1979, unpublished MS, unpublished Doctoral Dissertation).

The distribution of responses among the foraging tasks can be expressed in terms of the dominance of some tasks over others, or in terms of the perceived similarity among the tasks. The perceived similarity of the tasks is due to the proximity of the tasks along a subjective dimension of foraging outcomes. Both proximity and dominance can be

inferred from preferences (Gray, 1979, 1985). The dominant task is the one from which the greatest number or weight of seeds is taken. For example, an animal could use one task 100% of the time and another task 0%, or it could use one task 51% and another 49% of the time and show dominance of one task over another in both cases. The distribution of responses among the tasks in the two situations, however, is very different. A proximity measure (such as Shannon's Index described above) reveals an animal's perception of the similarity of the tasks. Dominance would not differ between the two situations of 100% vs 0%, and 51% and 49%, but proximity would. The diversity of preferences is better measured by proximity than dominance (Gray, 1979, 1985), but dominance can be used to illustrated overall preferences.

Results

Diversity of Preference

The diversity of preference (H') for the Naive group was 0.26 (SE = 0.013), and was taken as a baseline of diversity in the absence of prior experience with the 3 foraging tasks. The diversity of preference for the Naive group did not change over the 15 days of Preference testing (ANOVA F = 1.36, df = 14, P > 0.19). This result

demonstrated that adult experience did not affect diversity, and indicated that the Naive group was a valid baseline against which to test the diversity of the treatment groups in the later experiments.

Dominance of Preference

A Repeated Measures ANOVA of the number and weight of seeds taken from each of the three tasks over the 15 days of testing showed that the total numbers of seeds taken from Hang, Lift and Slide were significantly different (F= 4.34, df = 2, P < .03). Post hoc internal comparisons showed that the number of seeds taken from Lift (NL) was greater than the number taken from Slide (NS), and the number from Slide was greater than the number from Hang (NH) (LSD, α = .05, df = 70). Overall NL > NS > NH. The weight of seeds did not differ among the 3 tasks , nor was there a main effect of Trials, or an interaction between Trials and the number or weight of seeds taken from the 3 tasks. Based on the number of seeds taken, Lift was the dominant task for the Naive group.

Efficiency

Two efficiency measures (Remove and Total) were calculated for each task, giving six measures of efficiency

in all: Remove Efficiency Hang (REH), Remove Efficiency Lift (REL), Remove Efficiency Slide (RES), Total Efficiency Hang (TEH), Total Efficiency Lift (TEL), and Total Efficiency Slide (TES). Mean REH, REL, and RES are presented in Figure 2. The Remove efficiencies differ significantly for the three tasks (ANOVA, F = 20.84, df = 2, P < .001). Pairwise comparisons of the means indicated that the mean RES is significantly greater than the mean REL or REH (LSD, $\alpha = .05$, df = 22). Simple ranking of the three means resulted in REH < REL < RES. Comparisons of Total efficiency showed no significant differences. The comparisons of Remove efficiency showed that Naive mice had different efficiencies for the three techniques required by the tasks, and that the tasks can be ranked in order of efficiency as follows: Slide > Lift ≥ Hang. The lack of a significant difference between REH and REL makes the ranking of Lift over Hang somewhat arbitrary; the ranking given is derived from the means for the Remove efficiency measures. A clear superiority for the efficiency in removing seeds from the Slide task is statistically supported.

The relationship of efficiency and preference was analyzed using Pearson Product-Moment Correlation Coefficient, calculated for each efficiency measure correlated with the number and weight of seeds taken from the three tasks. No significant correlations were found. Figure 2: Mean Remove efficiencies of the Naive group for Hang (REH), Lift (REL), and Slide (RES) tasks.



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Figure 3 illustrates the lack of correlation between Remove efficiency and the total number of seeds taken from each task over the 15 days of testing. The lack of correlation between efficiency and the number or weight of seeds taken over all 15 days of Preference testing might have resulted from experience with the 3 foraging tasks during Preference testing. To determine if an initial correlation between efficiency and number or weight of seeds was present, Pearson Correlation Coefficients were calculated between the efficiency measures for each task and the number and weight of seeds taken from each task during the first 3 days of Preference testing. No significant correlations were found, indicating that efficiency was not related to preference for the first 3 days of preference testing.

Discussion

No animal can be a completely naive forager, but the behavior of the mice in the Naive group gives an indication of the efficiency of inexperienced mice performing the techniques required by the three foraging tasks, and the diversity of their preferences. H' for the Naive group indicated that inexperienced mice were not specializing on any single task. Their perception of the similarity of the techniques required by the various tasks can be best understood in relation to mice with different experience

Figure 3: Mean Remove efficiency and mean number of seeds taken over the 15 days of preference testing by the Naive group. The left panel contains Remove efficiencies for Hang (REH), Lift (REL), and Slide (RES), and the right panel shows the mean number taken from Hang (NUMH), Lift (NUML), and Slide (NUMS).



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with the techniques. Experiments 2 and 3 provide these comparisons. Correlations of the efficiency measures and the number and weight of seeds taken from the three tasks showed that, as a group, Naive mice do not prefer the task on which they are most efficient. Some dimension other than efficiency apparently underlies preference for these mice. The lack of a correlation between efficiency and preference, and the dominance of Lift even though efficiency was greatest for Slide, indicate that, in the absence of prior experience with the foraging tasks, no consistent relationship between efficiency and preference is evident. The lack of early experience with techniques of various efficiencies may have made these mice insensitive to efficiency as a relevant dimension for choosing among the techniques, and contributed to their diversity of preference. Experiments 2 and 3 were designed to provide mice with various types of juvenile experience with the techniques required by the three foraging tasks, and to assess the effects of early experience on efficiency and preference.

Experiment 2: The Effect of Practice on Efficiency and Diversity of Preference

Practice with a technique has been shown to increase its efficiency (Caro, 1980; Partridge & Green, 1985).

Experiment 2 tested the effect of restricted rearing with the Hang task on efficiency for Hang. The Hang Task was chosen for Restricted rearing because it ranked lowest in efficiency for the Naive group in Experiment 1. Also, if animals have equal preference for techniques that are perceived as similarly efficient, then practice with the Hang task may raise its efficiency enough for it to be perceived as similar in efficiency to Lift and Slide. If Hang were perceived as similarly efficient to the other tasks, then they should all be equally chosen, resulting in diversity of preference. Practice with a single task also increases the familiarity of the task. Familiarity alone has been shown to produce a preference for foraging techniques (Partridge, 1976a). If mice prefer the most familiar technique, then they should prefer that technique regardless of its efficiency. The two hypotheses (increase in efficiency and diversity of preferences with practice, and increased preference based on familiarity) are tested in Experiment 2 with the Restricted Hang (RH) treatment group.

Methods and Procedures

Three litters (12 mice) were bred and housed as in Experiment 1. As juveniles, mice in the Restricted Hang group were given 24 hr a day access to 50 seeds available from the Hang task. One mouse died during the experiment, leaving N = 11.

Results and Discussion

Diversity of Preference

As in Experiment 1, the diversity of preferences was analyzed with Shannon's Index of diversity (H'). Mean H' for the Restricted Hang group was 0.20, which did not differ from the Mean H' of the Naive group in Experiment 1 (t = 0.512, df = 21, P > .50). The equal diversities of RH and N indicate that practice with Hang did not increase diversity above baseline, suggesting that the perception of similarity of the techniques for RH was no different than for N.

Dominance of Preference

The Restricted Hang group showed a significant difference in the number (F = 12.70, df =2, P < .005) and weight (F = 14.06, df = 2, P < .003) of seeds taken from the tasks. Internal comparisons showed that significantly more seeds (LSD, α = .05, df = 48) and a significantly greater weight of seeds (LSD, α = .05, df = 48) were taken from the Lift than either the Slide or Hang tasks. RH's dominance for Lift confirms that familiarity with Hang did not produce a preference for Hang.

Efficiency

Mean Removal efficiencies for the Restricted Hang group are significantly different (ANOVA F = 5.03, df = 2, P < .02). Multiple comparisons of REH, REL and RES reveal that mean RES is significantly greater than REH or REL (LSD, $\alpha = .05$, df = 15). Figure 4 presents the Remove efficiencies for the 3 tasks. Mean Total efficiencies also differ for this group (ANOVA F = 5.06, df = 2, P < .02), and pairwise comparisons of the means shows TEH > TEL (LSD, α = .05, df = 15), but there were no other differences. Figure 5 shows the mean Total efficiencies for RH. The significantly greater RES than REH indicates that practice with Hang did not increase the efficiency for removing seeds from Hang to make it equal to the Remove efficiency for Slide. The higher TEH than TEL indicates that practice with Hang may have increased the efficiency of obtaining but not removing seeds. The Naive group showed no differences in Total efficiency among the three tasks, suggesting that the practice with Hang experienced by the Restricted Hang group had an effect on the ordering of Total efficiencies. Total efficiency is a better measure of the efficiency for Hang as it includes seeds that were

Figure 4: Mean Remove efficiency of RH for Hang (REH), Lift (REL), and Slide (RES).



Figure 5: Mean Total efficiency of RH for Hang (TEH), Lift (TEL), and Slide (TES). Total efficiency is calculated by dividing the weight (in grams) of seeds taken by the time taken to remove and eat the seeds.



not removed, but were partially eaten. Only the Hang task allowed mice to partially eat seeds without first removing them, so TEH is a better measure of the use of Hang than is REH. The superiority of TEH over TEL suggests that practice with the Hang task increased its relative Total efficiency by increasing efficiency for hanging beneath the walkway and eating seeds without removing them. Comparisons of REH and TEH between Restricted Hang and Naive showed no significant differences. Since neither Remove nor Total efficiencies differed between the groups, the only effect of practice that is evident from these data is that it changed the ordering of the Total efficiency for the Hang group.

The relationship between efficiency and the number and weight of seeds taken from the three tasks was analyzed by calculating separate Pearson Correlation Coefficients between the efficiency for each task and the number and weight of seeds taken from that task for the first 3 and for all 15 days of Preference testing. Correlations between efficiency and number and weight for the first 3 days of testing were examined to determine whether experience with the tasks during testing altered the relationship between efficiency and number and weight of seeds taken. A significant correlation would indicate that, as a group, the mice took from a task according to their efficiency for that task. The Restricted Hang group

showed no significant correlations between Remove or Total efficiency and the number or weight of seeds taken overall. Figure 6 shows the relationship between Remove efficiency and dominance for the 3 tasks. The only significant correlations found were negative correlations between REH and the number (r = -.71, P < .03) and weight (r = -.68, P< .04) taken from Hang, and, marginally, between TEH and , the number (r = -.63, P < .07) and the weight (r = -.59, P< .09) taken from Hang during the first 3 days of Preference testing. The negative correlation between efficiency and number and weight taken during the first 3 days of Preference testing indicates that mice with the greatest efficiency for Hang took the fewest seeds from Hang.

Correlations based on the whole group may have obscured the behavior of individuals who had a preference for the task on which they were most efficient. Five of the 11 (46%) mice in the Restricted Hang group took the greatest number or weight of seeds from the task on which they were most efficient. Three of the mice had highest Remove efficiencies for Slide and took the greatest number of seeds during the first three days from slide; one of these took the greatest number from Slide overall. One took the greatest weight from Slide overall and for the first 3 days, Another mouse had the highest Remove efficiency for Lift and took the greatest number and weight Figure 6: Mean Remove efficiency of RH for Hang (REH), Lift (REL), and Slide (RES) are presented in the left panel, and mean number of seeds taken over the 15 days of preference testing for Hang (NUMH), Lift (NUML), and Slide (NUMS) are in the right panel.



of seeds from Lift for the first 3 days of testing, and over all 15 days of testing. Another had the greatest Remove and Total efficiency for Hang, and took the greatest number of seeds from Hang overall, and for the first 3 days of Preference testing. The number measure for Hang is somewhat inflated as it includes any seed partially eaten. This mouse did not take the greatest weight of seeds from Hang so its preference for Hang is questionable.

The primary results of Experiment 2 were the dominance of Lift over Hang and Slide, the equal diversities (H') of Restricted Hang and Naive, the equal efficiencies (REH and TEH) of Restricted Hang and Naive, and the lack of a positive correlation between efficiency and preference.

Discussion

The dominance of Lift shows that mice did not prefer the technique with which they were most familiar, and the equal diversities of Restricted Hang and Naive show that practice with Hang did not make it more similar to the other techniques.

Practice with Hang had little effect on its efficiency when compared to the efficiency of inexperienced mice. The ineffectiveness of practice in

increase efficiency, or (2) the efficiency for Hang was near a ceiling in the Naive group.

The lack of a positive correlation between efficiency and the number or weight of seeds taken reveals that some dimension other than efficiency underlies preference for these mice. Since efficiency is not a relevant dimension for forming preferences, even if practice with Hang had equalized the efficiencies of the techniques, diverse preferences would not have resulted. Whatever the dimension underlying preference in this group, restricted rearing with Hang did not affect their experience so as to increase or decrease diversity of preference when compared to inexperienced mice.

Experiment 3: The Effect of the Opportunity to Compare Techniques on the Diversity of Preference

The suggestion that preferences are based on the perceived similarity of food items (Gray, 1985) or techniques implies that animals must have the opportunity to compare items or techniques in order to asses their similarity and to form preferences among them. This prediction still holds even if preferences are not related to efficiency, as suggested by the earlier experiments. All that is required is that the techniques differ along some dimension relevant to preference. Juvenile experience

with simultaneously available foraging tasks should provide the opportunity to compare the techniques required by the tasks, and promote specialization. Unpredictable access to the tasks should interfere with the opportunity to compare the techniques they require and so should promote diversity of preference. Unpredictable fluctuations in access to the foraging tasks that occur within an animal's memory window may not promote diverse preferences. If an animal has access to information about the efficiency (or some other relevant dimension) of the technique required by a previously encountered task while engaging in a different technique with a presently available task, then it may be able to compare the present technique to the past technique. In other words, very-short-term fluctuations may not promote diverse preferences because the fluctuations occur within the animal's memory window so that it can form restricted preferences. Fluctuations that occur over time periods longer than the animal's memory window should promote diverse preferences. The effect of having the opportunity to compare techniques, and the effect of short-term and longer-term fluctuating access to the tasks were tested in Experiment 3.

Methods

Three treatment groups were employed in Experiment 3, each having 3 litters of 4 mice. All mice were bred and housed as described in the General Methods. At weaning the litters were dispersed into individual plastic tubs and randomly assigned to one of the following treatment groups: Stable (S), Alternate-Day Fluctuating (AF) or Daily Fluctuating (DF). Each treatment group differed in its juvenile experience with the three foraging tasks (Hang, Lift and Slide). Mice in S were given simultaneous access to all three tasks, which were available in their home tubs 24 hrs a day. Each task was baited with 16 seeds so that each mouse had access to a total of 48 seeds. In order to obtain sufficient seeds, the animals in this group were forced to take seeds from all of the tasks each day. Daily intake was monitored to insure that mice were distributing their choices among all of the tasks. Mice were trained to use all of the tasks by leaving empty tasks unfilled until all of the tasks had been sampled. Within the first week of the juvenile phase all of the mice in this group were eating from all three tasks each day, although few mice took all available seeds each day. Animals in DF were given access to 50 seeds from a single task each day, and the tasks changed randomly every day. Mice in AF were given access to 50 seeds from a single task, changed

randomly, but only every other day. They were not fed on the days when a task was not presented. The only source of food for any of the mice was from the foraging tasks; no supplemental food was given. Two animals escaped, and several died, leaving N = 6 for Stable, N = 9 for Day Fluctuating, and N = 11 for Alt Fluctuating.

Results

Diversity of Preference

Shannon's Index of Diversity (H') was used to analyze the diversity of preferences among the groups as described in Experiment 1. Mean H' for the treatment groups are presented in Figure 7. The treatment groups differed significantly in their diversity of preference based on the number of seeds taken from each task each day (ANOVA F = 9.83, df = 4, P < .0001). Multiple comparisons of the mean H's show AF to be significantly more diverse than S, or DF (LSD, α = .05, df = 617). The Naive group (from Experiment 1) is also significantly more diverse than S or DF, and significantly less diverse that AF (LSD α = .05, df = 617). The diversity of S and DF does not differ. Comparison of H' based on the weight of seeds, also shows significant differences (ANOVA F = 10.16, df =4, P < .0001). Internal comparisons of the mean H's show AF significantly more Figure 7: Mean daily H' based on the number of seeds taken from all the tasks for Stable (S), Day Fluctuating (DF), and Alt Fluctuating (AF).



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diverse than S or DF (LSD α = .05, df = 617), and Naive significantly more diverse than S or DF (LSD α = .05, df = 617). The diversity of preference for the S and DF groups did not differ.

Dominance of Preference

The Stable and Day Fluctuating groups showed no significant difference in the number or weight of seeds taken from the 3 tasks. The Alt Fluctuating group showed a significant difference in the number (ANOVA F = 8.16, df = 2, P < .03) and the weight (ANOVA F = 7.80, df = 2, P < .003) of seeds taken from the 3 tasks. Internal comparisons indicated that NL > NS > NH (LSD, α = .05, df = 72).

Efficiency

Within-group comparisons showed no significant differences in mean REH, REL, or RES, or in mean TEH, TEL, or TES for the Stable group. Simple ranking of Remove efficiencies for the 3 techniques is REH < RES < REL. The Day Fluctuating group showed a marginally significant difference (ANOVA F = 3.29, df = 2, P < .06), with RES > REH. Mean Removal efficiencies for the Alt Fluctuating group differ significantly (ANOVA F = 37, df = 2, P <

.0001). Internal comparisons of the means showed RES > REL > REH (LSD, $\alpha = .05$, df = 20).

Pearson correlation coefficients showed no significant correlations between Remove efficiency and the number of seeds taken from each task over the 15 days of Preference testing for any of the groups.

The primary results of Experiment 3 were the higher H' of AF compared to S and DF, that most seeds were taken from Lift, and that the highest efficiency was for RES by AF and DF, and for REL by S.

Discussion

Each group's perception of the similarity of the techniques was measured with H'-scores (Gray, 1979, 1985). H' gives a measure of the diversity among the techniques, and differences in H' among the groups indicated that diversities differed. Mice in the S and DF groups showed lower diversity among the tasks than mice in the AF and Naive (Experiment 1) groups (see Figure 8). The higher H' of the AF group than of the other treatment groups supports the hypothesis that fluctuating environments produce diverse preference by interfering with the opportunity to compare events. An indication that the opportunity to the difference in diversity between the AF and DF groups.

Figure 8: Mean daily H' based on the number of seeds taken from all the tasks for Stable (S), Day Fluctuating (DF), Alt Fluctuating (AF), and Naive (N).



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The short-term fluctuations experienced by DF did not promote diversity, while the longer-term fluctuations of AF did.

Experiment 4: Diversity, the Opportunity to Compare Alternatives, and Food Scarcity

The significantly higher diversity of AF in Experiment 3 suggests that separating experience with the tasks by 48 hrs exceeds the memory window, and prevents comparisons of the techniques required by the various tasks. However, an alternative explanation for the difference in diversity of DF and AF cannot be ruled out with the data available from Experiment 3. Not only did the time between access to the various tasks differ between the AF and DF, but the amount of food available each day also varied. The every-otherday feeding regimen of AF may have also contributed to diversity. An increase in dietary diversity with resource scarcity is predicted by Optimal Foraging Theory and has been confirmed by experimental data from 3 species of Peromyscus (Ebersol & Wilson, 1980; Emlen, 1966; Maynard-Smith, 1974). Only adult mice were tested in these The influence of early experience with scarcity studies. on the subsequent foraging diversity of adults has not been tested. Early experience with food scarcity may influence later foraging strategies, and promote diversity of

preferences in adults even under conditions of abundance. Since juvenile mice in AF in Experiment 3 were given less food than those in DF or S, scarcity of food may have promoted diversity of the use of the 3 tasks, just as scarcity has been shown to promote dietary diversity. Experiment 4 was designed to resolve the confound between the opportunity to compare foraging techniques and food scarcity. Two alternative hypotheses were tested. If the opportunity to compare techniques accounts for diversity, then animals exposed to differences in food scarcity but given equal opportunity to compare techniques should have equal diversity of preferences. If, on the other hand, food scarcity accounts for diversity, then animals with equal opportunities to compare techniques, but differences in food scarcity should have different diversity of preference. Experiment 4 tests these hypotheses by comparing the diversity of preferences of AF, DF, and S in Experiment 3 to a treatment group (AF-Sup) identical to AF except for the addition of supplemental feeding on the days when no task was presented.

Methods

Three litters of 4 mice each (N=12) were bred and housed as described in the General Methods. At weaning the mice were dispersed into individual plastic tubs, and given

access to 50 seeds from a single task every other day. On the days when no task was presented, mice in the AF-Sup group were given 34 seeds in a plastic cup placed on the floor of the tub. The number of seeds provided as supplemental feeding was equal to the mean number of seeds taken by the Stable group during the juvenile phase of Experiment 3. The seeds were placed in the tubs at approximately the same position each day they were presented. At 50 days of age the mice were transferred into individual laboratory cages, and given Efficiency and Preference tests as in all previous experiments.

Results

Shannon's Index of Diversity (H') was used to analyze the diversity of preferences as described in Experiment 1. Mean H' for AF-Sup, AF, DF, and S are presented in Figure 9. The analysis of variance revealed a significant difference in diversity of preference (H') based on the number of seeds taken from each task each day (F = 7.61, df = 5, P < .0001). Multiple comparisons among the groups show that AF is significantly more diverse than AF-Sup (LSD, α = .05, df = 796). Diversity of the number of seeds taken each day by AF-Sup does not differ significantly from the diversity of DF or S. Comparison of H' among the groups based on the weight of seeds taken each day also Figure 9: Mean daily H' based on the number of seeds taken from all the tasks for Stable (S), Day Fluctuating (DF), Alt Fluctuating Suplemented (AF-Sup), and Alt Fluctuating (AF).



96
shows significant differences (ANOVA F = 7.92, df = 5, P < .0001). Internal comparisons of the mean H's show AF to be significantly more diverse than AF-Sup, and no difference in diversity between AF-Sup and either DF or S (LSD, α = .05, df = 792).

The primary results of Experiment 4 were the higher H' of AF compared to AF-Sup, and the equal H's of AF-Sup, DF and S.

Discussion

The lower diversity of AF-Sup than AF supports the hypothesis that food scarcity contributes to diversity of preferences. This finding indicates that a strict interpretation of diversity as due to memory limitations alone is inappropriate. The high diversity of AF indicates that juvenile experience with food scarcity can have longlasting affects, and influence the foraging strategies of adults even when an abundance of food is available.

Chapter III

General Discussion

The differences in diversity of preference among the treatment groups in this study indicate that early experience can affect adult foraging strategies. This result questions the validity of the basic assumption of Optimal Foraging Theory (OFT) that foraging strategies are genetically based and the result of natural selection for maximization of net gain. Since all of the animals in this study are members of the same species they share a common history of natural selection. If natural selection acted to maximize genetic programs for foraging strategies, then all of the groups should have had equal diversities of preferences, and efficiency should have been the dimension underlying the preferences. P. leucopus is usually labeled a generalist based on the diet diversity of species as a whole. If natural selection produced that diversity through selection for "generalist" genetic programs, then the early experience of the different groups should have had little effect on their diversity of preference. Selection for maximization of net gain should have been evident from efficiency as the underlying dimension of

preference. The differences in the diversities among the groups due to their different early experiences indicates that "generalist" genetic programs did not determine their foraging strategies, and illustrates the importance of early experience in determining adult foraging strategies. The lack of a correlation between efficiency and dominance in any of the groups indicates that the assumption of natural selection for maximization of net gain is also in Some dimension other than efficiency (as measured error. by grams of seeds/time) underlay preferences for the mice in this study. The general assumption of OFT that an economic dimension (measured by energy/time) is questioned by this study's results. Cost/benefit ratios may underlie foraging preferences, but energy/time measures may not demonstrate how the cost/benefit ratios are affecting foraging. More importantly, this study indicates that how an animal determines costs and benefits is affected by its early experience. An assumption that natural selection for maximization of net gain is the primary factor in determining foraging strategies is unwarranted based on the data presented here. A complete understanding of foraging must include investigations of developmental histories, and not rely solely on assumptions about natural selection for optimal genetic programs.

An ecological view of generalist and specialist foragers suggests that microhabitat differences among

individuals in the same species can contribute to differences in foraging diversity. An ecological continuum can be constructed based on a continuous range of ecological conditions, and animals placed along the continuum according to the conditions they experience. One such continuum is the predictability of available food resources. Animals who share microhabitat features, such as the same degree of predictability in available food resources, will have common experience, and occupy the same place on the ecological continuum. Since an animal's place on the continuum is determined (in part) by features of its microhabitat, different individuals of the same species could occupy the same or different places on the continuum depending on the similarity of their microhabitats. From an ecological view, foraging diversity is a function of some environmental feature, such as predictability, and an animal's response to it.

The differences in H' (diversity of preference) among the groups in Experiments 3 and 4 indicate that individual experience with unpredictable resources affects diversity, and suggests that differences in individual microhabitats can affect the range of variability in foraging behavior found within a species. Mice exposed to stable microhabitats will become specialists, while those in more unpredictable microhabitats will be more diverse. The foraging strategies of a species will include a mixture of the individual strategies developed in different microhabitats.

The width of a species' niche has been associated with the phenotypic variability of the species (Van Valen, 1965). Niche width is defined by Van Valen as the total multidimensional space of limiting resources used by a species. Release from competition, either intra- or interspecifically, has been shown to promote an increase in niche width in scorpions, <u>Paruroctonus mesaensis</u> (Polis, 1984) oystercatchers, <u>Haematopus ostralegus</u> (Ens & Goss-Custard, 1984; Goss-Custard, Clarke, & Durell, 1984), coal tits, <u>Parus ater</u>, (Alatalo, Gustafsson, Linden, & Lundberg, 1985; Gustafsson, 1988), and <u>Peromyscus maniculatus</u> and <u>P</u>. <u>truei</u> (Llewellyn & Jenkins, 1987).

Wider niches are associated with greater morphological and behavioral variability within a species (Van Valen, 1965). For example; coal tits on Gotland island occupy a wider niche than those on the mainland, foraging on the inner branches as well as the needles of pines (Alatalo et al, 1985; Gustafsson, 1988). On the mainland the inner branches and needles are occupied by two species, the willow tit (<u>Parus montanus</u>) and the crested tit (<u>P</u>. <u>cristatus</u>), that are not found on Gotland island. The wider niche of Gotland island coal tits is accompanied by morphological variations. Tarus length, body size and length of first primary feathers differ between branch and

needle foragers. All of the morphological features affect foraging ability. The wider niche of <u>P. ater</u> on Gotland, is, in part, due to release from interspecific competition that is common on the mainland. The lack of competition on Gotland has resulted in both a more generalized use of foraging sites by individuals (those intermediate between the branch and needle specialists), and a greater difference in strategies among specialized individuals.

Within-population variation in foraging strategies have been observed in a number of species. Partridge & Green (1985) list 3 mechanisms that can give rise to individual differences in foraging behavior: 1) patchy environments may have different foraging behaviors appropriate to different patches, 2) individual differences in phenotype, both behavioral and morphological may determine the most appropriate foraging strategy, and 3) competition among individuals may affect appropriate foraging strategies for individuals.

The different foraging strategies reflected in the diversity differences among the treatment groups reported here suggest some ways in which individual differences in foraging strategies could develop. They suggest that individual differences in experience with predictable and unpredictable food resources will affect the diversity of foraging behaviors. Individuals on the periphery of a population may be exposed to greater competition than more

central individuals, and thus be exposed to greater unpredictability, and exhibit greater diversity. With a release of competition, the more diverse individuals would be able to expand into previously unavailable environments, and broaden the niche of the species.

Diversity of preference depends on an animal's perception of the similarity of objects or events from which it is given the opportunity to choose (L. Gray, 1979, 1985, unpublished MS). Objects or events perceived as similar will be equally chosen, and those seen as dissimilar will be chosen differentially. Diversity of preference implies that objects or events are perceived as similar, or that the animal was prevented from comparing the objects or events so that similarities could not be established. Fluctuating environments could prevent comparisons, and thus enhance diversity of preference. The opportunity to compare is a co-function of the animal and its environment, therefore, the predictability of a food resource is due to ecological factors such as fluctuations in food supply, and to individual factors such as memory limitations. Short-term fluctuations that occur within an animal's memory window (Kacelnik & Krebs, 1985) would not prevent comparisons, and thus, could have the same effect on predictability as simultaneous experience with various food resources. Fluctuations that occur within the memory window would not interfere with comparisons, and thus not

prevent specializations. Longer-term fluctuations that exceed the memory window would prevent comparisons and thus prevent specializations.

The treatment groups in Experiment 3 had different opportunities, as juveniles, to compare the techniques required by the various foraging tasks. The Stable group had simultaneous access to all 3 tasks each day, the Day Fluctuating group were exposed to short-term fluctuations, and the Alt Fluctuating group to longer-term fluctuations. A prediction of diversity of preference can be made based on each group's opportunity to compare the techniques required by the various tasks. Based on the opportunity to compare the various techniques; Stable should be less diverse than Day Fluctuating (depending on the size of the memory window), and/or Alt Fluctuating. The low diversity of DF and S supports the hypothesis that short-term fluctuations do not promote diversity. However, the results of Experiment 4 indicate that the difference between AF and DF is affected by the differences in food scarcity between the groups. The difference in diversity between Alt Fluctuating and Day Fluctuating is only suggestive that longer-term fluctuations produce diversity of preference due to limitations of memory. Inherent in the memory window hypothesis is the idea that some sufficiently long period of time must elapse between eating bouts. The time between access to the various tasks for

the Alt Fluctuating group is confounded with food being available only every other day, which apparently contributed to diversity of preferences (Experiment 4). The total amount of time each group was exposed to the tasks also differed, and may have contributed to the diversity difference between them.

Unpredictability of food resources has two sources; variability in the amount of food available, and variability in the technique required to obtain the available food. Each of these situations presents a foraging animal with a different problem. In the first situation, the technique needed to obtain food is less important than whether or not food will be available. The relevant dimension of unpredictability is the availability of food. In the second situation, availability is predictable, but the technique needed to obtain it varies. The relevant dimension is the efficiency or some other aspect of the technique required to obtain available food. For AF both the availability of food and the technique needed to obtain it were variable. For AF-Sup only the technique varied.

If the two dimensions of unpredictability are hierarchical, with availability prior to efficiency or some other aspect of the techniques, then the AF group's diversity of choice comes from control of choice by availability of food rather than by differences among the

techniques. The AF group could not afford to pay attention to the differences among the tasks because they had to satisfy the more basic need of obtaining food before the less basic need of optimality could be satisfied. The AF-Sup group could afford to attend to the differences in the techniques because the environment was supplying a predictable abundance of food.

Gray & Tardif (1979) compared the diversity of choice for different food types among groups of Peromyscus exposed to predictable and unpredictable access to different food types. One group of mice was exposed to unpredictability in both amount and type of food. This group showed more diverse preferences than a group with predictable access to amount and type of food. In Gray & Tardif's study, amount and type of food were varied simultaneously, so the separate effects of unpredictability in amount versus unpredictability in food type cannot be assessed. Experiment 4 in the present study allows variability in amount of food and variability in type of foraging technique to be assessed separately. When both amount of food and type of technique needed to obtain food are unpredictable diversity of preferences is promoted. However, when the type of technique needed to obtain food is unpredictable, but the amount of food available is predictable, specialization of techniques is promoted. Food scarcity may be the primary factor in promoting

diversity in Experiments 3 and 4. However, dismissing the opportunity to compare techniques as a factor in the development of diverse preferences (based on the results from Experiment 4) would be premature. The time between encounters with various food types has been shown to affect the amount of information an animal has available for making foraging choices (Kacelnick & Krebs, 1985), and could affect the development of foraging strategies. In order to asses the separate contributions to diversity of opportunity to compare techniques and degree of food scarcity, they would have to be varied systematically to determine the relationship between the memory window and food scarcity.

Laboratory tests of foraging in which animals are able to initiate and terminate eating bouts show that animals alter their behavior in a number of ways in response to changes in the abundance or cost of food items. Cost/benefit analysis of foraging behavior reveals that animals will respond to increasing cost (search or handling time) of food items either physiologically by lowering body temperature (Rashotte, Henderson, & Phillips, 1989) or behaviorally by altering the frequency and size of meals (Collier, 1982, 1986; Collier & Rovee-Collier, 1981) or the type of food preferred (Kaufman & Collier, 1981; Caraco, Martindale, & Whitman, 1980). These studies are consistent with a basic tenet of OFT which predicts that animals will

select foods that maximize the value of food relative to cost (Emlen, 1966; MacArthur & Pianka, 1966; Pyke, Pulliam & Charnov, 1977; Schoener, 1971). Cost is usually defined as calories or grams of food/handling time (Stephens & Krebs, 1986).

Animals alter their foraging behavior based on their knowledge of the economics of their environments (Collier, 1986). In other words, they are sensitive to the risk of starvation or to the inefficiency that comes with some foraging choices. Models of risk-sensitive foraging have been developed that predict the conditions under which animals will be risk-averse or risk-prone. Shortfall models (Caraco et al, 1980; Stephens, 1981; Stephens & Charnov, 1982) predict that animals having enough food to meet their daily energy needs will be risk-averse, while those with less than enough food to meet daily energy requirements will be risk-prone. Food scarcity would promote risky foraging, and high-cost food items (those with longer handling times) would be included in the diet in a higher proportion than when food was abundant. The shortfall models are concerned with foraging situations in which an animal must stock up as a hedge against a time in the near future when food is expected to be scarce. For example, diurnal foragers must have energy stores that allow them to survive during the night. The choice of risk-averse or risk-prone behavior is made in anticipation

of the animal's needs in the near future. An animal's knowledge of the economic structure of its environment becomes important if one assumes that it is responding in anticipation of their energy requirements (Collier, 1986).

Applying the logic of risk-sensitive foraging to the juvenile rearing conditions of AF and AF-Sup, mice in AF would be predicted to be risk-prone in response to the shortfall created by the days when no food was available. Mice in AF-Sup would be risk-averse because their daily energy requirements were provided for by the tasks and supplemental feeding. The risk-prone mice in AF would had diverse preferences because they used both high- and lowcost techniques, while mice in AF-Sup would have been more specialized on low-cost techniques.

The diversity of preference of AF differs in one significant way from the diversity of preference predicted by risk-prone foraging. Risk-sensitive foraging models are concerned with the reaction of adult animals to the economics of their environments. Change from risk-averse to risk-prone behavior is predicted by a utility function that assumes an animal is able to anticipate shortfall. Adult <u>Peromyscus leucopus</u> have been shown to increase dietary diversity (become risk-prone) when food is scarce (Ebsersol & Wilson, 1980), and to decrease diversity (become risk-averse) when food is abundant. Since all of the mice in the present study experienced the same economic structure during preference testing (150 seeds available daily), they should all have responded as either risk-prone or risk-averse. The difference in diversity among the groups indicates that they were responding to the economic structure of preference testing in different ways due to the differences in the economic structures of their juvenile experience. The foraging strategy learned during the juvenile phase carried over into adult preference testing, and determined the mice's anticipation of the preference test economic structure.

One way in which the anticipation, or knowledge of the economic structure of preference testing could have been affected by the juvenile rearing condition is its effect on determining the relevant dimensions for making foraging choices. For mice exposed to unpredictability in both amount of food and the technique needed to obtain it, the relevant dimension of foraging choices may have been risk of starvation, thus promoting diversity as a hedge against the risk. Mice exposed to these conditions may have been indifferent to the relative costs of the techniques because their overriding concern was with survival. They developed a foraging strategy in which the relative costs of the techniques were irrelevant. When they were exposed to an economy in which the relative costs could be used to choose low-cost techniques without the risk of starvation they failed to attend to the dimension of relative cost.

Support for the view that groups attended to different dimensions of the economy comes from the observation that mice in AF did not decrease their diversity over the 15 days of preference testing. Kaufman & Collier (1981) show that adult rats (<u>Rattus norvegicus</u>) given a choice of sunflower seed with hulls and without hulls come to prefer hulled seeds within 3-7 days. The shift to hulled seeds is in response to the lower handling time, and thus lower cost of the hulled seeds. The stability of preference diversity in AF indicates that the differences in handling time among the tasks was irrelevant to their foraging decisions, and did not become relevant even in the face of food abundance over the 15 days of preference testing.

Models of foraging choice based on OFT has assumed a knowledgeable forager (Stephens & Krebs, 1986). Implicit in this assumption is that animals will learn about, and attend to, the relevant dimension of relative cost in making foraging choices. In other words, it has been assumed that all animals will rely on the same dimension to make choices: the dimension of cost. This study indicates that early experience with unpredictable environments has an effect on the dimensions animals will use to make adult foraging choices. Not only will the economics of foraging (cost/benefit ratios) affect choices, but an animal's perception of the economics must also be taken into account.

Determining an optimal response is problematical. What is optimal in one situation is non-optimal in another. The reliance on cost/benefit ratios in OFT reflects attempts to solve this problem by focusing on optimal choices as those that most enhance survival given economic limitations. Economic considerations alone, however, will not predict foraging behavior if early experience with a different economic structure affects the relevant dimensions on which choices are made. The ways in which relevant dimensions are established, and their effects on foraging adaptability must be included in order to have a complete foraging theory. Focusing on adult efficiency alone will not allow a complete foraging theory to be formed.

No clear relationship between efficiency and choice is evident from the experiments reported here. No significant correlations were found between Remove efficiency and choice of task. All of the groups took more seeds from Lift than from the other tasks. The dominance of Lift is statistically significant in N, RH, and AF, and the trend is clear in all the groups. However, all groups but one (Stable) were most efficient in removing seeds from the Slide task. RES is significantly greater than REH and REL in AF, N, RH, and marginally for DF. Since RES showed a statistically significant difference from the other Remove efficiency measures, the procedure for measuring Remove efficiency is adequate for differentiating among the techniques. Figure 10 illustrates the relationship between Remove efficiency and dominance for N, S, DF, and AF. Only the Stable group showed dominance for the technique that was also ranked as most efficient. However, since the relationship is not supported statistically it should not be taken as an indication that Stable rearing establishes efficiency as a relevant dimension for making foraging choices. The relationship does suggest that further study is needed to clarify the role of Stable rearing in establishing efficiency as a relevant dimension.

Partridge (1976a) assumed that great tits in the laboratory choose foraging techniques based on their efficiencies, but, she did not measure efficiency directly. Optimal Foraging Theory (OFT) predicts that animals choose among alternatives based on their different cost/benefit ratios. Items with the lowest cost and greatest benefit will be preferred by an optimal forager. The efficiency measures in these experiments are measures of cost (time to obtain and eat a seed) and benefit (grams of seeds obtained). However, the mice in these experiments did not chose the technique with the lowest cost/benefit ratio. Given the numerous examples of animals' sensitivity to costs and benefits (Stephens & Krebs, 1986; for an analogous view from the operant matching paradigm see Staddon, 1983) it seems unlikely that the mice in these

Figure 10: The relationship between Remove efficiency and the number of seeds taken over the 15 days of preference testing for Stable (S), Day Fluctuating (DF), Naive (N), and Alt Fluctuating (AF). The X axis represents mean Remove efficieny, and the Y axis mean number of seeds taken from each task. The leftmost point of each line is the efficiency/number for Hang, the center point is for Slide, and the rightmost point is for Lift. AF, DF, and N had the lowest efficiency/number for Hang, the highest for Slide, and Lift was intermediate between the two. S also had the lowest efficiency/number for Hang, but Slide is lower than Lift for this group.



experiments were totally insensitive to costs and benefits. One possibility for efficiency's failure to predict choice is that the handling-time measure used to evaluate cost did not adequately reflect an animal's actual cost. For example, if it takes less time to remove a seed from the Slide task than from the Lift task, but the energy expended is greater for Slide than Lift, then taking seeds from Slide would be more costly than taking them from Lift. The cost in terms of time may not be directly analogous to the cost in terms of energy. A speculation based on observations of animals retrieving seeds from the tasks is that the physiological costs differ, and are not reflected in the efficiency measures. One difference in Lift and Slide is the posture animals must assume in order to retrieve seeds from each task. The Slide task required a mouse to retrieve a seed from a hole bored in a flat piece of wood. To do this it had to open its mouth wide, with its upper jaw outside the hole on the board, and insert its tongue or lower jaw into the hole to retrieve the seed. Mice usually supported themselves with their from paws on either side of the hole. The Lift task, on the other hand, allowed a mouse to assume a more natural eating posture while retrieving a seed. To obtain a seed from Lift, a mouse had to open the cap and insert its tongue or lower jaw into the centrifuge tube to retrieve the seed. Inserting the tongue or jaw into the tube did not require

the wide stretch required by Slide. Mice usually held the tube with their front paws much as they held a seed while eating. The posture required by Lift was more like the normal eating posture than the posture required by Slide. The difference in the costs of the two postures may have been a factor in choosing between them. The posture required by Slide may have been physiologically more costly than that of Lift, or simply more uncomfortable. Neither of these costs would have necessarily been evident in a measure of the time taken to retrieve seeds from the two tasks.

Direction of Future Research

In sum, the results of this study showed that early experience with food scarcity and unpredictable access to various foraging tasks increases the diversity of preferences and that a relationship between efficiency and preference for foraging techniques by <u>P. leucopus</u> is not readily apparent.

A multidimensional analysis of the relevant dimensions underlying preferences for techniques would help in understanding the importance of efficiency in determining preferences. Species differences in the relevance of efficiency for determining preferences might reveal phylogenetic and early experience differences among

species that would help to clarify the relationship between efficiency and preference for foraging techniques. For example, rearing <u>P. leucopus</u> and <u>P. maniculatus blandus</u> in identical laboratory conditions, and testing their preferences for variations of a single task that differ only in the energy required by the variations would show the relevance of efficiency for determining diversity of preferences. If diversity differed for the two species, then efficiency would not be a relevant dimension for the more diverse species.

The memory-window hypothesis also deserves further study. By systematically varying the time between successive presentations of various tasks (with food scarcity kept constant) the separate affects of memory and food scarcity could be addressed. Another approach would be to compare the diversities of groups like AF and AF-Sup in the present study to a Stable group that had simultaneous access to various tasks every other day. In this way one group would be exposed to food scarcity and unpredictability of task, one group to food scarcity and unpredictability.

The relatively high diversity of the Naive group in this study also suggests a course of future research. Preweaning experience may have contributed to the diversity shown by this group. If the diversity of the Naive group

can be taken as a baseline, then stable juvenile rearing served to reduce diversity, while fluctuating juvenile experience helped to maintain, and enhance diversity. The features of pre-weaning experience that promote diversity have not been investigated. One way to approach an investigation of pre-weaning is with a manipulation of litter size. The normal litter size for P. leucopus is four, and females have 4 teats. The relatively high diversity of the Naive group could reflect the diversity supported by the 1:1 ratio of mice to nipples. Mice in litters of more than four may have more unpredictable access to teats, and this unpredictable access may enhance diversity of preferences even further. Small litters may be less diverse because of the predictability of access to milk. Cramer, Pfister, & Haig (1988) demonstrated differences in spatial learning among groups of rats in which the ratio of pups to nipples was 5:12 versus 5:4. When the ratio was 5:12 animals took fewer trials to learn an 8-arm radial maze. The difference in spatial learning was attributed to the experience of shifting nipples during suckling that enhanced performance in the 5:12 group. Nipple shifting seems to have enhanced the rats ability to adapt their behavior to the requirements of the maze. This adaptability of behavior may have correlates in adaptability to different foraging tasks. A female's behavior at weaning could also be a factor in the

predictability of a pup's access to milk. If females avoid pups, not allowing them to suckle, in order to wean them, then early weaning, before the mother imposes unpredictability, may enhance specializations.

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