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Early experience with food items of differing sizes and optimal foraging in golden hamsters (*Mesocricetus auratus*)

Turpin, Barbara, Ph.D.

The University of North Carolina at Greensboro, 1989

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EARLY EXPERIENCE WITH FOOD ITEMS OF DIFFERING SIZES AND OPTIMAL FORAGING IN GOLDEN HAMSTERS (*MESOCRICETUS AURATUS*)

by

Barbara Turpin

A Dissertation Submitted to
the Faculty of the Graduate School at
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Approved by

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APPROVAL PAGE

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The experiments in this dissertation were designed to examine the role of early experience on later food choice by golden hamsters.

In Experiment 1, the profitabilities of three sizes of Noyes food pellets (20, 45, and 94 mg) were assessed. The order of profitabilities were 94 > 45 > 20.

In Experiment 2, hamsters were reared, from birth to 35 days of age, on one of the three pellet sizes used in Experiment 1 and were later allowed to choose among the sizes. It was found that early experience had consistent effects on later food choice: Animals chose the size(s) most dissimilar to the size with which they were reared. This result is unexpected and fits into no extant theory of food choice.

Experiment 3 was conducted in order to see whether taste preference could be induced in hamsters as they are in other rodents. Animals were reared on either unflavored (control), banana-flavored, or coconut-flavored food, and, later, given a simultaneous choice between banana- and coconut-flavored food. Control animals showed no preference for either flavor; animals in the other groups showed a preference for the familiar flavor.

Taken together, the results of Experiments 2 and 3 reveal that size and taste are food-relevant cues that affect foraging behavior in hamsters quite differently.

Experiment 4 tested the hypothesis that animals in Experiment 2 treated the novel-sized pellets as objects to be explored rather than as food. Animals were reared on 20 or 94 mg pellets, and, during testing, were allowed to choose among 200 and 45 mg pellets and plastic beads of the same size and shape as the 94 mg pellets. The hamsters avoided the beads, but the results of the study showed that the animals, once again, as in Experiment 2, preferred the food pellets that were most dissimilar.

The results are discussed in terms of their implications for optimal foraging theory.

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Chapter I

Introduction

The acquisition of food is among the most basic behaviors animals must perform. The availability of food affects many aspects of animals' lives; most critically, without adequate food supplies, animals die. The food supply often sets the upper limit of the population of a species in an area and is the resource for which animals most often compete. Availability of food affects other decisions an animal must make, such as selection of a burrow or nesting site (Alcock, 1984; Hutchinson, 1959).

The problem of acquiring food is not easily solved. Not all the potential food items can be utilized by an individual, perhaps due to limitations in the efficiency with which a type of food can be digested. The availability of many types of food fluctuates seasonally so that during some times of the year food is abundant and during other times it is scarce. Competition among animals for the same resources also may limit the amount of food one animal can acquire. And while it is true that survival critically depends on the ingestion of enough calories, animals must avoid toxic compounds and acquire other nutrients (Pulliam, 1975; Rozin, 1976).

Feeding behavior has long been a central concern for both physiologists and psychologists (Hutchinson, 1959). Until recently, most physiologists and psychologists have dealt primarily with food consumption. Collier and Rovee-Collier (1981) point out that psychologists, influenced by operant methodology, have focused on the effect food has in changing the behavior of deprived animals, and that physiologists have emphasized the role of diet in maintaining homeostasis. There has been, these authors maintained, little emphasis on food-seeking behavior itself.

The relationship between feeding and the characteristics of animals' niches have been ignored by both groups. For example, much work in psychology has looked at the behavior of pigeons or rats acquiring food by performing an operant task. Collier and Rovee-Collier point out that key-pecking and maze-running bear little resemblance to the ways in which pigeons and rats find food in their natural habitats. Another ecological variable commonly ignored by both psychologists and physiologists is the social context in which animals normally live. Many birds and mammals live communally and forage in groups. Social organization is bound to play a role in food-seeking behavior as well as in the ingestion and utilization of food. Taking these factors into account would lead to a more thorough understanding of feeding behavior, according to Collier and Rovee-Collier. The recent behavioral ecology literature (Pyke, Pulliam, & Charnov, 1977), in which foraging behaviors are seen as involving all the factors that affect the active search, pursuit, and capture of food as well as its consumption, is an important contributor to this understanding.

Within psychology, there has been a shift away from the almost exclusive use of food as a motivator toward exploration of food-seeking as interesting in its own right. The role of early experience, especially social experiences, in the selection of food types has been the focus of most of these investigations.

Social Transmission of Food Preferences

Many young organisms are highly dependent upon parental care for their survival. In particular, mammalian young depend upon their mother's milk as the major source of nutrition for some time after birth. During the transitional period of weaning, the young gradually acquire fewer of their necessary calories from milk and more from solid food. When the process of weaning is complete, the animals are independent feeders.

Once rodents have become independent feeders, what determines the types of food they eat? Kuo (1967) proposed that food habits are formed on the basis of the kinds of foods animals were fed early in life, and he rejected the notion that there is a "genetic basis in the central neural organization" (p. 71) for determining food preferences. Galef and his colleagues (Galef, 1977) have accumulated convincing evidence to show that food preferences in rats are transmitted from dams to offspring. Rat pups eating their first meals of solid food chose the food their mothers had been fed rather than a novel food. New foods are more likely to be poisonous than are familiar foods, so the transmission of specific food preferences from mother to offspring is highly adaptive (Galef, 1970, 1977; Mitchell, 1976). If a preference for a particular diet did not develop before weaning is complete, weanlings would sample many foods indiscriminately and, therefore, be more susceptible to poisoning (Galef, 1977). Clearly, it is of adaptive advantage for the young to profit from the experience of their dams and of other adults in selecting solid food.

There are at least three mechanisms whereby a young rat's first meals of solid food can be influenced by adult conspecifics. First, as Galef and Clark (1971b) demonstrated, pups follow adults to feeding sites and eat next to the older animals. The onset of eating in young animals may, therefore, be affected by social facilitation (Neuringer & Neuringer, 1974). Second, adult rats leave olfactory cues in areas they visit and these cues may sway pups' choices of areas in which to begin feeding (Galef & Heiber, 1976). Finally, a female's diet may influence her pups' dietary preferences directly through gustatory cues passed through her milk (Bronstein, Levine, & Marcus, 1975; Capretta & Rawls, 1974; Galef & Clark, 1972; Galef & Henderson, 1972; Galef & Sherry, 1973). For example, Hepper (1988) fed pregnant rats a clove of garlic each day until day 21 of gestation. Other pregnant rats were fed a normal diet. At 12 days of age, their pups were placed in the middle of a testing arena. Two petri dishes, one containing garlic and the other onion, were placed under the wire-mesh floor of the arena at opposite ends; the position of the dishes was counterbalanced. Offspring of mothers who ate garlic showed a preference for the garlic side; control pups showed no consistent preference. Hepper interpreted these findings as showing that olfactory cues are available to rat pups _in utero_ and affect later preferences.

In order to demonstrate the role of social factors in the transmission of food preferences, Galef and Clark (1971a) established mixed-sex colonies of adult rats and trained them to eat one diet exclusively. The animals were presented with two diets, both nutritious and palatable, that differed in flavor. One diet was standard laboratory chow; the other was a high-sucrose compound, which is highly preferred in free-choice situations. Galef and Clark laced the high-sucrose diet with a sublethal dose of lithium chloride (LiCl); after eating this food, the animals became ill. Subsequently, they avoided this food and continued to avoid it after uncontaminated samples were made available during the daily three-hour feeding sessions. The avoidance was based on taste cues, not on location. When the pups first left the nest and ate solid food, they ate the safe diet exclusively despite never having been poisoned on the other diet. After they had eaten solid food for a few days, the young rats were transferred to a new colony cage without the adult rats. In this new situation, the preference for the safe diet persisted for 8 - 10 d after transfer. Bronstein et al. (1975) fed pregnant and lactating rats one of the two foods Galef and Clark (1971a) used and then measured their foster pups' food preferences by presenting them with the food the dam had eaten or the other, novel, food. Weanling rats showed relatively elevated intake if offered the diet eaten by their foster dams. This was a short-lived effect; prolonged presentation of the unfamiliar diet led to the pups preferring it if the new food had a high sucrose content.

Another demonstration of the potentially powerful effect of preweaning experiences with a particular flavor on postweaning food preferences was reported by Capretta and Rawls (1974). Pregnant rats were given either plain tap water or garlic-flavored water for the last 3 - 4 days before parturition and throughout the 21-day period during which they suckled their pups. Pups had no access to the water supply during this period. At weaning, the pups either continued on the water their mothers had received or were switched to the other kind of water for five days. Pups were then given a free choice of plain tap water or garlic-flavored water for eight hours a day for twelve days. The measure of preference employed was the amount of garlic water consumed. Rats that had had garlic flavor both before and after weaning consumed most of the garlic-flavored water, and those who had been given tap water both before and after weaning drank virtually no garlic water. The group that received garlic-flavored water before weaning and tap water after weaning drank more garlic-flavored water than did the group that received tap water first and garlic water second. Thus, preweaning experience appeared to be more important than post-weaning experience. After these tests were over, all the rats were given a month of tap water and then were tested again, as above, for 5 days. The same ordering of groups recurred, showing the persistence of the effect, which

> "demonstrate[s] . . . that adult rats can, in some fashion, lead their offspring to feed solely on a safe diet . . . [and] that food preferences learned in the presence of adults continue to affect the diet preference of pups for some time after the pups' removal from adult influences" (Galef, 1982, p. 284).

The social transmission of information about food is not limited to adult - pup interactions. Strupp and Levitsky (1984) showed that when an observer rat interacted with a demonstrator rat, the observer tended to eat the same food that the demonstrator had eaten, even though it was unfamiliar. A similar result was obtained by Posada-Andrews and Roper (1983); in their experiments, one rat was removed from a group of rats, fed a distinctively-flavored diet, and then returned to the group. Subsequently, the other animals in the group chose the diet the demonstrator had eaten. The effect was shown to be dependent upon olfactory cues and the observer rats were able to use the information from the demonstrator as long as 12 hours after interaction was ended (Galef & Wigmore, 1983). Live rats were more potent sources of information than were dead rats (Galef & Stein, 1985), anesthetized rats (Strupp & Levitsky, 1983), or a piece of cotton coated with one of the two flavors (Galef, Kennett, & Stein, 1985). Socially-induced diet preference was shown to ameliorate profound

LiCl-induced aversion to that diet (Galef, 1985b), suggesting that social influence may be important in the diet selection of free-living adults.

The role of experience in the development of taste preference seems clear. However, taste is not the only cue to which animals may respond when making foraging decisions. Other factors involved in food choice have been the concern of some behavioral ecologists, who have developed a set of models in order to describe food-seeking behavior by adult animals. For these theorists, the variables of interest are those that define the energy balance animals must maintain if they are to survive and reproduce.

Optimal Foraging Theory and the Optimal Diet Model

The behaviors that are included under the rubric of foraging have been the focus of a number of theoretical treatments over the years (e.g., Emlen, 1966; Krebs, Stephens, & Sunderland, 1983; MacArthur & Pianka, 1966). The literature in this area is collectively known as optimal foraging theory (OFT). The purpose of OFT has been to explain and predict many aspects of the foraging behavior of adult animals. One purpose is the determination of the ecological factors that affect the kinds of foods animals eat. The assumption common to all early OFT models is that "the fitness associated with an animal's foraging behavior has been maximized by natural selection, subject to certain constraints" (Pyke et al., 1977, p. 138). OFT models are based on general assumptions derived from neo-Darwinian theory (Post, 1984). All behaviors, including foraging, that animals engage in must contribute to their inclusive fitness. Pyke et al. (1977) explicitly outlined these assumptions with reference to foraging behavior:

1. Foraging behavior shows heritable variation within populations.

2. Natural selection favors those individuals in a population contributing the most genetic material to subsequent generations, and those that are optimal foragers should have higher inclusive fitness. Hence,

3. Natural selection will result in a shift of the average foraging behaviors in the population toward the foraging behavior giving maximum fitness.

The focus of optimization models of foraging (or of any behavior) is the determination of the ways in which the costs and benefits of alternative behaviors directly affect an individual's inclusive fitness. It is extremely difficult to determine how behaviors affect animals' inclusive fitness, because it is difficult to determine the absolute genetic similarity among related animals (Post, 1984). Most models rely on a more readily measurable currency, one that is assumed to contribute to inclusive fitness, such as number of matings, avoidance of predation, success in agonistic encounters, and, for OFT, rate of food intake.

OFT has been applied to four situations in particular: choice of an optimal diet, choice of an optimal patch in which to forage, optimal allocation of time to different patches, and optimal patterns of movement from one patch to another. The focus of this study was on the first of these, choice of an optimal diet; for a review of the literature pertaining to the others, see Krebs et al. (1983) and Pyke et al., (1977). Much work has been done on the composition of the optimal diet; indeed, the conclusions drawn from this work have been consistent and comprise what can be called the optimal diet model (ODM).

As in any optimization theory (Maynard Smith, 1978), it is necessary to identify the range of alternative behaviors and then to determine the relationship between particular behaviors and some currency that is to be optimized. There are three steps in finding the optimal behavior (Schoener, 1971). First, a currency must be chosen; that is, the theorist must decide what animals are maximizing or minimizing when they are foraging. In OFT, rate of caloric intake (the ratio of gross daily energy gain to total daily energetic costs) is the generally used currency, although other currencies are possible, such as net daily energy gain, time spent resting, or total daily caloric expenditure (Pyke, 1979). Second, the appropriate cost-benefit function must be determined. Animals gain calories as a result of eating, but they also expend energy while performing all the behaviors involved in survival. Both factors must be accounted for in any optimization model of foraging. In order to simplify the models, the general rule in OFT models has been to assume that animals make foraging decisions in order to maximize profitability (or rate of caloric intake), which is defined as gross energy gain (e) divided by handling time (h), or e/h. Although h is formally defined, in the model, as including all travel, search, and manipulation times involved in finding food, it is assumed that these are directly correlated with the gross daily energetic costs incurred by an animal and can, therefore, be used in the calculation of profitability.

Third, the solution must be found. Foods are included in or excluded from the optimal diet on the basis of their profitability. In every foraging situation there is a minimum profitability value at which an animal will "break even," and that varies from one situation to another. For example, if an animal has minimal handling costs or has to feed only itself, it will accept food items of a wider range of profitabilities than if it must travel a great distance to obtain food or must feed dependent offspring. ODM predicts that animals will not take food items that are below this minimum, or threshold, value. If adding a food type to the optimal diet would cause the value of the diet as a whole to fall below the threshold, that food type will not be included in the diet. In other situations, to maintain energy requirements, previously shunned items may be included. One environmental variable that affects the threshold is the abundance if food items of differing probabilities. A food will be included in or excluded from the diet according to the abundance of higher-ranking (i.e., more profitable) food types. For example, if three foods are available in the environment, of high, medium, and low profitability, and if all are equally abundant, the foraging animal should choose the highly profitable prey exclusively. As this type becomes scarce, the animal should still take it whenever it is encountered but should also begin taking prey of medium profitability. Finally, as both high- and medium-profitability prey are depleted, low-profitability prey will be taken. Conversely, as the abundance of more profitable prey increases, lower-ranking prey should be forsaken in reverse order of ranking, regardless of their abundance (Emlen, 1966; Krebs et al., 1983). As a corollary of these relationships, most ODM theorists predict that, for a given food type, there should be no partial preferences; that is, items of a particular food type should always be either accepted or rejected whenever they are encountered (Pyke et al., 1977). However, as Pulliam (1975) and Westoby (1974) have shown, if the theory is extended to include random fluctuations in abundance and/or nutrient constraints, partial preferences can be expected.

It has been shown that animals do respond to shifts in the abundance of food types by altering the range of items in their diets. Werner and Hall (1974) examined the diet of bluegill sunfish (Lepornis macrochirus). In this laboratory study, the fish were allowed to feed on three sizes of daphnia at three levels of abundance. At each level of food abundance, the number of daphnia present of each size class was equal. As predicted by the model, when food was scarce, the fish ate every daphnia they encountered, regardless of size; at a medium level of abundance, only the two largest size classes were consumed. At the highest level of abundance, only the largest prey were eaten. Werner and Hall concluded that, at low densities, the search time for the largest size is very long; accordingly, because time is probably an important cost in the economics of feeding for fish (insects are active for only a short time each day), the animals cannot afford to look for and capture only the largest prey. O'Brien, Slade, and Vinyard (1976) reinterpreted these results to show that under all conditions bluegill choose the prey which appeared largest; as large prey became scarce, smaller prey appeared relatively larger and the fish began to eat more insects from smaller size classes.

Barnard and Brown (1981) also confirmed an ODM profitability prediction; they showed that in the absence of competition, common shrews (Sorex araneus) were equally likely to take large and small mealworm pieces when the encounter rate with large pieces was relatively low. When the encounter rate with the large size was high, the shrews took more large prey than small. Encounter rate is directly related to abundance; a high encounter rate means that there are a great many prey of that type in the environment. Varying the encounter rate of the animals with small prey did not affect their preferences for large prey as long as the encounter rate for large prey was at least 0.03 encounters/second, the "switching point" (Houston, Krebs, & Erichsen, 1980). The switching point is the value at which the animal changes from choosing one prey type exclusively to taking two or more prey types; it is directly dependent on the abundance of foods of different profitabilities available to the foraging animal.

The research of both Werner and Hall (1974) and Barnard and Brown (1981) showed that animals chose larger prey preferentially when it was readily available and increased the range of prey sizes taken when the abundance of the largest sizes fell. In both sets of experiments, however, profitability was not measured directly. The positive correlation between size and profitability was assumed. Barnard and Brown admitted that the larger prey sizes might be less profitable than the smaller prey sizes, due to differences in handling time or to the fact that the larger mealworm pieces seemed "more chitinous" (p. 242) than the smaller pieces. Despite this problem, the conclusion that has been drawn from these studies as well as others that have examined prey size is that animals seem to use a rule of thumb when choosing prey items; lacking the ability to directly assess the net caloric value of food items, they use size as the most reliable index of value and select the largest prey available.

While most of the research on ODM has been done in the laboratory, ODM predictions have been supported in more natural situations. Lewis (1982) assessed the relative caloric contents of acorns of three species of oak (red oak > chestnut oak > white oak) and found that wild gray squirrels (Sciurus carolinensis), when given free access to all three types, chose acorns according to their profitability. The squirrels not only ate more of the red oak acorns, they buried more of them for use during the winter. However, hickory nuts, which are less profitable than any of the acorns, were preferred to the red oak acorns. Lewis attributed this to the fact that hickory nuts contain more protein than do acorns.

Few studies have confirmed the quantitative predictions of ODM (Gray, 1987), although most have shown that the qualitative predictions of ODM are correct. Experimenters have generally given animals different sized pieces of one food type (e.g., daphnia or mealworms) and have found that, in general, animals chose the largest pieces if there are a great many of them available. This exclusive preference for large prey decreases as prey becomes less abundant. It is important to realize that, while ODM does predict these results, so might other mathematical models. Aronson and Givnish (1983) point out that other models, which they refer to as "null hypothesis models," may fit the obtained data as well as does the optimality model. One such model is the "encounter rate model," which is based on the assumption that animals take food as it is encountered and that larger food items are more likely to be found because they are more likely to be detected. Nonetheless, the results from ODM studies are important because they show that under certain, somewhat restricted conditions, adult animals forage for the most profitable food items available.

An assumption crucial to ODM is that the individuals of a population of a species will always forage according to certain rules that restrict the content of the optimal diet. These are, essentially, that the strategies employed in looking for food will not change and that the diet will be relatively stable over long periods of time (Gray, 1987; McNair, 1980). However, these assumptions do not necessarily hold. McNair (1981) showed that as few as one or two prey encounters could lead to rapid and reversible changes in feeding behavior. In particular, three types of training were considered: formation of a search image, training in the probability of succeeding when a capture is attempted, and training in the time to pursue, capture, and eat prey. If these training effects have occurred, "a given prey type is more likely to be captured if it was the last type with which the predator had experience" (p. 147). These three types of training can lead to "nonstandard" optimal diets that cannot be predicted from the standard rules for optimal diet calculations. Such calculations assume that encounters with one prey type do not affect encounter with subsequent prey and that the rate at which a predator encounters a particular prey type is dependent upon its abundance and not on the abundance of other types of prey. A nonstandard optimal diet may also result from increased encounters with unprofitable prey (Hughes, 1979). If an unprofitable prey item becomes abundant, and if the animal must handle each prey item before accepting or rejecting it, then the predator may learn to handle the items more efficiently. This would have the effect of making these prey items more profitable by reducing their handling costs. Partridge (1981) studied the role of experience in changing an optimal diet. She first tested four species of wild-caught rodents to determine which of two foods, oats or wheat, was preferred by each one. The modal choice for each species was assumed to be the optimal diet. She then restricted the animals to the other, nonoptimal food and after six weeks gave them simultaneous access to both oats and wheat. They preferred the food to which they had been restricted, a result which raises some problems for the assumptions underlying studies of optimal food choice. As she wrote, "if food preference changes with experience, then either optimal food choice has changed, or food choice is sometimes not optimal" (p. 215). As Partridge's statement clearly indicates, the role of experience in determining an optimal diet has been ignored by most people working in ODM. The work of Galef and others, as reviewed above, has clearly established that experience can alter one aspect of food-seeking behavior, selection of food by gustatory cues. Many animals have a great deal of experience with food before they have to select food on their own, and these experiences will affect the foraging behaviors animals display as adults.

Central-Place Foraging

Some animals do not eat their prey where it is captured but return with it to a central place where it is eaten, stored, or fed to dependent offspring. These animals are called central-place foragers, and the theory that deals with their behavior is referred to as central-place foraging theory or CPF (Orians & Pearson, 1979). In those species that show parental care, central-place foraging occurs at least some of the time, while parents are feeding their young. Many mammals, particularly rodents (Brown & Lieberman, 1973; Giraldeau & Kramer, 1982), and some birds (Sherry, 1985) cache food to be used during periods of prey scarcity.

Although Orians and Pearson originally developed their model of CPF to explain the behavior of parent birds feeding their young, it is applicable in many other contexts. Some animals are single-prey loaders - they bring back one food at a time; others, multiple-prey loaders, bring back many items per trip. The profitability of prey varies systematically with traveling time, just as ODM predicts; the difference is that in CPF the return trip and the energy expended in carrying prey are calculated as part of the handling costs. At farther distances, selectivity increases, so that the variability of prey sizes taken decreases. One application of CPF has been analysis of the rate at which multiple prey loaders load food in order to take it back to the central place (Giraldeau & Kramer, 1982; Kasuya, 1982; Kramer & Nowell, 1980). Giraldeau and Kramer (1982) found that load size increased with increased travel time between the foraging site and the animals' burrows, as Orians and Pearson (1979) predicted. This finding has been confirmed with Japanese paper wasps (Kasuya, 1982), European starlings (Tinbergen, 1981), and wheatears (Brooke, 1981). However, in all cases, the CPF prediction about the selection of food items corresponded to the basic ODM prediction. To maximize the relationship between load size and profitability, only the largest available items that an individual animal can carry should be taken. This was demonstrated by Kramer and Nowell (1980), who showed that Eastern chipmunks (*Tamias striatus*) filling their cheek pouches with sunflower seeds became more selective as their pouches filled. The loading rate decreased as the animals searched for the largest seeds available.

The Development of Optimal Diets

The role of social factors in the transmission of preference for a particular food type has been well-established (e. g., Galef, 1985a). Yet, adult animals discriminate not only between food types but also, as the results of studies of ODM revealed, within a kind of food, preferring more profitable (larger) food items. How is it that animals become able to discriminate profitable from unprofitable food? It is clear that animals learn to forage optimally, and a number of mechanisms have been invoked to explain how this ability is acquired (Fantino & Abarca, 1985; Pulliam, 1981). It is logical to suppose that social transmission processes, as reviewed by Galef (1985b), are involved in this learning, although their potential roles have been ignored.

The purpose of the present set of studies is to investigate the predictions and assumptions of ODM in a developmental context. The research on socially-mediated food choice makes it clear that some information about food selection is learned through interaction with conspecifics, and that this learning can occur early in the life of an animal. If young rodents can come to prefer a specific flavor of food because of early experience, then it seems likely that other aspects of food choice are affected by experience as well. Optimal foraging theory was developed in order to predict animals' food choices when energy maximization is the focus of concern. An assumption of ODM is that animals choose profitable food because there is a genetic tendency to do so. In other words, there is some sort of innate recognition device so that animals know what food items are profitable and, therefore, will choose those items. However, this assumption is not logically necessary in order to predict ODM results. Profitability is defined as the relationship between energy gained and energy lost, and, although animals may not be able to assess these factors directly, they have access to cues that reflect them, such as hunger and satiation. Animals behave appropriately in response to these cues (Collier & Rovee-Collier, 1981). Before some animals become independent feeders, they have available to them a great many food-related cues; not only are they exposed to information about taste, but information about profitability is also available to them. For those animals, such as hamsters and some other rodent species that cache food, the items in the hoard are probable sources of that information. It is also the case that, before they are weaned, rodent pups accompany their dams on foraging trips, and they tend to eat from the same food patches. If the adult animal chooses food items of optimal sizes, the young may learn to do so as well.

The storage of food for later use has been documented in a number of families of birds and mammals, and a few investigators have been interested in examining the ways in which these animals establish, use, and rely upon stores of food (Smith & Reichman, 1984; Vander Wall & Balda, 1981). Much of the research has focused on animals' memories for cache sites (Macdonald, 1976; Vander Wall, 1982) as well as on the social consequences and economics of hoarding (see Sherry, 1985, for review). However, little work has been done on the functions of hoarding and of hoards. Wong and Jones (1985) concluded that hoarding has many functions, both across species and within species, but that it serves generally as an activity performed to avoid future food shortages. This is, most likely, more relevant for adults than for young, for it is the adult animal that actively forages for and returns to the central place with food. Very little is known about the function hoards may serve for young animals that are exposed to them. For young animals, the hoard may serve a discrimination function in that they may equate "what is in the hoard" with "food." The contents of the hoard represent a sample of the food types available in the environment and, when the young begin searching for food on their own, they may choose primarily the food types to which they were exposed in the hoard. By manipulating what is in the hoard, then, it may be possible to affect the initial food choices of young animals when they begin independent foraging.

Foraging Behavior in Hamsters

Golden hamsters (Mesocricetus auratus) seem to have a diverse diet in their natural habitat, although they are primarily granivorous. Although grain and seeds make up the bulk of their diets, hamsters also prey upon arthropods, especially nocturnal ground-dwelling insects such as crickets (Murphy, 1985). A great deal of research has been done on the behavior of golden hamsters preying on insects. Polsky (1977a; 1977b; 1978a), in an extensive series of experiments, found that hamsters' skill in catching insects greatly improves once they have caught an insect. This one-trial learning was attributed to strong genetic programming (Polsky, 1978b), although the important role of experience seems clear.

Langley (1985) examined the relative importance of olfaction, audition, and vision in the predatory behavior of golden hamsters. These senses were blocked in five hamsters either singly or in combination. The hamsters were then required to locate either a live, tethered cricket or a dead cricket. All three senses were found to play a role in locating the live cricket (which could move around), whereas vision and olfaction played a role in locating the stationary cricket. In both cases, Langley found that vision was the dominant sense in locating the prey. The obvious dependence of hamsters on vision for locating and capturing prey is interesting in the light of the research of Rahmann, Rahmann, and King (1968) who demonstrated that hamsters had less well-developed visual acuity than did members of a number of other rodent species. Rahmann et al. had hamsters and other rodents discriminate between stationary striped patterns. Hamsters could not discriminate as finely as could other rodents. In Langley's studies, the hamsters did not have to make a visual discrimination; vision was needed in order to orient themselves toward the prey.

Another aspect of hamsters' foraging behavior that has been studied is hoarding. The most salient physical characteristics of hamsters are their fur-lined cheek pouches. These are filled quite full during a foraging trip. Hamsters return to their nest burrows with filled pouches, where they are unpacked into a hoard. Hamsters are known as prodigious hoarders (Morgan, 1947; Smith & Ross, 1950); in fact, their name was derived from the German hamstern, "to hoard" (Roberts, 1981). Much laboratory research on hoarding has used golden hamsters as subjects; the emphasis of these studies has been on the development of the motor aspects of hoarding (Daly, 1976; Etienne, Emmanuelli, & Zinder, 1982). Bevan and Grodsky

(1957) examined the role of early experience with solid food on the development of adult-like foraging behavior and found that young animals that had been given solid food showed mature hoarding behavior earlier than did those that had been given liquid food. More recent research (Etienne et al., 1982; Turpin, Johnston, & Fulk, 1988) has shown that dispersal from the family group at the end of weaning induces the establishment of individual hoards in hamsters.

The four studies presented in this dissertation are designed to examine the potential role of early experience on later food selection behavior in golden hamsters. The emphasis in these experiments is on size, because of its theoretical importance in ODM, as reviewed above. The specific question addressed is whether early experience with food items of one size will induce a preference for that food size in later foraging.

Chapter II

Experiment 1: Profitability

As discussed in Chapter 1, profitability is the currency of choice in most optimization models of foraging. The optimal diet model (ODM) predicts that animals will select the most profitable food items available when more than one food item is available. The propensity to take the most profitable prey available is seen as being sensitive to environmental context, such as the availability of foods of different values, the distance animals must travel to get to food and search for it, competition among animals for scarce resources. and the presence or absence of predators. Learning is seen as involved, therefore, in animals' reactions to changes in the environmental context in which food is found, but animals do not need to learn what profitable food is. In an ideal situation - abundant food of a variety of sizes with adequate nutritional composition, negligible travel and search times, and the absence of competitors and predators - the most profitable food will be chosen. The role of early experience in the establishment of what is profitable has not been considered. However, in light of the effects of early experience on taste preference, it seems highly likely that experience may affect the relationship between food profitability and food choice.

The more experience animals have with one food size, the easier that food size will be to detect, decreasing search time, and the easier it will be to handle (Hughes, 1979). Making detection easier and handling more efficient would serve to decrease the energy expended in foraging. In effect, food of a particular size would become more profitable even though its caloric content would not change. Therefore, for an ODM prediction to be confirmed, two things must be true: Larger pieces must contain more energy than small pieces, and handling time for the sizes must differ only negligibly. The first requirement is a given, in most cases; however, the second requirement, that handling times differ only slightly, if at all, is not. Many tests of ODM have been done on the basis of these assumptions; different-sized pieces of one kind of food have been presented to many different kinds of animals.

The purpose of Experiment 1 was to measure the profitability of three sizes of Noyes food pellets. All had the same caloric content (3.9 KCal/g) but it seemed likely that different-sized pellets would have different handling times. If handling times are different for different sizes, then profitability may not be proportional to size, and this may affect pellet choice in the free-foraging situation.

General Procedure

Subjects

All the animals used in the studies reported here were golden hamsters (*Mesocricetus auratus*) born to members of the breeding colony in the psychology department at the University of North Carolina - Greensboro.

Adult hamsters are considered semi-isolates, and, in the wild, adults meet only to mate (Murphy, 1985). In the breeding colony at UNC-G, adult hamsters are kept in individual cages. Female hamsters go into estrus every four days and give birth after 16 days of pregnancy. There may be as many as 15 or as few as 3 pups in a litter. Average litter size varies among laboratories; in the UNC-G colony, the average litter contains 8 - 10 pups. Weaning in the laboratory generally occurs at 21 days of age, although Siegel (1985) reported that weaning can occur as early as 19 days. In the UNC-G laboratory, pups have been successfully weaned at 16 days of age if they weighed at least 20 grams. Rowell (1961) concluded, from her studies of golden hamsters in semi-natural conditions, that complete mother - young separation in the wild occurred at 30 - 35 days of age.

At birth, the pups are altricial. Physical development proceeds relatively quickly; the young begin eating solid food at 9 - 10 days of age, before they begin walking (10 - 12 days) and before their eyes are open (12 - 15 days).

Methods

The subjects used in this study were three litters of golden hamsters (*Mesocricetus auratus*). Only litters with four or more pups were used in this study; in order to maintain a constant litter size of four, larger litters were culled using halothane anesthesia when the pups were 5 days old.

Until postpartum day 9, the dams of the experimental litters were maintained on *ad lib* Purina Laboratory Chow 5001 (Ralston-Purina Company). They were kept in polypropylene breeding cages, 45.7 x 35.6 cm, and allowed free access to water. On day 10, the dams and their litters were transferred to clean cages. Each litter was provided with one of three sizes of Noyes food pellets (Noyes Pharmaceutical Company, Formula A: Small Rodent Diet): 20, 45, or 94 mg pellets. These sizes were chosen because they reflect the sizes of food that are probably available to hamsters in the wild. Initially, dams were provided with 24 g of food; 12 g were added daily. This was enough to maintain normal growth and development of the pups. On day 35, the pups were removed from their mothers and placed in individual cages, 26.7 x 12.7 x 15 cm, each containing 12 g of the familiar-sized pellets.

On days 36, 37, and 38, each animal was presented with a plastic petri dish containing 12 g of either 20, 45, or 94 mg pellets. Each size was presented singly and the order of presentation was counterbalanced across days, animals, and rearing conditions. The hamsters were allowed one foraging trip for each pellet size; the weight of the pellets remaining in the dish was determined and subtracted from 12 to determine the amount of food (in g) each animal took. The duration of each foraging trip was also measured using a hand-held stopwatch.

The measure of profitability used was (mg/sec) x 1000. The multiplication was done to clear all decimals from the analysis and does not alter relationships among the variables (Kirk, 1968). A 3 (Rearing) x 3 (Days) x 3 (Size) Latin Square split-plot ANOVA was performed on these data. Statistical values reported here were reconverted to mg/sec.

Results

The only significant source of variance in the ANOVA was the main effect for Size ($\underline{F}$ (2, 18) = 20.16, $\underline{p} < .01$). Figure 1 shows the means and standard errors for these data. A Scheffe's post-hoc analysis of this effect showed that the means for all three sizes were different from one another ($p < .05$): for 20 mg pellets, $M = 9.88$ mg/sec; for 45 mg pellets, $M = 31.37$ mg/sec; for 94 mg pellets, $M = 77.9$ mg/sec). The 94 mg pellets were more profitable than the 45 mg pellets, which were more profitable than the 20 mg pellets. These results are shown graphically in Figure 1.

Analysis of the handling times showed that the mean number of pellets taken per second did not differ across sizes (F (2, 69) = 0.29, n.s.; for 20 mg pellets, $M = 0.291$; for 45 mg pellets, $M = 0.298$; for 94 mg pellets, $M = 0.257$).

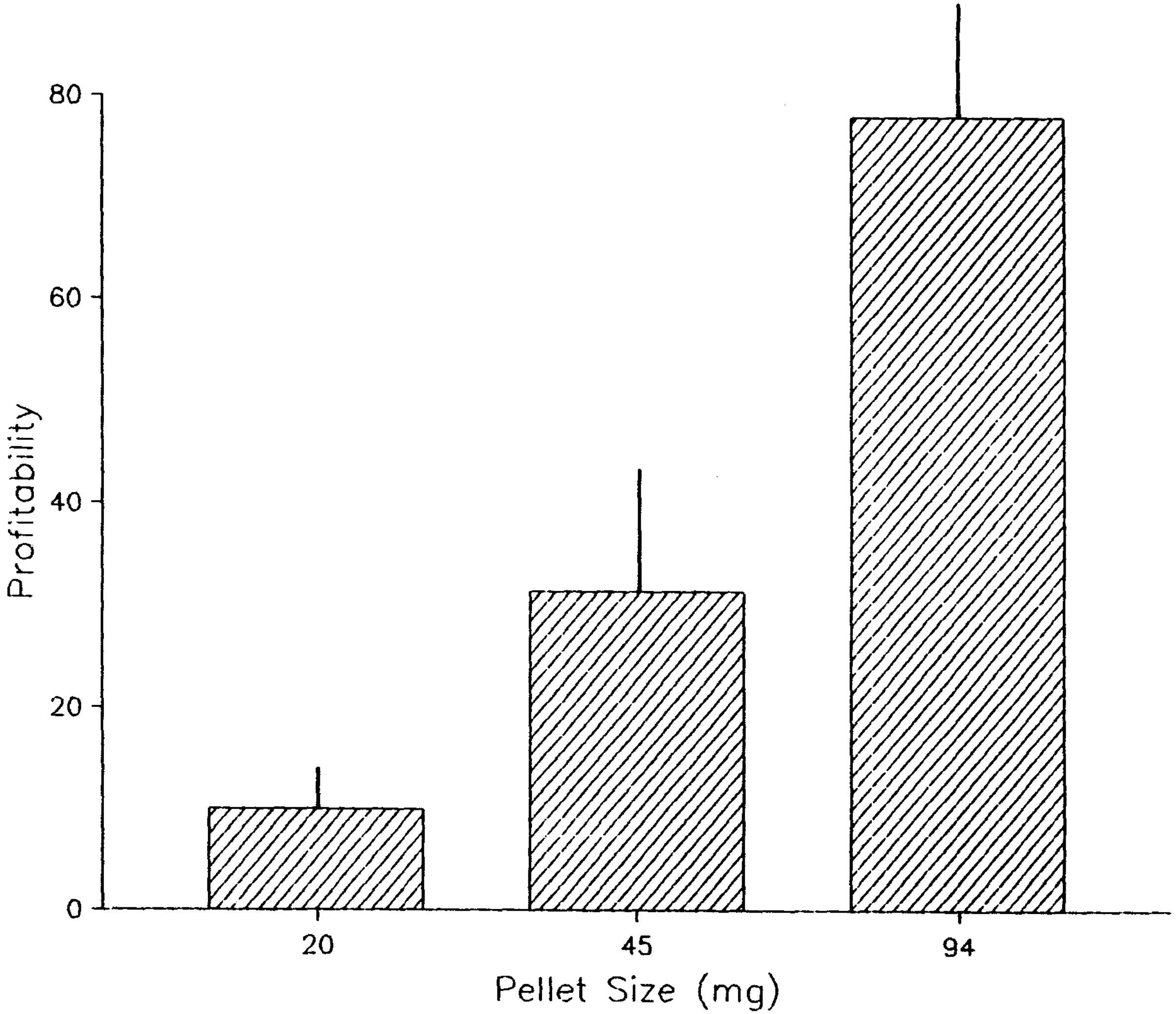

FIGURE 1: Profitability for 20, 45, and 94 mg Pellets, Experiment 1

Discussion

The results of this study indicate that, at least for the range of sizes used in this experiment, size is a direct reflection of profitability. The largest size (94 mg) is 2.5 times as profitable as the middle size (45 mg), which is 3.2 times as profitable as the smallest size (20 mg). Thus, over the range of sizes to be used in Experiment 2, profitability is indeed proportional to size. In order to maximize foraging efficiency, according to ODM predictions, a hamster should take the largest pellets available whenever possible.

There was no main effect of Rearing and no Rearing x Size interaction, indicating that the experience with different sizes of pellets prior to testing did not affect food-handling ability.

Chapter III

Experiment 2: Size Preference

Experiment 1 established, for the range of pellet sizes employed, that profitability is directly related to size and that early experience with a particular size did not decrease handling time and, thereby, increase profitability of that size. However, Experiment 1 revealed nothing about preference; food types were presented successively, so the animals could not make choices based on the size of food. In the natural habitat of hamsters, it is likely that many kinds of food are available simultaneously. It may be the case that the effects of early experience on foraging are manifested only in situations in which animals are confronted with a choice between two or more food sizes. Experiment 2 was designed to mimic such a situation. Three possibilities exist:

1. Early experience has no effect, and hamsters will take the most profitable (largest) size available regardless of the size they had experienced earlier in life.

2. Early experience has no effect and hamsters are not sensitive to profitability. In this case, hamsters will take prey items as they come upon them; that is, at encounter rate.

3. Early experience has an effect; hamsters will, at least initially, prefer items of the size with which they have had experience.

If animals in Experiment 2 respond merely to profitability, so that early experience does not play a role in the choice among items that vary in size, the results of Experiment 1 lead to the prediction that hamsters should begin taking 94 mg pellets from the beginning of testing. If hamsters are responding neither to profitability nor to familiarity, they should take pellets at encounter rate. And, if early experience has an initial effect, the animals should take the familiar item size.

Methods

Subjects The subjects used in Experiment 2 were nine litters (4 animals per litter) of golden hamsters.

Rearing Conditions Five days before their litters were due, female hamsters were placed in a rectangular wooden arena (0.61 x 1.22 m). The floor of the arena was covered with about 5 cm of corn cob bedding (Bed-O-Cobs). Attached near one corner of the arena was a plastic tub (30.5 x 22.9 x 15 cm) which served as a nest box. The nest box was covered with a top made of hardware cloth and was connected to the arena by a metal tube, 5 cm in diameter. The floor of the nest box was covered with the corn cob bedding material and shredded newspaper was provided for nest building. Water bottles were suspended so that their sipper tubes protruded into the nest boxes through the hardware cloth of the tops. Until the day the litters were delivered, the dams were fed Purina Laboratory Chow 5001. The animals were kept on a reversed light cycle (14 light: 10 dark) for the duration of the experiment.

On the day a litter was born (day 0), the remaining chow was removed from the nest box. A baking tray (25.4 x 15.2 cm) containing approximately 1.27 cm of sand (Bonsal Play Sand) was placed in the arena. Each day, 24 g of one of the same three sizes of food pellets used in Experiment 1 were spread across and pushed into the sand so that, although the pellets were not completely covered, the animals had to dig the pellets out of the sand. On day 35, dams were removed from the arenas and returned to the breeding colony. Littermates continued to live together in the arena until the end of testing.

Testing Beginning on day 36 and continuing through day 45, littermates were tested individually. For five minutes, the animals were kept blocked in their nest box. The baking tray was emptied and the sand was sifted to remove bedding material and feces that had accumulated. The sifted sand was returned to the baking tray and enough clean sand was added so that approximately 1.27 cm of sand remained in the tray. After each animal was tested, sand was added to the tray as needed. The sand and tray used by one litter were never used by another; after the testing of a litter was completed, the trays were thoroughly washed and dried. To allow individual identification of littermates, animals were marked with indelible ink near their tails on their ventrums. The markings were renewed daily after each animal's test session was completed.

Three hundred food pellets (100 of each of the three sizes) were spread randomly over the sand and pressed into it. One animal was allowed to leave the nest box and enter the arena. Each animal was allowed one foraging trip, which was defined as the period of time between walking onto the tray and walking off the tray. The maximum time allowed for a foraging trip was 10 minutes. At the end of the foraging trip, the animal was removed from the arena and placed in a holding cage. The tray was removed from the arena; the sand was sifted to remove any remaining pellets and was returned to the tray. The remaining pellets were placed in a plastic cup which was labeled with the animal's identification number. This procedure was repeated for each animal until all members of the litter had had a foraging trip. At that point, the animals and sand tray were returned to the arena and the nest box was opened.

Dependent Measures The pellets remaining in the tray after each animal had completed its foraging trip were sorted into sizes and counted. The value obtained from the count was subtracted from 100 to determine the number of pellets of each size the animal had taken. This indirect measure was chosen for several reasons. First, animals would often stop to eat a pellet while foraging, so that counting pouch contents would have been inaccurate. Second, group-living animals do not remove the contents of their pouches as readily as do individually-housed animals (Turpin, Johnston, & Fulk, 1988) and it is difficult to induce hamsters to unpack their pouches. Third, the pouch emptying they do is in the nest box or in the arena, where the pellets become mixed up with the bedding. There, they are hard to find and are likely to get combined with pellets collected on previous days or by littermates. Finally, even if the above problems could be solved, some of the pellets are wet and adhere to one another and others are crumbled or partially eaten.

Once the number of pellets taken of each size was determined, it was transformed into a proportion: p = (number of pellets taken of a given size)/(total number of pellets taken).

Analyses As recommended by Abbey and Howard (1973), litters were used as the unit of analysis.

For each litter, a chi-square analysis was done on the number of pellets of each size taken each day. If the value of the daily chi-square was not significant, it meant that the animals were taking one size independently of the others, that is, at encounter rate. The daily chi-square values are shown in Table 1. Of the 90 values reported, 79 (87%) are significant, indicating that the hamsters were not taking pellets at encounter rate; rather, some preference was being shown. However, the chi-square analyses could be reflecting one of two things: Each litter could be showing an individual preference not shared by other litters in the same rearing condition, or all litters in one rearing condition could be showing the same preference. To resolve this ambiguity, ANOVAs were performed for each rearing condition (3 (Litter) x 3 (Size) x 10 (Days)). Before the ANOVAs were calculated, the proportion data were converted using the arcsin transformation recommended by Kirk (1968).

Results

Examination of the ANOVAs showed that there were no significant effects of Litter or Days nor were there any significant interactions. The only reliable effect was Size. This pattern held true for all rearing conditions: for animals reared on 94 mg pellets, $\underline{F}$ (2, 27) = 98.2; for animals reared on 45 mg pellets, F (2, 27) = 22.3; for animals reared on 20 mg pellets, F (2, 27) = 599 (all ps < .01). To further analyze the Size effect, post-hoc analyses were done using Scheffe's method (Kirk, 1968). Animals reared on 94 mg pellets preferred 20 mg pellets (P = 0.46) to 45 mg pellets (P = 0.34) and both 20 and 45 mg pellets to 94 mg pellets (P = 0.20). Animals reared on 45 mg pellets preferred 94 and 20 mg pellets equally (Ps = 0.39 and 0.36, respectively) and both sizes were preferred to 45 mg pellets (P = 0.25). Animals reared on 20 mg pellets preferred 94 mg pellets (P = 0.47) to 45 mg pellets (P = 0.35) and both sizes to 20 mg pellets (P = 0.18). (See Table 2 and Figures 2, 3, 4, and 5 for the results of this experiment.)

Table 1

Daily Chi-Square Values, Experiment 2

Reared on 94 mg Pellets

Day	Litter 1	Litter 2	Litter 3
1	59.80c	23.42c	12.48b
2	16.56c	1.53	5.82
3	109.16c	7.62a	45.55c
4	72.06c	1.25	22.32c
5	13.40b	2.17	47.50c
6	102.39c	10.03b	20.92c
7	4.71	8.79a	45.14c
8	38.57c	22.88c	88.71c
9	106.17c	10.10b	71.11c
10	52.79c	19.73c	16.03c

Reared on 45 mg Pellets

Day	Litter 1	Litter 2	Litter 3
1	8.64a	17.95c	3.71
2	19.01c	17.91c	0.96
3	28.43c	3.52	21.92c
4	7.80a	2.00	39.59c
5	16.72c	9.11a	32.44c
6	1.00	14.29c	70.99c
7	33.07c	10.35b	41.61c
8	8.76a	18.53c	34.72c
9	12.70b	14.80c	8.36a
10	17.47c	30.03c	52.39c

Table 1

(continued)

Reared on 20 mg Pellets

Day	Litter 1	Litter 2	Litter 3
1	26.33c	15.68c	27.03c
2	42.98c	50.59c	28.62c
3	49.16c	49.81c	41.33c
4	22.07c	38.01c	42.48c
5	78.57c	23.48c	8.61a
6	75.85c	17.27c	26.75c
7	51.28c	33.18c	13.68c
8	51.98c	22.69c	24.68c
9	87.30c	15.00c	27.38c
10	10.39b	18.08c	0.22

Note: all *df* = 2; a: *p* <.05, b: *p* <.01, c:*p* <.001

Table 2

Mean *P* with Standard Errors, Experiment 2

Reared on 94 mg Pellets

Day	20 mg	45 mg	94 mg
1	.42 (.03)	.39 (.02)	.19 (.03)
2	.40 (.04)	.32 (.02)	.27 (.02)
3	.48 (.07)	.39 (.03)	.13 (.07)
4	.51 (.08)	.29 (.01)	.20 (.07)
5	.41 (.04)	.36 (.01)	.23 (.05)
6	.48 (.06)	.34 (.03)	.18 (.04)
7	.43 (.05)	.34 (.01)	.23 (.05)
8	.43 (.05)	.34 (.01)	.23 (.05)
9	.50 (.05)	.34 (.02)	.16 (.04)
10	.52 (.09)	.29 (.06)	.19 (.03)
M	.46 (.06)	.34 (.02)	.20 (.04)

Reared on 45 mg Pellets

Day	20 mg	45 mg	94 mg
1	.43 (.08)	.22 (.06)	.35 (.06)
2	.29 (.05)	.26 (.06)	.45 (.05)
3	.30 (.12)	.27 (.02)	.42 (.10)
4	.39 (.07)	.23 (.03)	.38 (.01)
5	.38 (.08)	.27 (.02)	.35 (.08)
6	.45 (.07)	.25 (.01)	.30 (.06)
7	.38 (.10)	.23 (.03)	.39 (.06)
8	.45 (.04)	.25 (.02)	.30 (.05)
9	.38 (.05)	.27 (.01)	.35 (.05)
10	.48 (.04)	.26 (.03)	.26 (.06)
M	.39 (.07)	.25 (.03)	.36 (.07)

Table 2

(continued)

Reared on 20 mg Pellets

Day	20 mg	45 mg	94 mg
1	.18 (.04)	.38 (.06)	.45 (.04)
2	.17 (.04)	.35 (.01)	.47 (.04)
3	.15 (.04)	.35 (.003)	.50 (.04)
4	.19 (.006)	.32 (.04)	.49 (.05)
5	.19 (.08)	.34 (.03)	.48 (.10)
6	.16 (.07)	.35 (.03)	.49 (.08)
7	.20 (.04)	.33 (.03)	.47 (.07)
8	.17 (.08)	.36 (.02)	.47 (.08)
9	.15 (.07)	.34 (.03)	.51 (.10)
10	.22 (.07)	.36 (.02)	.41 (.05)
M	.18 (.06)	.36 (.02)	.47 (.06)

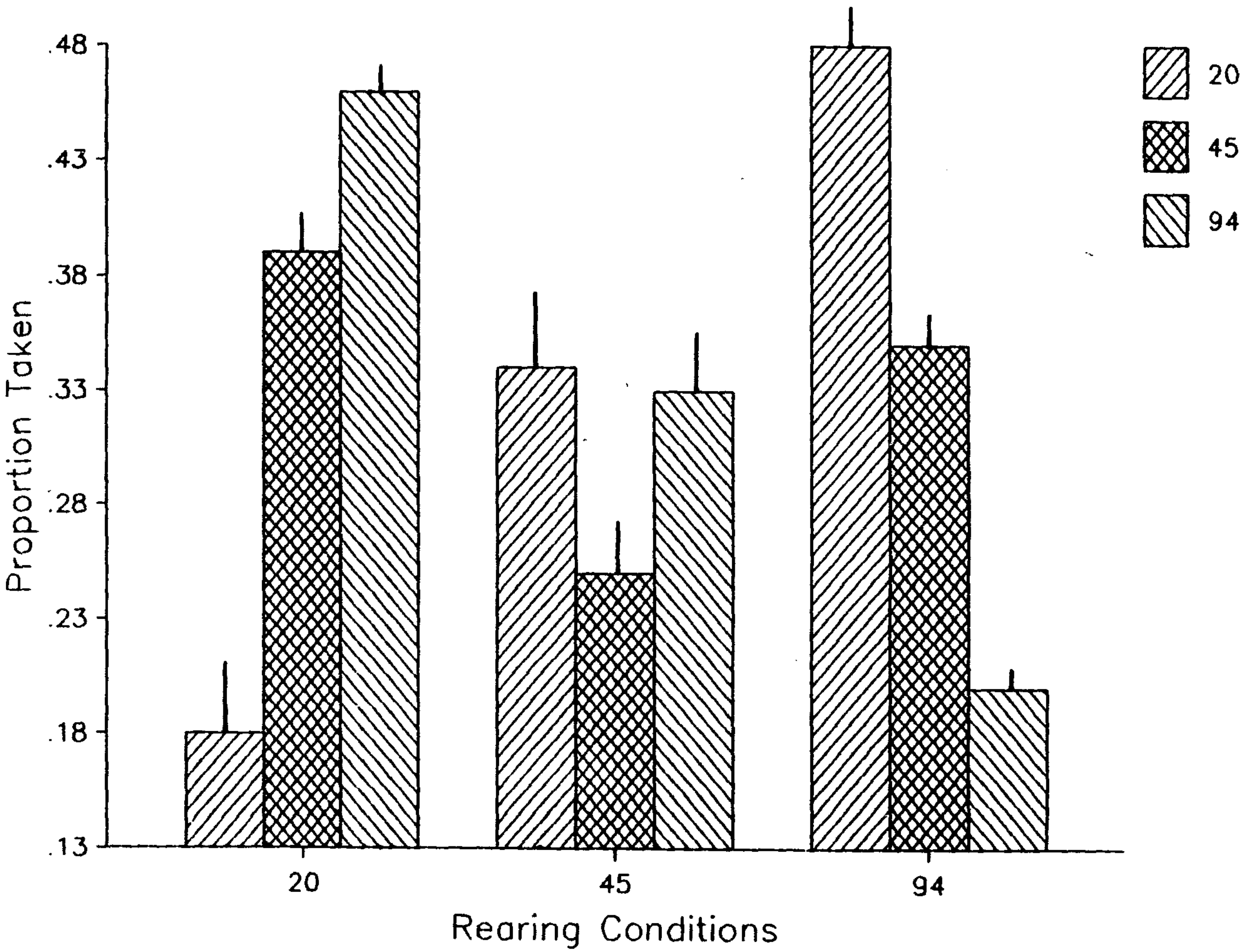

FIGURE 2: Proportion Taken, Experiment 2

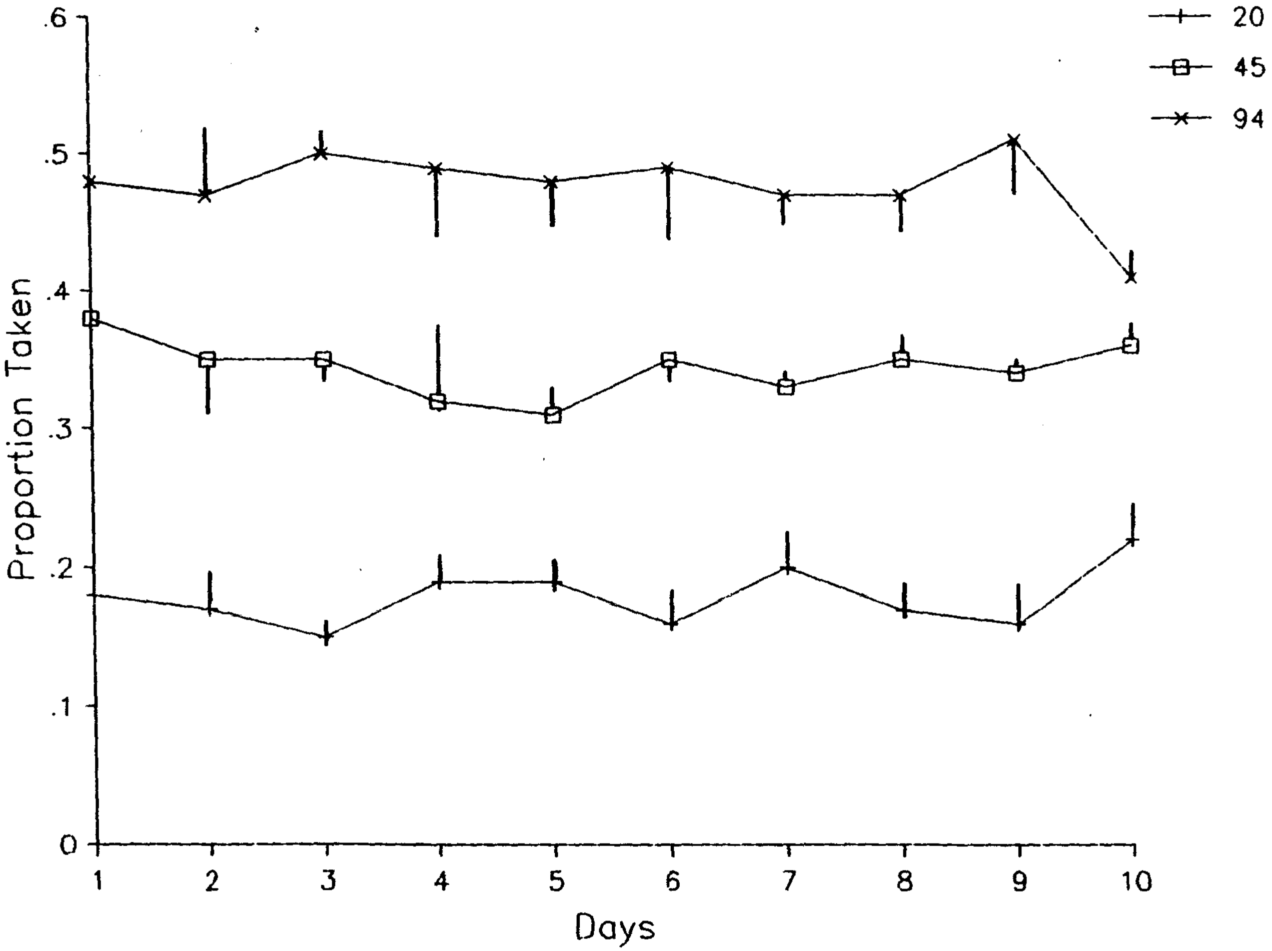

FIGURE 3: Proportion Taken Across Days, 20 mg Rearing Condition, Experiment 2

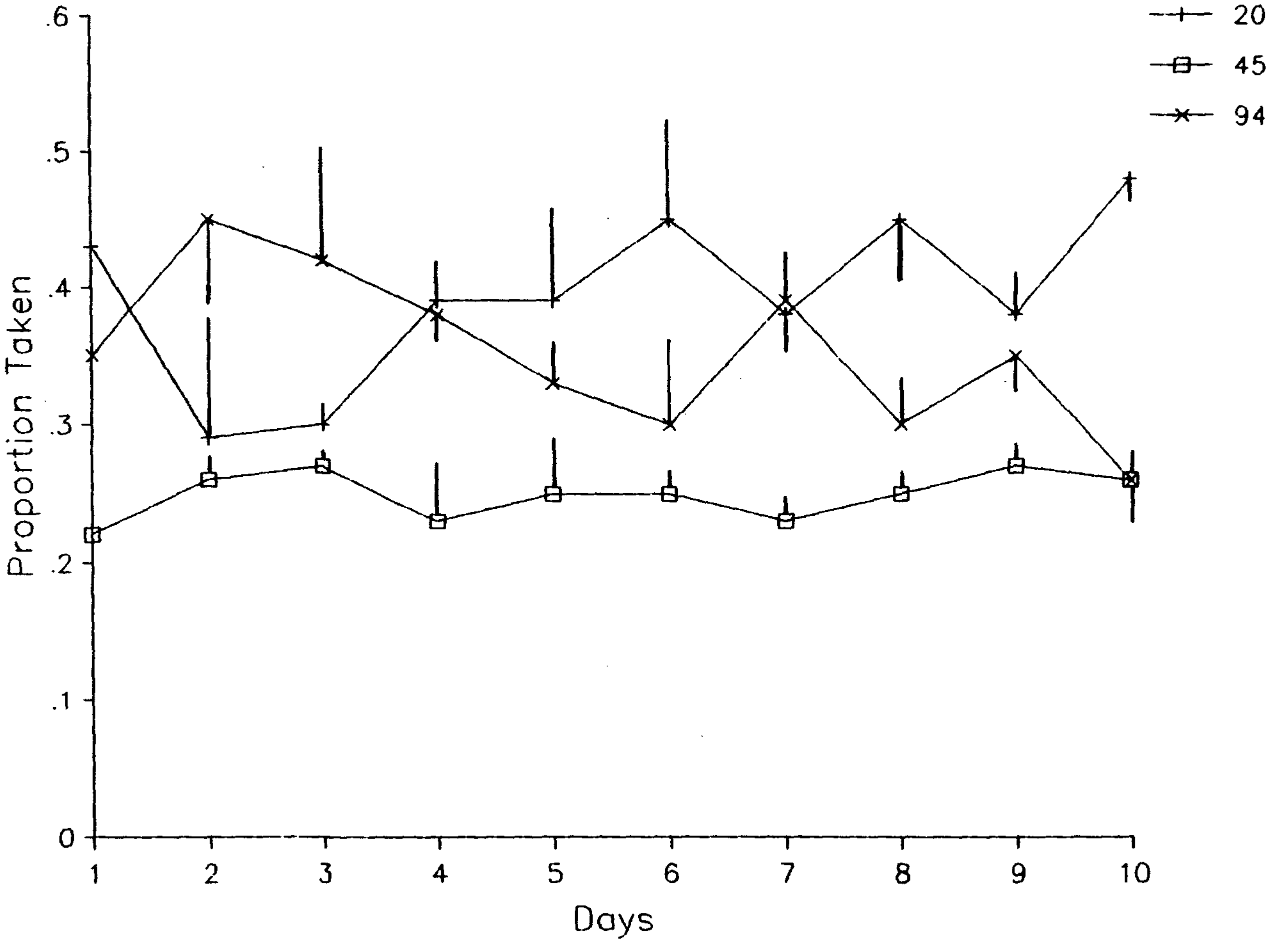

FIGURE 4: Proportion Taken Across Days, 45 mg Rearing Condition, Experiment 2

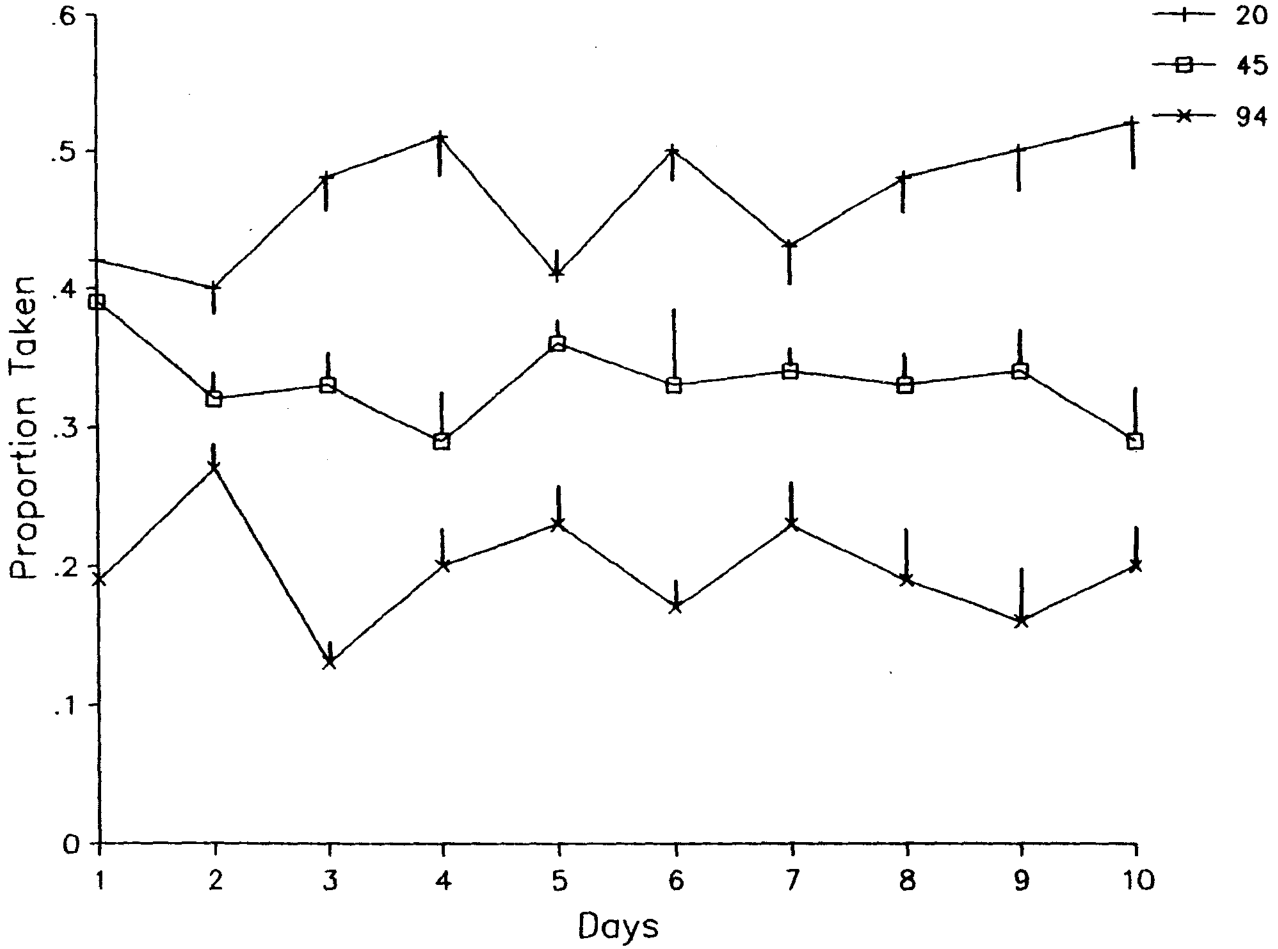

FIGURE 5: Proportion Taken Across Days, 94 mg Rearing Condition, Experiment 2

Discussion

The results of Experiment 2 show that hamsters do not take food items as they are encountered, do not always take the most profitable food, and do show a preference that depends upon early experience with food items of a particular size. However, the preference shown was not the predicted preference. Instead of preferring the most familiar size, animals took, from the first day of testing, the food size(s) most dissimilar from the size with which they were reared. The preference for the most novel size (neophilia) is clearest in the 94 and 20 mg rearing conditions. The neophilia effect is unexpected and is consistent with none of the extant literature on food choice, except for some of the research reviewed by Rozin (1976). This research showed that in situations in which animals are fed nutritionally incomplete diets, they will sample among novel foods and select those that correct the deficiencies. However, the Noyes food pellets used in this study are a complete diet for small rodents so it cannot be the case in this experiment that nutritional deficiency is mediating the neophilia. The results are also reminiscent of the results of taste-aversion studies, in which animals made ill on one food will avoid it in the future. Results of those studies have shown that rodents are sensitive to the relationship between taste and illness; but, because all the pellets were composed from the same formula, it is unlikely that a taste-aversion-like mechanism led to the preference for novel size shown by the animals in Experiment 2.

Chapter IV

Experiment 3: Taste Preference

The results of Experiment 2, that hamsters prefer the food size that is most novel to them, could be explained if it were the case that hamsters do not form food-related preferences as do other rodents. As reviewed in the introduction, many researchers have found that early experience with food of a particular flavor induces a later preference for that flavor. However, the preponderance of work in this area has been done with rats, and other rodents may behave differently. It is reasonable to assume that most rodents do respond to taste cues because they have been shown to be very dependent upon olfactory information when foraging (Langley, 1985), and the olfactory and gustatory senses are very highly related. However, hamsters have not been used as subjects in taste preference studies. The purpose of this experiment was to determine if hamsters are influenced by early restriction to one flavor as are members of other rodent species. If hamsters do not prefer familiar tastes, there is no reason to expect that they will prefer familiar food sizes, although it would not explain why novelty is prepotent in hamsters' food choices. If hamsters do show preference for familiar food flavors, then the preference for novel size demonstrated in Experiment 2 indicates, at least for hamsters, that size and taste differ in their effects on food choice.

If hamsters do make choices based on taste, we would have a clearer picture of the characteristics of food that are important when hamsters forage. Sensitivity to one of the characteristics of food to which other rodents are sensitive would indicate that hamsters may be sensitive to other food-related cues, such as profitability.

Methods

Subjects and Rearing Conditions The subjects used in Experiment 3 were six litters of golden hamsters. As in previous experiments, litters were culled to four pups, using halothane anesthesia, at 5 days of age. Littermates were housed together until they were 35 days of age; dams were removed when the pups were 21 days old. When the pups were 35 days old, they were placed in individual polypropylene cages (26.7 x 12.7 x 15 cm). Water was freely available at all times.

Control Animals Two litters were reared on granulated laboratory food (Noyes Pharmaceutical Company, Formula A: Small Rodent Diet) mixed with water and dried (unflavored food) until they were 35 days of age. For the next five days (days 36 - 40) they were given two plastic petri dishes containing 15 grams of granulated food flavored with either banana or coconut extract. The two flavors were presented simultaneously in the home cage. Position of the dishes were counterbalanced (front - back) across animals and days. After 20 minutes, the dishes were removed, the remaining food weighed, and the amount taken from each dish was calculated.

Flavor Experienced Animals Four litters were reared on granulated food to which artificial flavors had been added. Two litters received banana-flavored food and the other two received coconut-flavored food. The dams began receiving the food the day they were mated, and the pups continued receiving it until they were 35 days of age. These litters were tested as the control animals were.

Food composition The unflavored food was made by mixing 50 ml of water with 0.24 l granulated Noyes food. The flavored foods were made by mixing 45 ml of water with 5 ml of banana- or coconut-flavored extract (Sauer Company) and then adding it to 0.24 l of granulated food pellets. The mixtures were spread out on waxed paper and allowed to dry overnight. The foods were then kept in covered plastic containers. The finished product consisted of granulated food with a few small pieces, slightly moist. Pretesting indicated that hamsters will readily eat this food, although they do not pouch it.

The dependent variable used for analysis was the weight of food (in grams) taken from the petri dishes. For all three rearing conditions, a 2 (Flavor) x 5 (Days) ANOVA was run.

Results

Preferences of Control Animals There were no significant sources of variance in this analysis. Animals reared on unflavored food preferred neither banana nor coconut (_F_ (1, 70) = 1.37, n.s.). On average, these animals took 7.00 g of banana-flavored food and 5.89 g of coconut-flavored food per day (Table 3).

Preferences of Experienced Animals

Banana-reared Animals Table 3 also shows that animals who experienced only banana-flavored food until they were 35 days old preferred familiar-flavored food. Flavor was significant at $p < .05$ ($F(1, 70) = 4.02$). On the average, these hamsters took 6.80 g of banana-flavored food per day and 5.06 g of coconut-flavored food.

Coconut-reared Animals The animals that had experienced coconut-flavored food also reliably preferred familiar food. The effect for Flavor was significant at $p < .01$ ($F(1, 70) = 28.52$); the animals took a mean of 3.92 g of banana-flavored food and 7.66 g of coconut-flavored food per day.

There was no effect for Days and no Days x Flavor interaction. The results of this experiment are shown graphically in Figure 6.

Table 3

Mean Amount Taken (g) with Standard Errors, Experiment 3

Control Animals

	Day 1	Day 2	Day 3	Day 4	Day 5
Banana					
	4.81	6.95	8.00	6.59	8.95
	1.63	1.44	1.58	1.22	1.96
Coconut					
	3.29	6.61	6.78	6.90	5.88
	1.17	1.24	1.12	1.56	1.58

Banana-reared Animals

	Day 1	Day 2	Day 3	Day 4	Day 5
Banana					
	5.01	6.74	7.19	7.92	7.16
	0.89	1.51	1.90	1.42	1.81
Coconut					
	2.94	6.04	6.50	4.06	5.78
	0.48	1.59	1.85	1.08	1.41

Coconut-reared Animals

	Day 1	Day 2	Day 3	Day 4	Day 5
Banana					
	1.72	3.35	5.23	3.35	5.95
	0.67	0.94	1.29	0.80	1.02
Coconut					
	4.29	7.15	8.91	8.82	9.10
	1.17	1.57	1.03	0.93	1.12

Summary, Across Days

	Banana	Coconut
Control	7.00 (0.72)	5.89 (0.61)
Banana	6.80 (0.67)	5.06 (0.63)
Coconut	3.92 (0.48)	7.66 (0.58)

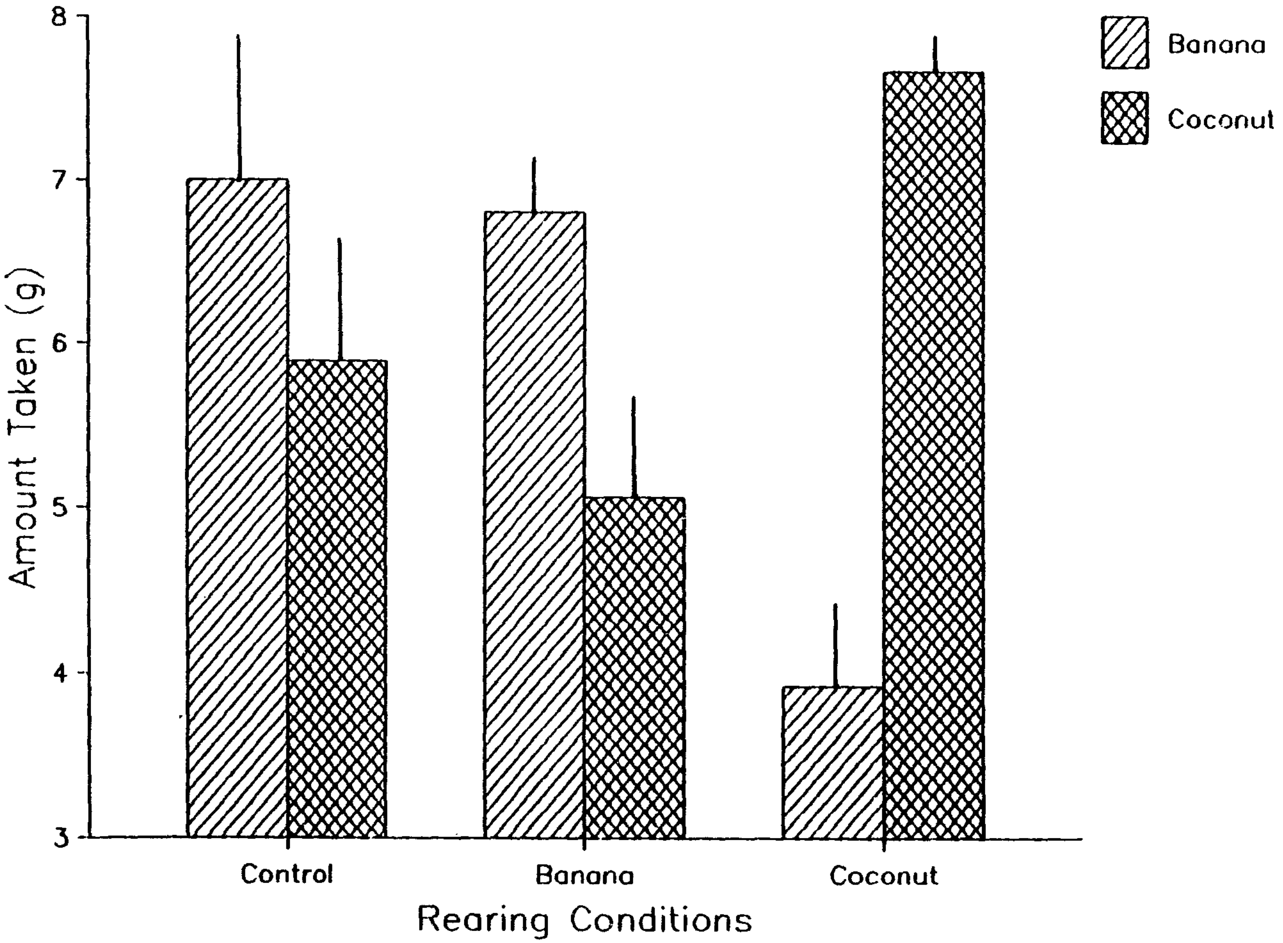

FIGURE 6: Amount Taken (g) Across Rearing Conditions, Experiment 3

Discussion

Hamsters, it appears, are like other rodents when it comes to choosing food on the basis of taste. Although the design of this experiment was somewhat different, the results replicated the findings of Capretta and Rawls (1974), Strupp and Levitsky (1984), and the work conducted by Galef and his colleagues (Galef, 1982): Early experience with taste affects food choices made later in life.

It is clear from the results of Experiments 2 and 3 that size and taste are food cues that have very different effects on foraging behavior in hamsters. Perhaps it is the case that, for hamsters, foraging can be thought of as comprising two separable components, pouching and eating.

Hamsters' foraging behaviors differ from those of most of the species studied in experiments on food choice. They rarely eat as they are collecting food; their pouches are filled and then emptied into a hoard at the nest site. When these animals do eat, they select food items from their hoards, and the choices they make at that point are unknown. Perhaps it is the case that, for hamsters, pouching can be thought of as comprising two separable components, pouching and eating. While eating, hamsters may respond to food-relevant properties of items that are in the hoard, such as taste and nutrient composition. When collecting food, they may respond to other, unknown properties of what is available. Experiment 4 was designed to examine the possibility that novelty is one property which hamsters respond to when foraging.

Chapter V

Experiment 4: Novel Objects

Research on the spatial memory of hamsters and gerbils has shown that slight changes in the position of a familiar object leads to increased exploration of that object to the level of exploration shown to unfamiliar objects (Poucet, Durup, Chapuis, & Thinus-Blanc, 1986; Thinus-Blanc & Ingle, 1985). Pouching may be one of the things that hamsters do when they explore novel objects, and, if so, the novel properties of the pellets (size, in this case) may be more salient than taste cues to the hamsters. When they eat, taste may be more salient. The results of Experiments 2 and 3 fit into this reasoning: The flavored food, which was in granulated form, could not be pouched, unlike the pellets, which were hard and easily pouched. In fact, hamsters are likely to pouch almost anything that is the correct size and firmness, such as paper and other bedding materials and pieces of wood and plastic. Pouching may be a behavioral response serving two or more systems, feeding and exploration. At least, it may be the case that factors that influence pouching are separable from those that influence eating. Experiment 4 was conducted to effect this separation and, therefore, to provide a tentative explanation for the unexpected results of Experiment 2. In

Experiment 4, novel objects were substituted for one pellet size. If the hamsters are taking unfamiliar-sized pellets because they are treating them as items to be explored, then the results of Experiment 4 will parallel those of Experiment 2.

One of the most striking aspects of the results of Experiment 2 was that initial preferences persisted across the ten days of testing. The perseveration of preference for novel sized food may have been due to the fact that initial choice was based upon a preference for novel objects to explore; it continued because the animals discovered that the unfamiliar objects were food. However, if the new objects were discovered not to be food, they should not be taken. Hogan (1971) reported such a finding in his studies on the ontogeny of feeding in chicks. When his chicks first started to scratch and peck for food, they pecked at anything of the appropriate size and shape, including pebbles. With repeated experience, however, they began to make fewer and fewer errors, so that in a relatively short time, they virtually never pecked at anything other than kernels of grain.

The hamsters used in this study were reared as were the animals in Experiment 2, the size preference study, except that no group was reared on 45 mg pellets. The results of the 94 and 20 mg groups showed a clear preference for one size - 20 and 94 mg pellets, respectively - so, because the animals reared on 45 mg pellets showed mixed preference, that rearing condition was eliminated from Experiment 4. At the time of testing, both groups of animals were presented with 45 mg and 20 mg pellets, and, instead of 94 mg pellets, plastic beads of the same size and similar shape. If the animals are responding to size novelty, at least initially, the results will parallel those of the size preference study: Animals reared on 94 mg pellets will avoid the beads whereas those reared on 20 mg pellets should take them. However, after the animals become familiar with the beads and discover that they are not edible, preference should decrease, a result similar to that Hogan (1971) found with chicks.

Methods

Subjects and Rearing Conditions Six litters of golden hamsters were reared as were the litters in Experiment 2; in this experiment, however, the 45 mg rearing condition was omitted so that three litters were reared on 94 mg pellets and three on 20 mg pellets. All other treatments until the time of testing were the same as in Experiment 2.

Testing The test procedure of Experiment 2 was also used in Experiment 4. Animals were restrained in their nest boxes for five minutes and then allowed out, one at a time, to forage in the baking tray. In the tray were 100

45 mg and 100 20 mg pellets, and 100 plastic beads, 5 cm in diameter (The Beadery Craft Products). All the objects in the tray were pressed down into approximately 1.27 cm of sand. The hamsters were allowed one foraging trip or 10 minutes to fill their pouches. At the end of the testing period, animals were removed to a holding cage where they stayed until the last animal in their litter had completed its foraging trip. They were then returned to their arena. The determination of the number of pellets of each size and the number of beads each animal took was determined by counting what remained in the tray and subtracting that value from 100.

The dependent measure, P, employed in Experiment 2 was also used for this experiment. The proportions were transformed using the arcsin transformation recommended by Kirk (1968), and following Abbey and Howard (1973), litters were used as the unit of analysis. Two 3 (Size) x 3 (Litters) x 10 (Days) ANOVAs were run, one for the 20 mg rearing condition and the other for the 94 mg rearing condition.

Results

The main effect for size was the only significant source of variance in both analyses; for animals reared on 20 mg pellets, F (2, 27) = 6,683, p < .0001 and for animals reared on 94 mg pellets,

F (2, 27) = 743, p <.001. Post-hoc analyses showed that, for those animals reared on 94 mg pellets, 20 mg pellets were preferred to 45 mg pellets, and both were preferred to beads; for animals reared on 20 mg pellets, 45 mg pellets were preferred to 20 mg pellets and both were preferred to beads (for both post-hoc analyses, ps < .05, Scheffe's test). These results are summarized in Table 4 and Figures 7, 8, and 9.

Daily chi-square analyses were also done; they revealed that animals did not take pellets at encounter rate (see Table 5).

Table 4

Mean $\bar{P}$ with Standard Errors, Experiment 4

Reared on 94 mg Pellets

Day	20 mg	45 mg	Beads
1	.48 (.02)	.48 (.02)	.05 (.007)
2	.52 (.05)	.42 (.05)	.06 (.01)
3	.49 (.05)	.45 (.02)	.06 (.02)
4	.49 (.02)	.47 (.002)	.04 (.02)
5	.59 (.06)	.38 (.06)	.03 (.007)
6	.50 (.04)	.45 (.04)	.03 (.007)
7	.50 (.02)	.48 (.02)	.02 (.003)
8	.52 (.03)	.46 (.03)	.02 (.003)
9	.50 (.01)	.48 (.003)	.02 (.01)
10	.50 (.03)	.47 (.003)	.03 (.02)
M	.51 (.03)	.45 (.02)	.04 (.01)

Reared on 20 mg Pellets

Day	20 mg	45 mg	Beads
1	.45 (.005)	.53 (.009)	.02 (.005)
2	.45 (.01)	.54 (.01)	.01 (.003)
3	.43 (.005)	.56 (.005)	.01 (.003)
4	.43 (.01)	.55 (.01)	.02 (.005)
5	.44 (.01)	.55 (.02)	.02 (.003)
6	.44 (.01)	.55 (.01)	.01 (0)
7	.45 (.02)	.54 (.01)	.01 (.003)
8	.45 (.005)	.54 (.005)	.01 (0)
9	.47 (0)	.52 (0)	.01 (0)
10	.46 (.01)	.53 (.01)	.01 (.003)
M	.45 (.008)	.54 (.009)	.01 (.002)

Table 5

Daily Chi-Square Values, Experiment 4

Reared on 94 mg Pellets

Day	Litter 1	Litter 2	Litter 3
1	191.86	141.58	50.08
2	214.83	30.76	23.54
3	149.73	108.12	111.27
4	219.78	230.78	56.63
5	202.54	236.58	59.40
6	161.70	207.85	117.06
7	241.61	267.99	142.36
8	258.84	247.20	154.86
9	255.57	168.45	281.28
10	306.99	151.29	228.39

Reared on 20 mg pellets

Day	Litter 1	Litter 2	Litter 3
1	317.18	279.50	282.82
2	202.70	299.29	355.54
3	305.99	331.79	271.68
4	340.46	282.55	282.27
5	322.09	289.55	281.57
6	329.38	309.59	313.06
7	314.44	280.61	248.97
8	304.91	278.65	285.88
9	330.94	251.73	276.66
10	317.24	278.97	312.66

Notes: all *df* = 2; all values significant, *p* < .001

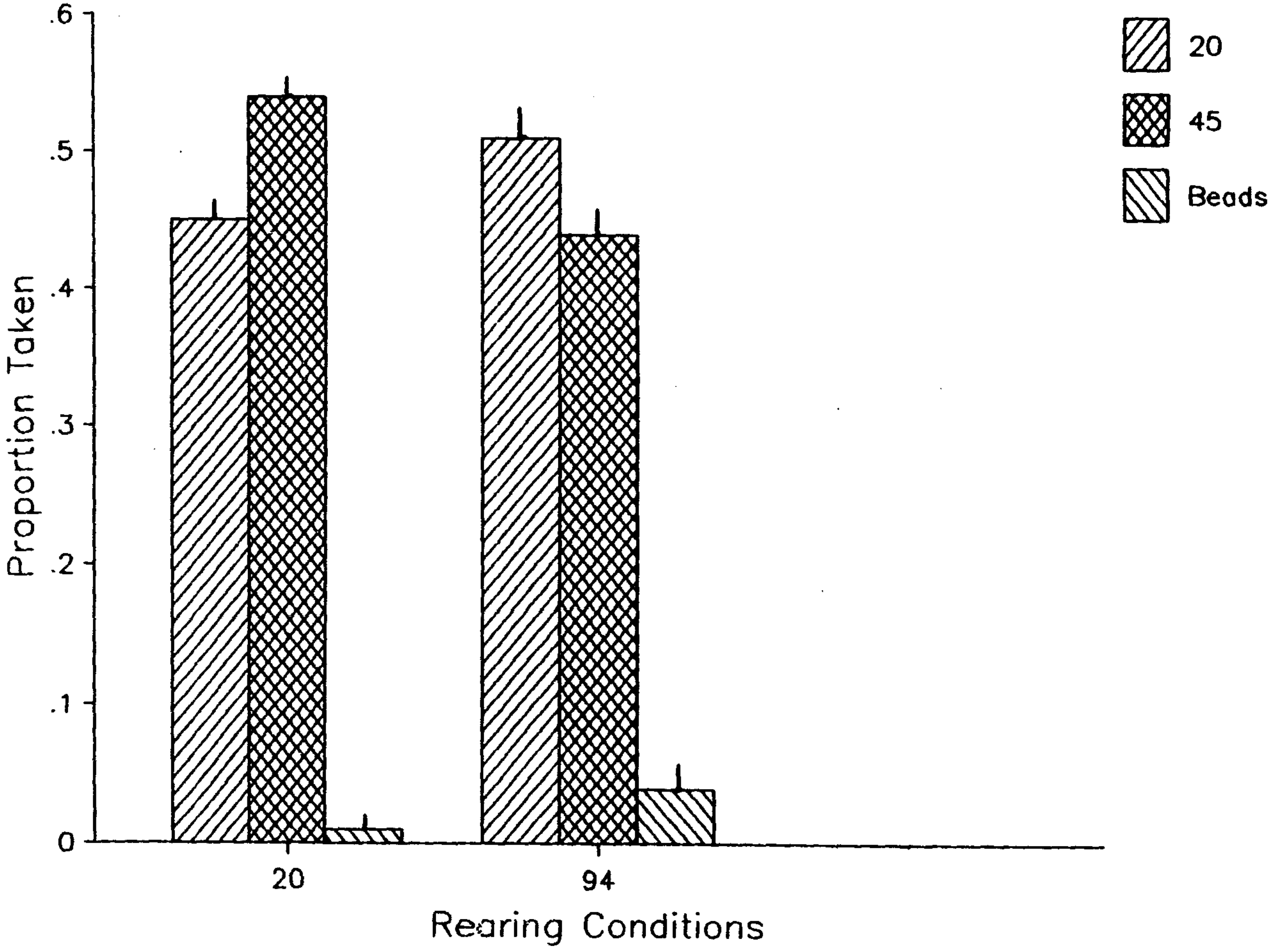

FIGURE 7: Proportion Taken Across Rearing Conditions, Experiment 4

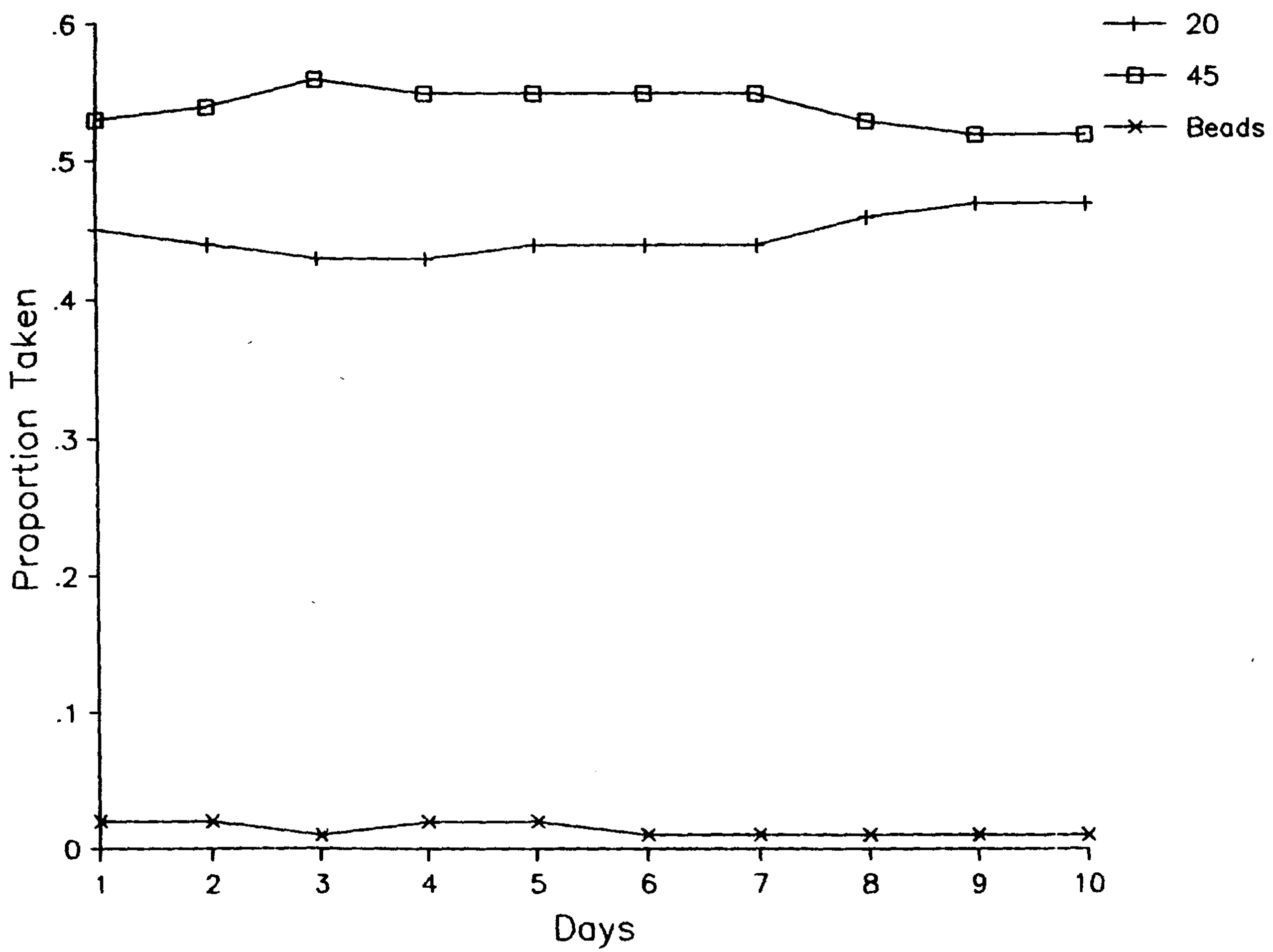

FIGURE 8: Proportion Taken Across Days, 20 mg Rearing Condition, Experiment 4

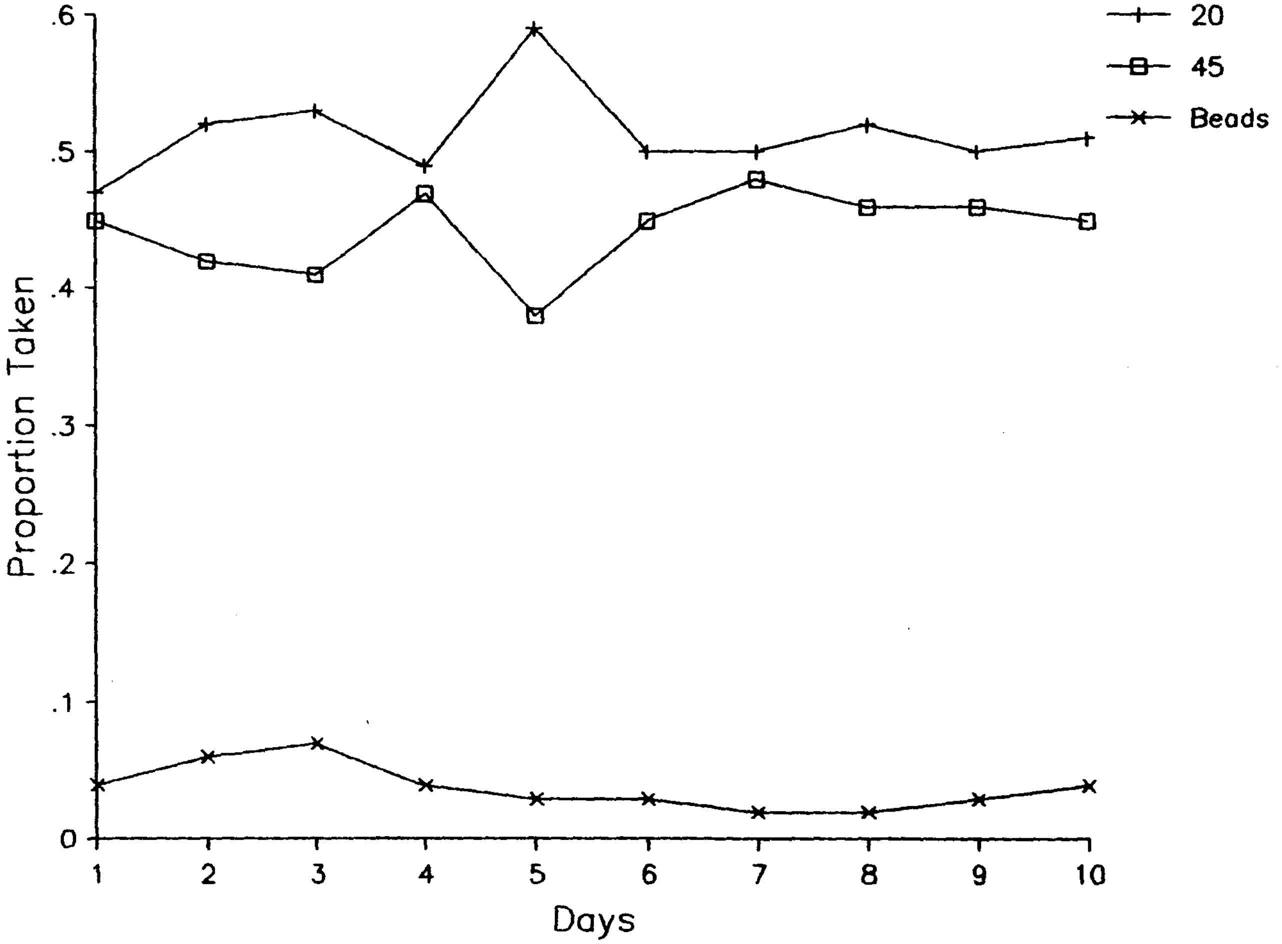

FIGURE 9: Proportion Taken Across Days, 94 mg Rearing Condition, Experiment 4

Discussion

The effect demonstrated in Experiment 2, that hamsters preferred food pellets most dissimilar in size from those with which they had early experience, was replicated in Experiment 4. Animals reared on 94 mg pellets once again preferred 20 mg pellets; those reared on 20 mg pellets preferred 45 mg pellets. Neither group took many beads; the proportion of beads taken by the 94 mg group was higher than the proportion taken by the 20 mg group ($\underline{M}(94) = 0.04$, $\underline{M}(20) = 0.01$; $\underline{t}(18) = 5.27$, $\underline{p} < .001$), but the proportion of beads taken by the 20 mg group was so low that any elevation in the number of beads taken would have been significantly different.

The results of Experiment 4 disconfirmed one hypothesis tendered to explain the results of Experiment 2: Animals did not respond to sheer novelty. The beads were not taken as much as would be expected if size novelty alone was leading to the preference for novel food item sizes reported in Experiment 2. The novelty effect appears only when the objects are food. Of course, it could have been the case that the beads were too novel; not only were they an unfamiliar size for those animals reared on 20 mg pellets, they had a different smell, they were inedible, and the shape of the beads was somewhat different from the shape of the pellets.

Chapter VI

Summary and Discussion

The experiments presented in this dissertation were designed to examine the role of early experience on later food choice by golden hamsters (_Mesocricetus auratus_). The four experiments can be summarized as follows:

Experiment 1 Animals were reared with food pellets of one size and later were allowed to take food pellets from dishes containing the familiar-sized food and food items of two unfamiliar sizes. Within the range of sizes tested, the largest (94 mg) available food pellets were the most profitable (ratio of calories to handling time), the middle-sized (45 mg) pellets were the next most profitable, and the smallest (20 mg) pellets were the least profitable. All sizes had approximately equal handling times; experience with pellets of a particular size did not decrease handling time for that size.

Experiment 2 Experiment 1 showed that experience with pellets did not affect their profitability; however, experience may affect preference for food items without affecting their profitability. In Experiment 2, animals were reared with food pellets of one size, and, as adults, were given free choice among pellets of each of three sizes: the familiar size and two unfamiliar sizes. The food items were 94 mg, 45 mg and 20 mg pellets of Noyes

Formula A. Three mutually exclusive predictions were made: (1) If the assumptions of the optimal diet model (ODM) are correct, the animals should have chosen the largest, most profitable pellets available regardless of their early experience. (2) If size is not a relevant cue for food choice, early experience should not make a difference nor should profitability; the animals should have taken food at encounter rate. (3) If early experience with size has the same effect as early experience with taste, the hamsters should have shown preference for the size with which they were reared. In fact, the results of this study showed that early experience affected food choice in a consistent manner, but not in the way outlined in the third prediction. Hamsters chose the food sizes that were most different from the familiar size: those reared on 94 mg pellets preferred 20 mg pellets, those reared on 20 mg pellets preferred 94 mg pellets, and those reared on 45 mg pellets split their choices equally between 94 and 20 mg pellets.

Experiment 3 In order to see whether taste preferences could be induced in hamsters as they are in other rodents, animals were reared on unflavored, banana-flavored, or coconut-flavored granulated food. Later, the animals were given a simultaneous choice between banana- and coconut-flavored food. Control animals (those reared on unflavored food) showed no preference for either flavor. Animals in the other groups showed a preference for the familiar flavor. Thus, hamsters are sensitive to at least one food-relevant cue, taste, and behave as do rats with regard to that cue.

Experiment 4 One explanation of the unexpected results of Experiment 2 was that the animals were not treating the pellets as food but as objects to be explored. Research has shown that hamsters spend more time exploring novel objects than familiar ones; it seemed possible that one way a hamster might explore an object is to pouch it and take it to the hoard. To examine this possibility, hamsters were reared on either 94 or 20 mg pellets and later tested with plastic beads replacing the 94 mg pellets. If, in Experiment 2, the animals were responding to size novelty, those reared on 94 mg pellets (in Experiment 4) should have rejected the beads whereas those reared on 20 mg pellets should have taken the beads. This result was not obtained; the animals reared on 94 mg pellets did reject the beads but so did the animals reared on 20 mg pellets. However, both groups preferred the most novel food size available at the time of testing: The 94 mg rearing group preferred 20 mg pellets, and the 20 mg rearing group preferred 45 mg pellets. It is clear that preference for unfamiliar-sized food is consistent.

What is it about novel-sized food that makes it so attractive to hamsters? The results of Experiment 4 showed that it is not size novelty *per se* that led to animals taking such items. The beads were unfamiliar on other characteristics than size; for example, they were a different color, smelled differently, and had a slightly different shape than did the beads. For the animals reared on 94 mg pellets, the only familiar characteristic of the beads was their size; for those reared on 20 mg pellets, no characteristics were familiar. In other words, the beads may have been too novel. Bateson (1973; 1976) proposed that preferences develop as a result of exposure to objects; objects that are slightly dissimilar to the training stimulus are preferred. If this line of reasoning is followed, it may mean that the hamsters were responding to novelty when they took the pellets of the most unfamiliar size; however, the beads were simply too novel. One important experimental strategy to use to discover if this is the case would be to make the novel objects more like food; for example, they could smell the same as the food pellets. Because it is the case that novelty itself is not enough to bring about preference, it seems likely that some aspect of "foodness" is important; if an object is not food (in this experimental situation) it does not get pouched, and if it is too familiar, even if it is food, it does not get pouched either. The interaction of food properties and novelty is one which needs further investigation. By manipulating the properties of the novel object, the nature of this interaction and the roles such factors play in the development of food choice in hamsters will be elucidated.

In none of the experiments was there complete rejection of any food or non-food item. All animals took at least one bead or one pellet of the familiar size. In fact, the animals were quite diverse in their foraging, especially in Experiment 2. This observation is consonant with the findings of Reichman (1981) on the foraging behavior of a variety of species of desert rodents in the Southwestern United States. There is little information about the natural history of hamsters, but examination of the diet selection of ecologically similar species may offer some clues. The species Reichman studied were members of the family Heteromyidae, and have external, fur-lined cheek pouches in which they store seeds while foraging. In this respect they are similar to hamsters, which are cricetid rodents. In addition, the heteromyids occupy an ecological niche similar to that of hamsters. The members of all four of the heteromyid species Reichman studied gathered a great variety of seeds, although they preferred the seeds that had the highest caloric values.

They did not take the seeds available in the substrate at encounter rate. The selectivity shown in collecting was even more pronounced later, when the seeds were consumed; sampling of stomach contents revealed that animals ate the seeds that were highest in energy content from those that they had collected. This finding is contrary to the predictions of ODM: The seeds had been found, collected, and taken to hoards, so the majority of the energy that had been invested in them had been spent. Not eating the seeds, therefore, resulted in a loss of energy. Reichman proposed that heteromyids fill their cheek pouches rapidly to avoid hostile environmental conditions and sort the seeds later in the relative safety of their borrows. Sorting the seeds while foraging may represent an even greater potential loss of energy than carrying seeds that will not be eaten back to the hoard. Perhaps the hamsters are behaving in a similar fashion. They collect slightly novel items as well as some familiar ones; later, they may eat more selectively. When a method is devised to examine what hamsters eat from their hoards, a different pattern of preferences may be found. Reichman could not distinguish within seed types; that is, to the extent that he could determine, rodents ate all of one kind of seed, regardless of the size of the seeds.

When heteromyids gather seeds and grain in the field, taste information is not immediately available. The seeds and grain are covered with shells and husks. If taste cues were made available to the animals at the time of foraging, perhaps their foraging selectivity would be more closely related to their ingestion selectivity. Size and taste were not covaried in the experiments reported here. In Experiment 3, taste was varied but size was not; in Experiments 1, 2, and 4, size was varied but taste was not. If size and taste were independently varied, so that animals were reared on one size and one flavor and later tested on combinations of familiar and unfamiliar size with familiar and unfamiliar flavor, a clearer picture of how novelty operates in the selection of foods by hamsters and other pouching rodents may emerge.

The results of Experiments 2 and 4 showed that neophilia in food choice was consistent and relatively long-lasting. It could be argued that ten days was not long enough to show a shift in preference. This may be true; however, most studies on the development of food choice have shown a shift away from familiar tastes within 3 or 4 days (Galef, 1977). In Experiment 2, one litter, reared on 94 mg pellets, was inadvertantly tested for 13 days instead of 10; those animals continued to show the same pattern of preferences characteristic of other animals in their rearing condition. While this is not conclusive evidence, it supports the conclusion that the effect is persistent.

The pellet sizes were chosen to reflect the sizes of seeds hamsters are likely to encounter in their natural habitats. The sizes were easy for the hamsters to pouch and in most cases hamsters filled their pouches quickly. There may be a range of sizes that are too dissimilar to the original sizes; items of those sizes may not be pouched because they are too large or too small to be handled or because, as Bateson's (1973; 1976) model would predict, they are outside the preference continuum that is established by restricted exposure.

Implications for the Optimal Diet Model

The results of these experiments do not refute the optimal diet model (ODM). The body of work on ODM is too large and too diverse and too many ODM predictions have been confirmed experimentally to reject it. However, the findings of these studies should lead researchers to more carefully examine the assumptions of the model.

Optimality and Choice In ODM, the optimal diet is the one in which energy gain offsets energy loss. As discussed earlier, if handling time and search times are kept constant, or nearly so, and caloric content per gram and nutrient composition are the same across sizes, larger sizes should be more profitable than smaller sizes, a prediction that was confirmed in Experiment 1. According to ODM predictions, the largest size should be taken most often if all sizes are equally available. However, this did not happen; the results of Experiments 2 and 4 revealed that animals do not automatically take the most profitable available food. Adult food choice is strongly influenced by the kinds of foods animals are exposed to while young. It holds true for taste (Capretta & Rawls, 1974; Galef, 1977; Neuringer & Neuringer, 1974; Partridge, 1981) and, as these experiments have shown, it holds true for size. If animals do not always choose an optimal diet, why should ODM be considered at all? Under certain circumstances, adult animals do choose optimally, but the choice does not spring from a phylogenetic tendency to pick foods that meet the optimal diet model. Even when all the conditions under which animals should choose according to the optimal diet model are met, the animals may not do so. In Experiment 2, in which the situation was devised to meet the most stringent requirements of ODM, the animals did not choose the most profitable food under all conditions. If an animal chooses an optimal diet, it does not mean that the animal is responding to profitability. Partridge (1981) suggested that, in order to predict what foods an animal will choose to eat, one should look at what they have most recently eaten, which is influenced by food availability.

However, this is not to say that animals cannot learn about the profitability of foods and respond in the way predicted by ODM. If animals have had a great deal of experience with a variety of foods that vary in profitability, they should be able to learn about the relationship between choice and energy gain and act accordingly (Fantino & Abarca, 1985). As Rozin (1976) established in his review of the literature on food choice, animals can change their diets in response to nutritional deficiencies as well as to unpleasant consequences that result from ingesting certain foods. Why not in response to profitability?

Development of Optimal Food Choice These considerations make it clear that, when studying foraging, whether one is concerned with the selection of a diet or of a search strategy, the behaviors of interest are under developmental control. They are influenced by a complex set of environmental and organismic events, which interact and influence the performance of the behaviors. Partridge (1981) attributed the non-optimal diet choices shown by her mice to changes in digestive system efficiency brought about by restriction to one type of grain in their diets. Animals are not aware of these changes, of course, but their behaviors are affected nonetheless (Balagura & Harrell, 1974). Experience with food does not have to have dramatic physiological effects to induce or maintain the choice of a particular food. McNair (1981) derived a mathematical model, which he confirmed experimentally, that showed that training effects can occur and do lead to alterations in later food choices. Animals can learn, with experience, to handle a specific food type more efficiently or to find it more easily. Therefore, an animal's diet may contain nothing but items that a particular model predicts to be below the threshold of profitability. In other words, animals may and often do choose a non-optimal diet.

Recognition of food as food is often influenced by specific early experience. Galef and his colleagues (see Galef, 1977; 1985a for reviews) have shown that information about the flavor of food is transmitted through mother's milk; when rat pups are able to feed on solid food, they choose the flavor to which they were exposed while suckling, even if a food that is preferred by most rats is also available. The conclusion from this research and that of Capretta and Rawls (1974) is clear: If an animal has not been exposed to a particular kind of food, the animal will avoid it when it is first presented and prefer familiar food throughout life. As Galef (1982) showed, rats do not eat every possible food item available to them, but are strongly influenced by the foods eaten by other conspecifics. Although the diets of their dams have the most profound effects, other animals can serve as demonstrators. Given a supply of a new food, rats will sample it sparingly until they learn that it is safe; however, if an animal interacts with a conspecific that has eaten the unfamiliar food, the rat will eat much more of it. The effect is as strong with adults as it is with pups (Galef, Kennett, & Stein, 1985; Galef & Stein, 1985; Posada-Andrews and Roper, 1983).

The results of the size preference studies reported here lead to much the same conclusions. Before the hamster pups could forage on their own, they were exposed only to the pellets their dams collected and brought back to the nest box. When they were old enough to forage independently, they followed their dams into the arena and found the same food size that they had encountered in the hoard. They did not, when given a choice among many different sizes of food, prefer the familiar size, but their preferences were systematically influenced by the early experience they obtained. The preferences were consistent within rearing conditions and different between rearing conditions. Why the hamsters chose unfamiliar food item sizes is still open to investigation. What is clear is that ODM does not provide a complete explanation of food choice; it is a description of what happens when animals with certain kinds of experience with food are given a choice among different kinds of food. A more complete explanation of food choice behavior, as well as other behaviors animals display, must include the examination of the factors that contribute to the preferences that are demonstrated. What experiences lead animals to choose foods optimally? Are these likely to be the experiences they have during early development? These are among the questions that need to be answered in order to reach an explanation of food choice behavior.

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Appendix

Raw Data

Appendix

Raw Data, Experiments 1, 2, 3, and 4

Experiment 1: Profitability

Reared on 20 mg Pellets

Subject No.	Pellet Size	Day 1	Day 2	Day 3
86-66	20	4.5	2.9	7.1
	45	64.3	13.3	6.4
	94	16.8	91.7	15.4
86-67	20	20.3	8.0	28.9
	45	42.2	22.4	43.5
	94	21.6	27.6	85.4
86-68	20	1.4	15.0	19.5
	45	7.9	12.7	35.6
	94	147.5	7.7	88.6
86-69	20	11.7	1.6	9.6
	45	35.8	11.0	3.6
	94	50.5	58.2	38.4

Reared on 45 mg Pellets

Subject No.	Pellet Size	Day 1	Day 2	Day 3
86-74	20	4.5	15.6	22.2
	45	15.5	129.9	30.4
	94	36.1	43.9	46.6
86-75	20	3.8	11.9	8.3
	45	7.4	14.4	104.1
	94	69.9	24.2	67.8
86-76	20	2.5	11.7	8.5
	45	12.2	28.3	36.7
	94	27.4	20.9	42.9
86-77	20	8.5	3.1	24.5
	45	13.1	10.1	13.0
	94	74.2	285.7	31.1

Reared on 94 mg Pellets

86-70	20	21.8	7.0	2.9
	45	8.3	50.0	64.8
	94	41.1	118.3	85.1
86-71	20	1.2	15.9	2.6
	45	14.0	65.5	6.7
	94	122.2	33.9	20.0
86-72	20	2.3	0.0	18.9
	45	16.2	0.0	97.1
	94	56.9	289.0	75.6
86-73	20	6.5	0.0	21.0
	45	67.1	0.0	25.9
	94	287.3	147.1	107.6

Handling Times

(pellets/sec)

20 mg	45 mg	94 mg
0.108	0.293	0.109
0.391	0.312	0.690
0.676	0.625	0.142
0.310	0.676	0.380
0.441	0.298	0.126
0.410	0.508	0.298
0.546	0.202	0.222
0.513	0.145	0.645
0.172	0.087	0.103
0.351	0.140	0.057
0.351	0.392	0.347
0.061	0.127	0.153
0.092	0.321	0.356
0.083	0.050	0.806
0.312	0.164	0.235
0.090	0.088	0.249
0.031	0.529	0.251
0.442	0.347	0.064
0.176	0.071	0.223
0.088	0.353	0.082
0.176	0.071	0.223
0.676	0.084	0.223
0.483	0.420	0.223
0.095	0.830	0.049
0.096	0.081	0.146

Experiment 2: Size Preference

Reared on 94 mg Pellets

	Litter 1			Litter 2		
Day	20 mg	45 mg	94 mg	20 mg	45 mg	94 mg
1	0.37	0.42	0.21	0.48	0.40	0.12
2	0.33	0.36	0.31	0.43	0.31	0.26
3	0.34	0.40	0.26	0.58	0.34	0.08
4	0.35	0.31	0.34	0.61	0.27	0.12
5	0.36	0.35	0.29	0.38	0.35	0.27
6	0.38	0.37	0.25	0.58	0.28	0.14
7	0.39	0.36	0.25	0.37	0.33	0.30
8	0.48	0.31	0.21	0.42	0.35	0.23
9	0.40	0.37	0.23	0.58	0.31	0.10
10	0.47	0.35	0.18	0.69	0.17	0.17

Litter 3

Day	20 mg	45 mg	94 mg		20 mg	45 mg	94 mg
1	0.41	0.36	0.23	6	0.54	0.33	0.13
2	0.45	0.30	0.25	7	0.54	0.32	0.14
3	0.53	0.43	0.04	8	0.54	0.33	0.13
4	0.57	0.29	0.14	9	0.52	0.33	0.15
5	0.49	0.37	0.14	10	0.40	0.35	0.25

Reared on 45 mg Pellets

	Litter 4			Litter 5		
Day	20 mg	45 mg	94 mg	20 mg	45 mg	94 mg
1	0.44	0.14	0.43	0.56	0.20	0.24
2	0.36	0.14	0.50	0.20	0.30	0.50
3	0.09	0.30	0.61	0.32	0.28	0.40
4	0.27	0.17	0.56	0.40	0.28	0.32
5	0.23	0.25	0.52	0.47	0.25	0.28
6	0.33	0.25	0.42	0.47	0.25	0.28
7	0.24	0.27	0.49	0.33	0.26	0.41
8	0.38	0.22	0.40	0.48	0.27	0.25
9	0.29	0.26	0.45	0.44	0.28	0.28
10	0.40	0.23	0.37	0.51	0.33	0.16

Litter 6

1	0.29	0.33	0.38	6	0.56	0.24	0.20
2	0.31	0.33	0.36	7	0.56	0.17	0.27
3	0.50	0.24	0.26	8	0.49	0.27	0.24
4	0.51	0.23	0.27	9	0.41	0.27	0.32
5	0.47	0.24	0.20	10	0.53	0.23	0.24

Reared on 20 mg Pellets

	Litter 7			Litter 8		
Day	20 mg	45 mg	94 mg	20 mg	45 mg	94 mg
1	0.20	0.28	0.52	0.09	0.50	0.41
2	0.10	0.37	0.53	0.18	0.33	0.49
3	0.08	0.34	0.58	0.18	0.35	0.47
4	0.19	0.24	0.57	0.18	0.32	0.50
5	0.04	0.29	0.67	0.23	0.34	0.43
6	0.02	0.34	0.64	0.23	0.30	0.47
7	0.12	0.27	0.61	0.23	0.34	0.43
8	0.02	0.35	0.63	0.24	0.39	0.37
9	0.03	0.27	0.70	0.22	0.36	0.42
10	0.10	0.40	0.50	0.23	0.36	0.41

Litter 9

1	0.24	0.35	0.51	6	0.23	0.40	0.37
2	0.24	0.36	0.40	7	0.26	0.37	0.37
3	0.19	0.35	0.46	8	0.25	0.33	0.42
4	0.20	0.39	0.41	9	0.22	0.38	0.40
5	0.29	0.38	0.33	10	0.34	0.33	0.32

Experiment 3

Control Animals

Sub. No.	Flavor	Day 1	Day 2	Day 3	Day 4	Day 5
87-85	Banana	2.9	13.8	10.2	3.6	14.6
	Coconut	0.6	12.9	11.9	2.8	5.9
87-86	Banana	0.2	9.6	6.5	12.0	12.8
	Coconut	2.8	6.0	9.0	8.8	9.8
87-87	Banana	4.8	8.1	11.8	7.7	14.0
	Coconut	0.1	5.9	7.9	13.9	4.3
87-88	Banana	0.5	4.4	7.2	9.2	5.1
	Coconut	1.5	2.5	7.6	7.2	12.7
87-118	Banana	10.1	6.3	13.9	6.9	13.7
	Coconut	2.3	7.2	2.9	8.7	1.5
87-119	Banana	0.0	0.2	2.6	1.2	3.7
	Coconut	4.0	2.0	2.2	0.9	1.7
87-120	Banana	9.4	8.7	10.6	4.1	3.2
	Coconut	4.4	7.0	6.8	10.1	1.2
87-121	Banana	10.6	4.5	1.2	8.0	2.1
	Coconut	10.6	9.4	5.9	2.8	5.9

Reared on Banana-Flavored Food

87-94	Banana	5.8	12.0	4.6	2.7	14.6
	Coconut	0.0	10.2	2.8	1.6	2.3
87-95	Banana	8.7	8.3	9.9	7.2	2.7
	Coconut	2.1	8.7	12.9	5.2	8.3
87-96	Banana	5.5	7.0	13.6	5.4	4.4
	Coconut	2.5	7.8	13.0	2.5	13.6
87-97	Banana	4.7	12.1	10.7	9.4	13.5
	Coconut	4.0	12.6	11.3	4.4	4.7
87-114	Banana	2.7	2.6	9.5	8.2	7.4
	Coconut	6.6	1.4	2.5	1.3	2.6
87-115	Banana	0.9	1.7	0.8	0.5	2.8
	Coconut	0.3	2.1	1.5	0.0	1.3
87-116	Banana	7.6	8.3	0.4	8.7	1.5
	Coconut	3.7	0.7	0.4	6.4	4.8
87-117	Banana	4.2	1.9	0.0	13.3	10.4
	Coconut	2.7	5.4	2.1	9.9	7.9

Reared on Coconut-Flavored Food

87-102	Banana	6.1	5.5	5.2	2.1	2.6
	Coconut	4.5	9.9	9.7	9.8	8.5
87-103	Banana	2.4	1.8	2.3	0.8	3.1
	Coconut	9.3	2.0	11.0	8.5	4.9
87-104	Banana	1.5	0.4	6.0	4.3	10.3
	Coconut	0.6	12.6	11.7	8.8	11.7
87-105	Banana	0.4	0.5	2.1	5.6	8.1
	Coconut	0.9	6.2	7.4	6.3	6.6
87-110	Banana	0.5	4.2	8.4	0.0	4.0
	Coconut	8.5	5.0	3.5	5.1	14.6
87-111	Banana	0.7	2.5	2.9	5.9	7.8
	Coconut	5.1	12.6	8.4	9.3	9.7
87-112	Banana	1.3	3.6	2.6	2.8	3.8
	Coconut	1.6	1.0	7.2	8.8	6.4
87-113	Banana	0.9	8.3	12.4	5.3	7.9
	Coconut	3.8	7.9	12.4	14.0	10.4

Experiment 4: Novel Objects

Reared on 94 mg Pellets

	Litter 1				Litter 2		
Day	20 mg	45 mg	Beads		20 mg	45 mg	Beads
1	0.48	0.47	0.05		0.44	0.45	0.03
2	0.48	0.48	0.04		0.43	0.48	0.09
3	0.49	0.47	0.04		0.51	0.38	0.11
4	0.51	0.48	0.01		0.50	0.47	0.03
5	0.58	0.41	0.01		0.48	0.48	0.04
6	0.59	0.35	0.06		0.46	0.49	0.02
7	0.53	0.46	0.01		0.46	0.52	0.02
8	0.57	0.41	0.02		0.46	0.53	0.01
9	0.52	0.47	0.01		0.47	0.48	0.05
10	0.53	0.47	0.0		0.46	0.43	0.11
			Litter 3				
1	0.51	0.44	0.05	6	0.46	0.52	0.02
2	0.64	0.31	0.05	7	0.52	0.46	0.02
3	0.60	0.37	0.05	8	0.54	0.44	0.02
4	0.45	0.47	0.08	9	0.51	0.44	0.02
5	0.72	0.25	0.03	10	0.53	0.46	0.00

Reared on 20 mg Pellets

	Litter 4				Litter 5		
Day	20 mg	45 mg	Beads		20 mg	45 mg	Beads
1	0.46	0.51	0.03		0.44	0.55	0.01
2	0.41	0.56	0.03		0.43	0.56	0.01
3	0.44	0.55	0.01		0.44	0.56	0.00
4	0.43	0.56	0.01		0.40	0.58	0.02
5	0.43	0.56	0.01		0.41	0.57	0.02
6	0.41	0.58	0.01		0.44	0.55	0.01
7	0.44	0.55	0.01		0.46	0.53	0.01
8	0.47	0.52	0.01		0.46	0.53	0.01
9	0.47	0.52	0.01		0.47	0.52	0.01
10	0.44	0.55	0.01		0.48	0.51	0.01
			Litter 6				
1	0.46	0.53	0.01	6	0.47	0.52	0.01
2	0.48	0.51	0.01	7	0.41	0.57	0.02
3	0.42	0.57	0.01	8	0.46	0.53	0.01
4	0.45	0.52	0.03	9	0.47	0.52	0.01
5	0.47	0.51	0.02	10	0.48	0.52	0.00