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UNIVERSITY OF ALBERTA

Taste Aversion Learning as a Mechanism of Diet Selection

by

Pamela J. Reid

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

Department of Psychology

EDMONTON, ALBERTA

SPRING, 1986

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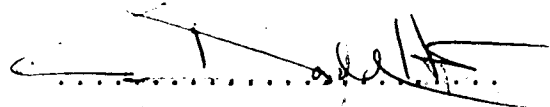
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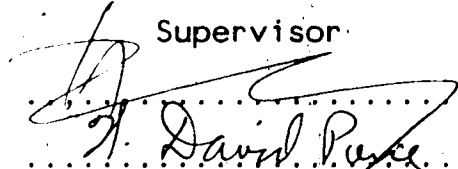
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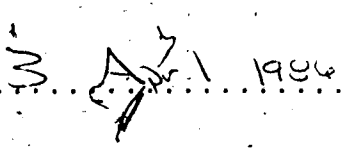
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Dedication

The author wishes to dedicate this work to NiK Burchell, whose understanding, patience, and motivation was a strong source of inspiration throughout the project.

Abstract

A proposed means of assessing the role of taste aversion learning as a proximal mechanism of diet selection is to examine any changes that occur in foraging patterns with different levels of conditioned aversion to a prey type. If the patterns match those expected of animals foraging on different quality prey types, aversion conditioning may be a mechanism permitting foragers to discriminate prey types according to an energy maximization scale. Two groups of rats foraged for food in a room by climbing wire ladders to "patches" containing sucrose pellets mixed in animal litter. Food density in each patch was alternated daily, with two patches of 10 pellets each and two patches of 20 pellets each during a session. The match between an optimality model of patch use and the behavioral data was tested for three levels of conditioned aversion to the pellets. The purpose of group division was to counterbalance order of aversion level. Group O-W-S was initially tested with no aversion, then with a weak aversion, and finally, with a strong aversion. In contrast, Group O-S-W was initially tested with no aversion, then with a strong aversion, and finally, with a weak aversion. While foraging did decline with increasing aversion, the changes were not in accord with the predictions of the optimal foraging model. Instead, consistent underutilization of the high density patches and overutilization of the low density patches occurred. Although several explanations of this deviation from

optimality were discussed, it is worth noting that on several occasions, especially in the strong aversion, the optimal left-over-constant exceeded the initial amount available in the low density patches, resulting in the prediction that these patches should not have been foraged in at all. With a tendency toward exploitation of only the high density patches, foraging patterns would not be expected to match the theoretical predictions. In addition, an interpretation suggested by the overutilization of the low density patches is that an assumption of exclusive use of an immediate maximization foraging strategy is invalid. Overutilization of low reward alternatives is often attributed to the use of a sample-then-exploit foraging strategy, which strikes a balance between the need for energy and information. An examination of the residence time data suggests the rats may have begun each session with a short period of sampling in order to determine density location. Substitution of a sample-then-exploit strategy into the optimal patch use model would predict foraging patterns more akin to those observed in the study.

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The author is especially grateful to Dr. Don Heth for his invaluable guidance, advice, and encouragement during the course of this project. His influence will hopefully remain with me for many years to come. I am also indebted to Nik Burchett for his unfailing assistance with all aspects of the project, particularly with conducting the experiment and analyzing the data. In addition, special thanks are due to John Turtle for graciously helping with the figures.

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I. INTRODUCTION

When considered from an evolutionary perspective, it is commonly assumed the ultimate function of behavior is the maximization of reproductive fitness. Given this assumption, optimal solutions which are more effective than any available alternatives are conceivable for all ecological problems. Determination of an optimal solution for a particular behavior pattern and a given set of circumstances gives rise to an optimization model of behavior which can be used to derive predictions about actual behavior.

MacArthur and Pianka (1966) extended the concept of optimization to the specific behavior pattern of foraging, by suggesting that natural selection should tend to turn each species into "optimal foragers". Optimal foraging theory assumes that natural selection enhances the reproductive success of those animals whose foraging patterns maximize exploitation of the environment and eliminates those whose patterns deviate from the optimum. Unfortunately, the currency of reproductive fitness is difficult to measure and so, for the sake of practicality, net energy intake, which is assumed to be related to fitness, has traditionally been used as the forager's short-term goal (Krebs & McCleery, 1984).

MacArthur and Pianka's (1966) classical foraging model was designed to be as general as possible and therefore includes only a small number of assumptions about constraints on the animal's performance. For instance,

optimal foraging theory assumes that prey types are perfectly discriminable to the predator and that the predator searches for all prey types simultaneously, although items are encountered sequentially. Each encounter with a prey item is assumed to be a random and independent event. Given these assumptions, a solution that maximizes food intake during a foraging bout is the optimal solution. When restricted to the problem of diet selection, the theory makes two predictions about the optimal solution:

1. Food types must be rated according to their ratio of net energy gain to handling time (E/h). Handling time refers to the total time between the forager's decision to pursue a food item and when it is next possible for him to forage for another item. This includes the time taken to pursue, capture, prepare, and consume the item (Krebs, 1980).
2. If a particular food item is encountered in the environment, the decision of whether or not to take it depends on its value of E/h and the average net energy intake that can be achieved if the type is consistently not taken. Thus, a particular food type is either never or always taken and an animal will become increasingly selective as overall food density increases. The prey type with the highest E/h value should always be preferred, regardless of its abundance. Whether or not a food type is included in the diet depends only on the densities of all other food types with higher E/h values.

and is unaffected by its own density (Vickery, 1984).

Optimality models are analytic tools, with the predictions generated describing how animals ought to behave if they are designed to optimize foraging strategies. Therefore, empirical tests of the predictions provide an assessment of how well animals are adapted to their environments and an indication of the validity of the assumptions inherent in the model (Kamil & Roitblat, 1985).

Field studies of diet selection are especially difficult because the variables influencing foraging are harder to identify. Nevertheless, several researchers have attempted field tests of the hypotheses generated by optimal diet theory. Barnard and Stephens (1981) found that as the overall density of earthworms increased, lapwings became more selective and accepted only the larger prey. Davidson (1978) observed that harvester ants specialized on higher E/h value seeds with increasing overall seed density. Davies (1977) reported that spotted flycatchers became more selective with increasing densities of high E/h insect types and that no specialization occurred when the density of low E/h insect types rose. Goss-Custard (1977) reported similar results in his field study of the redshank preying on marine worms. He also noted that the birds occasionally preyed on less profitable worms when optimal diet theory would have predicted a disadvantage in doing so. In a recent field experiment, Vickery (1984) observed that three different rodent species consistently preferred the food type

associated with the highest E/h ratio, but the densities of both high and low types influenced acceptance. In addition, the animals continued to forage on low quality food, even with increasing abundance of the preferred type. Other researchers have reported similar findings in a variety of species (e.g. Lewis, 1980; Mittelbach, 1981; Waddington & Holden, 1979).

In contrast, laboratory studies of diet selection have been conducted to isolate and manipulate factors believed to be influential in the foraging process. Often the studies are characterized by imaginative and unusual designs, in an attempt to reconcile the need for control with the desire to keep the situation as natural as possible. For example, Krebs, Erichsen, Webber, and Charnov (1977) examined the decisions of great tits feeding off conveyor belts attached to their cages. The belts permitted the researchers to control the encounter rates of two prey types. The birds were observed to make the predictable shift from feeding on both types to specializing in only the more profitable type with an overall density increase. Increasing only the density of the less profitable prey had no effect on choice behavior.

Moermond and Denslow (1983) offered individual wild-caught, fruit-eating birds choices between pairs of different fruits. The birds were reliably sensitive to fruit differences, showing consistent preferences on 67-100% of the trials. Even more important, the choices of the birds

were transitive: a finding which strongly supports the notion that foragers respond to prey items in accord with an E/h type scale.

Lea (1979) attempted to simulate the foraging situation by utilizing reinforcement schedules in a traditional operant paradigm. A modified concurrent chain schedule was used, with responses on an initial "search" schedule resulting in one of two terminal "handling" schedules. Each terminal schedule represented a prey type, with the shorter schedule being the more preferred. Prey density was manipulated by varying the accessibility of the schedules. By increasing overall prey density, Lea was able to show an increased tendency to accept only the preferred prey. Increasing the density of the preferred prey affected the rate of acceptance of the nonpreferred prey in the predicted manner. Increasing the density of the nonpreferred prey was found to have a slight effect on its rate of acceptance. Abarca and Fantino (1981) and Peden and Rohe (1984) adopted Lea's design with slight schedule alterations and reported similar results. Collier and his colleagues (e.g. Collier & Rovee-Collier, 1981; Jensen, 1980) have also shown comparable results using rats in operant simulations.

In summary, the empirical research on diet selection suggests that the foraging model proposed by MacArthur and Pianka (1966) does, with limitations, an adequate job of describing the foraging behavior of animals. The hypothesis that animals rank food types according to an energy

maximization criterion has been almost universally supported. (For an exception, see Shettleworth, 1985.) In addition, animals do shift toward selectivity with increasing density, but the hypothesis of an all-or-none shift has received almost no support (but see Snyderman, 1983).

Diet selection is a survival problem that has been addressed almost entirely at the ultimate level. The classical optimal diet model of MacArthur and Pianka (1966) requires that the forager be extremely sensitive to the E/h values and densities of all potential prey types. But few have speculated on the proximal mechanisms permitting the forager to monitor these features of its environment. Proximal mechanisms include specific procedures which enable animals to function in certain ways. A common example comes from the learning psychology literature, in which choice behavior is studied by examining the distribution of responses an animal makes on two available schedules of reinforcement. Sensitivity to reinforcement rates permits the animal to choose between two concurrently available alternatives. Similarly, an optimality analysis of foraging describes general rules for maximizing energy intake but does not specify the procedures which would enable the animal to follow the rules. As such, optimal diet theory is a model of performance outlining how animals should behave. But, as the previous review of foraging studies indicates, animals consistently do not behave in a strictly optimal

manner. With a mismatch between the optimization model and behavioral data, it is appropriate to search for constraining factors, such as limited physiological investment and the need to meet conflicting demands, which may have exerted opposing selective pressures on the species. In dealing with the possibility of selection resistance to the development of complex physiological machinery necessary for fully optimal decisions, behavioral ecologists have postulated that very simple strategies or automatic response algorithms may be sufficient to allow an animal to exhibit near-optimal behavior (e.g. Barnard, 1984; Shettleworth, 1984). The identification and understanding of such proximal mechanisms is necessary for the incorporation of these constraints into models of foraging behavior.

Lea (1981) has suggested that the general processes used during foraging are likely the same as those underlying conditioned behavior in the psychology laboratory. This is particularly likely in the selection of diet, as all foraging animals have the goal of acquiring sufficient food resources to survive, even though the types of prey in the diet and the methods of procurement differ widely across species. Thus, with regard to the ranking of prey types, presumably there is a general mechanism permitting foragers to determine which prey types to select for their diet.

The experiment described in this report is based on a specific application of Lea's hypothesis to the problem of how the forager goes about a monotonic ranking of potential

prey types. A well-studied learning mechanism of the psychology laboratory that is undoubtedly relevant to prey selection is the phenomenon known as taste aversion learning. In brief, taste aversion learning is a form of associative conditioning, in which an animal decreases consumption of a particular substance following the pairing of ingestion with poison-induced illness. (See Riley & Baril, 1976, for a bibliography of taste aversion studies.) This conditioning paradigm is easily displayed in species that identify their prey by means of gustatory and olfactory cues, for which the development of a mechanism permitting the rapid association of tastes and gastrointestinal effects would be especially advantageous (Kamil & Yoerg, 1982).

Brower, Ryerson, Coppinger, and Glazier (1968) first alluded to the possibility that aversions could form part of the mechanism of diet decisions by suggesting that there may be an entire palatability spectrum, with highly preferred items at one end and items to be avoided at the other. Mellgren (1985) clarified this proposal further by suggesting that a forager may acquire all the information necessary for prey selection by means of an aversion learning mechanism. Specifically, a high E/h prey item, when frequently included in the forager's diet, could result in the formation of an aversion to lower-ranking items, if ingredients contained in the high E/h prey have the effect of altering the taste sensitivities to items lower on the scale, making them less palatable. A mechanism of this

nature would provide the forager with information about both the relative qualities of the potential prey types and their associated encounter rates because lower-ranking items would be increasingly accepted with a decrease in the density of higher-ranking items. If a high E/h type is rarely encountered, then any aversions previously conditioned to lower-ranking items would extinguish, resulting in an increase in their acceptance.

The purpose of this research was to investigate the aversion hypothesis by experimentally conditioning different levels of taste aversion to a prey type and observing the resulting foraging patterns. A paradigm used in a laboratory experiment simulating the natural environment, reported by Mellgren, Misasi, and Brown (1984), is ideally suited for the investigation of variables purported to affect foraging, such as taste aversion conditioning, because it provides easy control of relevant environmental variables. Prior to a description of the Mellgren et al. (1984) study, a basic introduction into the theoretical basis is necessary.

In the natural environment, the assumption that prey are encountered in a sequential fashion is often unrealistic. For many species, food items are distributed in clumps or patches rather than continuously. Hence, an animal needs to determine not only what type of patch to visit, but also, how long to remain in a specific patch.

Charnov (1976) has developed an optimal decision model, the marginal value theorem (MVT), which deals with the

forager's problem of when to leave a patch. Like the optimal diet model, the MVT is based on several simplifying assumptions. The animal is assumed to spend all of its time either searching for prey within a patch or travelling between patches. While a forager is in a patch, food intake decreases with time spent, due to depletion of the resources. Also, the number of prey present within a patch cannot be observed directly. Instead, the predator must sample the patch in order to form an expected value for the patch. The forager is also assumed to possess knowledge of the overall average capture rate for the habitat and the instantaneous marginal capture rate (which is dependent on the amount of time already spent in the patch). This information is necessary for the forager to determine the point at which it is optimal to desert the patch, which is when the marginal capture rate in the patch drops to the average capture rate for the habitat. In other words, in order to acquire the maximum amount of food available from an entire habitat, the forager should remain in any one patch long enough for the number of prey items to deplete to a point that is equal to the overall rate of return available from the remainder of the habitat.

Predictions of the MVT are displayed graphically in Figure 1. Patch A is characterized by a high rate of return, which means that an animal could forage for a relatively long time before the net return rate drops to a point where foraging elsewhere would yield a higher return per unit

time. Patch B should be foraged in for a shorter time period, while Patch C should not be exploited at all because the net return rate would never equal or exceed the average rate of return for the entire habitat.

Insert Figure 1 about here

Precise quantitative tests of the MVT are problematic, as it is difficult to validate the restricting assumptions. The forager's expected value for the patch is a function of the rate of capture during sampling, while the instantaneous marginal capture rate is a function of the ongoing rate of capture. Consequently, much of the evidence cited in support of the MVT is qualitative. For instance, birds have been observed to remain longer in high density foraging areas when the overall availability of food is low (Smith, 1974 a, b). Unicellular predators display an increased frequency of turning in high density areas, a behavior pattern that results in a more intensive search of the surround (cited in Charnov, 1976).

Fortunately, Krebs, Ryan, and Charnov (1974) have extended the MVT by proposing an algorithm that would result in a foraging strategy approximate to that predicted by the theorem. They reasoned that if animals use the simple rule, "leave patch if no prey items have been encountered within t seconds of arrival or since last capture," this would produce close to optimal patch use. The giving-up time

(GUT), the time between the forager's last capture and patch desertion, is then used as a measure for testing the model, rather than rate of food intake. The GUT hypothesis predicts that, regardless of the initial densities of prey, a forager will have a constant GUT for all patches within a habitat and that this time will decrease as the average capture rate for the habitat increases.

Mellgren et al. (1984) derived a second prediction from the MVT which permits a less obtrusive measure of patch use than time. To recount, the MVT assumes that the longer a forager remains in a patch, the lower the rate of return. This rate of return will fall to the marginal value when the patch has been depleted to a particular level. Hence, the rate of capture in a patch is a function of the number of prey still remaining in the patch. Therefore, regardless of the initial density of prey in a patch, the number of prey remaining in the patch after a forager abandons it should be, on the average, a constant. The left-over-constant (LOC) provides an easily calculable measure of optimal patch utilization.

Mellgren et al. (1984) designed a simulated foraging environment in which factors expected to influence patch use, such as prey density, interpatch distance, and foraging bout duration, could be explicitly controlled. Rats were trained to dig for food pellets buried in sandboxes ("patches") in a small room. The patches were placed on ledges attached to posts reaching from floor to ceiling,

which permitted manipulation of patch height. The rats were tested under various environmental conditions and their foraging patterns were compared with the predictions of the LOC model.

Initially, Mellgren et al. (1984) kept patch height and, therefore, interpatch distance, constant, while prey density was varied in order to determine consumption of available prey as a function of differing densities. The LOC model predicts this to be a straight line function, with a slope of 1.0 and a y-intercept of $-(LOC)$, as in: amount consumed = $-(LOC) + (1.0)$ amount available + error variability, which is in the form of a least squares model of regression: $Y = B_0 + B_1X + e$. Mellgren et al. (1984) found a close match between the LOC model predictions and the actual foraging behavior of the rats, which means that the animals did leave a constant number of pellets in each patch, regardless of the amounts available at the beginning of a session. Residence times also increased with increasing prey density, but the effect was more variable than that indicated by the LOC measure. This probably reflects the fact that residence time can include both foraging and non-foraging directed activities, while the amount left is a more direct measure.

Mellgren et al. (1984) then introduced unequal prey densities within a session, with each density consistently located in the same patch across successive sessions. Under these conditions, Mellgren et al. (1984) noted a systematic

deviation from predicted optimal behavior. The rats tended to overutilize low density patches and underutilize high density patches. When the locations were rotated so that each density appeared in each location only once across a set of sessions, the deviation was still present, although not as pronounced.

Finally, Mellgren et al. (1984) investigated the influence of travel costs on patch use. Making travel between patches more costly should increase the value of staying in a patch longer, as the average profitability of the habitat is lowered and the rate of return from the patch will take longer to drop to the marginal value for the habitat. In other words, increasing travel time is predicted to increase patch residence time and decrease the LOC. While the general predicted trends were observed, Mellgren et al. (1984) found a close match between the observed foraging patterns and the model only at high travel costs. When the patches were only 1 foot off the floor, the LOC model did not fit the data. The match was improved at 4 feet and was best at 7 feet. Mellgren et al. (1984) concluded that increasing the difficulty of travel appears to facilitate optimal patch exploitation.

Having surveyed the Mellgren et al. (1984) paradigm, it is important to understand how a conditioned taste aversion might operate in such a foraging situation. Recall that the MVT of patch use predicts that the forager behaves so as to maximize the net rate of energy intake during a feeding

session. Therefore, an important factor for animals foraging in a patchy environment is the energy intake obtained while in a patch, which is a direct function of the type of prey contained in the patch. Each prey type, then, has its own specific energy-intake-over-time curve, as is displayed in Figure 2. In order to maximize energy intake, a forager should remain longer in patches containing high quality prey than in patches of low quality prey. In measurable terms, the lower the value of the prey type in the environment, the greater the LOC for each particular patch.

Insert Figure 2 about here

An implicit necessity of the MVT, then, is that a mechanism is required permitting foragers to discriminate prey types of high quality from types of low quality. As noted previously, Brower et al. (1968) and Mellgren (1985) have proposed that conditioned taste aversions could provide this mechanism.

Consider, for example, a forager in a patch of prey items of a given quality. If the number of items in the patch does not replete as the animal forages, the rate of energy intake decreases with time in the patch. Such a condition is depicted in the top panel of Figure 3. However, with a weak taste aversion conditioned to the prey type, the palatability mechanism would result in an effective energy intake that is lower than the nominal energy intake. In

other words, the forager behaves as if the quality of the prey type had lowered. All else being equal, the effective energy intake function would look like the middle panel of Figure 3. A stronger taste aversion would presumably result in an even lower effective energy intake function, such as that depicted in the bottom panel of Figure 3. This lowering of the effective quality of the prey type would be reflected in the forager's behavior, such that with an increase in the level of aversion conditioned to the type, foraging patterns typical for a prey type of poorer quality would be observed (with a corresponding increase in the LOC).

 Insert Figure 3 about here

The LOC model predicts that the function describing patch exploitation should take the form of a line with a slope of 1.0 and a y-intercept of $-(LOC)$. If the ingestion of an averted prey type operates functionally like the ingestion of a low quality prey type, it is expected that increasing the level of aversion would affect patch use by decreasing the y-intercept of the best-fitting line (in other words, increasing the LOC), while leaving the slope unchanged. In addition, the error variance or "degree of fit" with the model should remain constant. A second prediction about the pattern of foraging observed under the described conditions concerns the optimal amount of time spent in each patch. Patch residence times would be expected

to decrease with increasing levels of conditioned aversion because the asymptote of the energy-intake-over-time function is lower for poorer quality prey. These predictions were tested in the present study by comparing the patterns of foraging observed under three aversion conditions, using a simplified version of the Mellgren et al. (1984) simulation paradigm. All environmental features were held constant, with the exception of prey density and level of taste aversion.

II. METHOD

Subjects

Eight male Long-Evans rats, approximately 11 months old at the start of the experiment, were maintained at 85% of their free-feeding weights. The rats were not experimentally naive, having previously participated in a standard spatial memory study on the eight-arm radial maze.

Apparatus

The experimental room was a small empty room, measuring 301 cm x 327.5 cm in size. A square, with sides 140 cm long, was drawn on the floor, with the outside corners designating patch locations. At each of the four corners, a plastic box, measuring 21.5 cm x 21.5 cm x 7.5 cm in size, was placed on a wooden stand, 31 cm high. A thin piece of bordered wire mesh ran from the top of the stand to the floor, as a "ladder" for the rats. Each box, or "patch," was filled with The Andersons Bed-o'cobs Bird and Animal Litter, 1/4 inch size, to a depth of approximately 4 cm. Standard 45-mg Noyes pellets were used as "prey" during the initial preliminary training, while 45-mg Noyes sucrose pellets were used during the remainder of the experiment.

Procedure

General Overview.

The intention of the procedure was to train animals to forage in a patchy environment containing two prey densities (10 pellets and 20 pellets). After measuring the parameters of the LOC model, each rat was then tested under two aversion conditions. This was accomplished with a multiple-phase experiment. Phase 1 was a test of foraging under conditions of no aversion. Phase 2 was a test of foraging at either a weak or a strong level of aversion. Lastly, Phase 3 was a test of foraging at the alternate level of aversion. The order of aversion levels was counterbalanced across two groups. A general schematic of the procedure appears in Table 1. The specific procedure follows.

Insert Table 1 about here

Preliminary Training.

All subjects were given training finding food buried in litter by systematically introducing the components of the foraging room over a 76-day period. Initially, each rat was required to find food in one patch placed on the floor, with the amount of litter contained in the box gradually increasing to the desired level across sessions. Within 14 days, all the rats were

displaying consistent and stable foraging patterns and an additional patch was introduced. Subsequently, the rats took an average of 12 days to achieve stable foraging with each additional patch introduction. After the rats were foraging from all four patches, the stands and ladders were introduced for a seven day period. Following this, unequal prey densities within a session were presented, with 10 pellets in each of two of the patches diagonally across from each other, and 20 pellets in each of the remaining two patches. The location of each density was rotated on consecutive sessions. Stable foraging was judged to have been achieved after five days and the data from the following five days were analyzed to determine if the results could be described by the LOC model. It was thought that if the results indicated significant deviations from optimality, it would be necessary to increase patch height, as Mellgren et al. (1984) reported a close fit between their experimental results and the LOC model only at patch heights greater than 1 foot. A least squares regression line was fit to the data for each subject and a test of the null hypothesis that each slope equalled 1.0 was computed. Out of the eight line slopes, only one was found to be significantly different from 1.0, at a probability level of 0.05. This was judged to be a sufficiently close match, and the heights of the patches remained at 31 cm. Experience with

unequal prey densities continued for a total of 21 days. Introduction of the sucrose pellets occurred last, to ensure that the taste would still be relatively novel in Phase 1. The rats received experience foraging for sucrose pellets three days prior to initiation of the experiment.

Phase 1.

Following preliminary training, each subject was tested in the experimental room for 30-minute sessions on eight consecutive days. At the beginning of a session, each rat was placed in a random orientation at the center of the room. Two of the patches diagonally across from each other contained 20 pellets each, while the remaining two contained 10 pellets each. The densities were rotated, such that each density was located in each patch exactly four times, alternating with each consecutive session, to guard against position preferences. During the session, the amount of time the rat spent in each patch was recorded by an experimenter, blind to the experimental hypotheses. Times were measured by means of a battery-operated LED stopwatch. Patch entry was defined as "that moment when all four feet of the rat are in contact with or inside the box", while patch exit was "that moment when all four feet of the rat lose contact with the box". Two independent observers recorded residence time data during three separate 15-minute sessions to determine cross-observer

reliability of the behavioral definitions. A correlation of 0.99 was achieved between the times recorded by the observers. At the completion of a session, the rat was removed and the amount eaten from each patch was determined by sifting the litter through a screen. The litter from all patches was periodically mixed together to prevent patch preferences due to idiosyncratic odor.

Phase 2.

At this point in the experiment, subjects were randomly divided into two equal-sized groups, hereafter referred to as Group O-W-S or Group O-S-W, depending on the particular procedural order experienced by the group. All rats were averted to the sucrose pellets by means of a taste aversion conditioning procedure adapted from Holland and Rescorla (1975). In the home cage, each rat was presented with 50 sucrose pellets for a 10-minute period. Immediately following this access, the rat was removed from the cage and given an intraperitoneal injection of 0.6 M Lithium Chloride, at a dosage of 5cc per kg. The injection caused approximately 10 seconds of localized pain around the area of the injection, followed by a 60-minute period of general lethargy. The number of pellets consumed during the 10 minutes was recorded. Two hours later, the rats were fed sufficient food to maintain their 85% weight. The conditioning procedure was carried out for two consecutive days.

As it was essential to ensure that all subjects in a group were equally averted to the sucrose pellets, an extinction procedure was implemented following the conditioning. On consecutive days, each rat was presented with 50 sucrose pellets in the home cage for 10 minutes. The number consumed at the end of the period was recorded and two hours later, the rats were fed sufficient food to maintain the 85% deprivation level. Extinction trials continued for Group O-S-W until each rat was ingesting at least 10 pellets (which represents 20% of the 50 pellets originally consumed prior to conditioning). Thus, the rats in Group O-S-W were tested with an equivalently strong aversion to the sucrose pellets. In contrast, extinction trials for Group O-W-S continued until each rat consumed at least 40 pellets (80% of the original 50 pellets), such that the rats all had an equivalently weak aversion to the pellets.

As each rat reached the criterion level set for its group, it was tested in the experimental room for 30-minute sessions on four consecutive days. Densities were again rotated to guard against position preferences. Residence times and the amounts eaten from each patch were measured. Following the four-day testing period, each rat was maintained on deprivation in the home cage, until all rats in that group had completed the testing. Once the entire group had finished the four-day test, each rat spent two additional days in the

home cage, in an attempt to ensure the experiences of all subjects were roughly similar. On the third day, the rats were again presented with 50 sucrose pellets for 10 minutes in their home cages and the number eaten was recorded. Once all the rats in the group were consuming at least 30 pellets (60% of the original 50 pellets) they were forwarded, as a group, into the next phase.

Unfortunately, at this point in the experiment, one subject from Group O-W-S was excluded from the remaining procedures. While the other subjects in the group reached the determined criterion for ingestion after an average of 20 extinction trials, one rat still exhibited no signs of extinguishing after 21 consecutive days. At this time, it was decided to attempt an approximated "implosion therapy" with the rat. Following each extinction trial, the rat was force-fed a liquid sucrose concentration (2 pellets dissolved in 1 ml of water) through a syringe. This procedure was employed for nine consecutive days, with no apparent affect on consumption. The concentration was increased to 10 pellets dissolved in 1 ml of water, for 12 additional days. This also had no observable affect on the rat's consumption of pellets and, for practical reasons, it was decided to proceed with the three remaining rats. As a consequence of this complication, the two groups received different experimental procedures, with Group O-S-W having a minimum of two "rest days" before

continuing with the next phase, and Group O-W-S having a minimum of 11 "rest days."

Phase 3.

Phase 3 was identical in all respects to Phase 2, with the exception that the criterion levels for extinction were reversed. Following completion of the second testing, each group of rats received a second aversion conditioning to the sucrose pellets. Group O-S-W was then extinguished to an 80% level, while Group O-W-S was extinguished to a 20% level of aversion. Again, upon reaching the determined aversion level, each rat was tested in the experimental room for 30-minute sessions on four consecutive days. Residence times and the amounts eaten from each patch were recorded. A detailed description of the experiences of individual subjects is presented in Table 2.

Insert Table 2 about here

III. RESULTS

Preliminary Training

During the preliminary training, subjects were allowed 30-minute daily foraging sessions over a 76-day period, while each component of the foraging situation was gradually introduced. The only datum recorded was the number of pellets obtained from each patch.

The rats appeared to acquire the response of digging for food pellets easily. With only one patch in the room, the subjects ate virtually all the pellets during a session. Once all the rats were consistently obtaining 15 out of the 20 available pellets buried in the full amount of litter, a second patch was introduced. With two patches full of litter, most of the rats were again able to obtain virtually all of the 40 available pellets during a session. Two rats were the exception, consuming an average of 16 pellets out of each patch during the last session prior to the introduction of a third patch. With three full patches, the rats were consuming a mean of 18.2 pellets from each patch during a session. At this point, only two of the rats were consistently leaving more than one or two pellets in each patch. With the introduction of the stands and ladders, the mean number of pellets consumed from each patch dropped to 12.8, a figure based on data from the day prior to the incorporation of unequal prey densities. After five sessions with unequal prey densities, the rats were foraging

consistently under these conditions (leaving similar LOCs in each patch over three consecutive sessions) and a best-fitting line was fit through the data from the following five days for each subject. The analysis revealed that the LOC model of foraging described the data well, with an overall mean y-intercept of -1.34 (range = -3.10 to 0.30) and an overall mean slope of 0.88 (range = 0.53 to 1.08). Over the five days, a mean of 47.5 pellets were consumed per session, out of the total 60 pellets available. There were few instances of any of the rats failing to visit patches during a session. The final change during the training part of the experiment was the introduction of sucrose pellets. Over the three days, the rats appeared to react to the replacement of standard pellets with sucrose pellets, consuming a mean number of only 21.3 out of the total 60 pellets available per session.

Phase 1

During Phase 1, the rats were allowed eight 30-minute foraging sessions on consecutive days. Overall, the mean total amount eaten per session was 43 out of the 60 pellets available per session. There were no instances of a rat not visiting a patch during Phase 1. The average number of patch visits in a session was 10.5 (range = 5.4 to 16.5). Time spent in a patch increased as a function of food density, with a mean residence time of 7.07 minutes for 10-pellet

patches and 10.12 minutes for 20-pellet patches. The mean number of pellets consumed per minute over both prey densities was 2.4. These behavioral measures of foraging are summarized in Table 3.

 Insert Table 3 about here

Search paths were highly efficient. The probability of a repeat visit to a patch as a function of the ordinal number of the visit for the two experimental groups is shown in Figure 4. Two theoretical extremes of performance, the cases of "perfect memory" and "no memory," are also displayed for comparative purposes. A subject with no memory, choosing patches strictly on a random basis, would visit a previously visited patch on the k th visit with probability $P_k(\text{repeat})$,

$$P_k(\text{repeat}) = 1 - \frac{\binom{N}{k}}{N^k}$$

where N is the number of patches (Mellgren et al., 1984). The actual performance of the rats is clearly closer to the perfect memory case.

 Insert Figure 4 about here

A least squares regression analysis determined the subjects' utilization of the available pellets as a function of differing densities, with the results shown in Figure 5.

The mean y-intercept over all the subjects was -1.29, while the mean slope was 0.81 ($r = 0.80$ between amount available and amount consumed).

Insert Figure 5 about here

Conditioning 1

On the first day of the initial conditioning, all subjects consumed the total 50 pellets offered for 10 minutes in the home cage, prior to the injections. On the second day, the mean consumption rate was 4.2 pellets during the 10 minutes. Only two rats consumed any pellets on the third day, with one subject eating two pellets and the other eating a single pellet.

Following the aversion conditioning, the subjects were randomly divided into two groups for the extinction procedure. Over the course of the extinction trials, consumption of the pellets gradually increased to approximately 10 pellets; subsequent to this, the consumption rate increased much more drastically. Group O-W-S required a mean number of 19.3 extinction days to reach the criterion of 80% of the original 50 pellets (range = 10 to 27). In contrast, Group O-S-W took a mean number of 11.8 extinction days to achieve the criterion of 20% of the

original 50 pellets (range = 10 to 13).

Phase 2

During Phase 2, the rats were allowed four 30-minute foraging sessions on consecutive days. For Group O-W-S, the overall average amount eaten was 38.5 pellets per session. There were no instances of a rat not utilizing all of the four patches in a session. The average number of patch visits in a session was 10.6 (range = 6.5 to 15.8). Time spent in a patch increased as a function of food density, with a mean residence time of 6.32 minutes for 10-pellet patches and 9.08 minutes for 20-pellet patches. The mean number of pellets consumed per minute over both prey densities was 2.6.

For Group O-S-W, the mean total amount eaten during Phase 2 was 32.1 pellets per session. There was only one instance of a rat not utilizing a 20-pellet patch during a foraging session. The average number of patch visits in a session was 7.1 (range = 5.8 to 9.8). Time spent in a patch increased as a function of food density, with a 5.12 minute residence time for 10-pellet patches, and a 6.43 minute time for 20-pellet patches. The mean number of pellets consumed per minute over both prey densities was 2.5. Refer to Table 3 for a summary of these foraging measures organized according to level of aversion.

As in Phase 1, search paths were again highly efficient. The probability of a repeat visit to a patch as a

function of the ordinal number of the visit for the two groups is shown in Figure 6. As before, the performance of the rats is very close to the perfect memory case.

Insert Figure 6 about here

A least squares regression analysis determined the subjects' utilization of available pellets as a function of differing densities. The results are shown in Figure 7. The mean y-intercept was -0.54 and the mean slope was 0.68 for Group 0-W-S ($r = 0.83$ between amount available and amount consumed). For Group 0-S-W, the mean y-intercept was -0.19 and the mean slope was 0.52 ($r = 0.58$ between amount available and amount consumed).

Insert Figure 7 about here

Conditioning 2

On the first day of the second conditioning to the sucrose pellets, the rats in Group 0-W-S consumed a mean number of 45.7 pellets during the 10 minutes prior to the first injection. On the second day, the mean consumption rate was 0.3 pellets. On the third day, the rats again consumed an average of 0.3 pellets. Following the aversion

conditioning, the rats in this group were extinguished to a 20% criterion. The group required a mean of 11.7 extinction days to reach the criterion (range = 4 to 26).

On the first day of conditioning, the rats in Group 0-S-W consumed a mean of 46.5 pellets during the 10 minutes prior to the first injection. On the second day, the mean consumption rate was 3.8 pellets. On the third day, the rats consumed an average of 0.5 pellets during the 10 minutes. Following conditioning, rats in this group were extinguished to an 80% criterion, requiring a mean number of 23 extinction days (range = 14 to 45).

Phase 3

During Phase 3, the rats were permitted four 30-minute foraging sessions on consecutive days. For Group 0-W-S, the overall mean amount eaten was 14 pellets per session. There were two instances of the same rat failing to utilize all the patches during a session. The average number of patch visits in a session was 6.2 (range = 3.3 to 7.0). Time spent in a patch increased only marginally as a function of food density, with a mean residence time of 5.08 minutes for 10-pellet patches, and 5.83 minutes for 20-pellet patches. The mean number of pellets consumed per minute over both prey densities was 1.3.

For Group 0-S-W, the mean total amount eaten during Phase 2 was 29.7 pellets per session. There were instances

of rats not utilizing all the available patches, with one rat not visiting a 20-pellet patch during a session, and a second rat failing to visit a 10-pellet patch in one session and during the final session, not utilizing any patches. The average number of patch visits in a session was 5.8 (range = 4.1 to 8.6). Time spent in a patch increased as a function of food density, with a 4.93 minute mean residence time for 10-pellet patches, and a 6.35 minute time for 20-pellet patches. The mean number of pellets consumed per minute over both prey densities was 2.7. See Table 3.

As in the previous phases, search paths were highly efficient. The probability of a repeat visit to a path as a function of the ordinal number of the visit for the two groups is shown in Figure 8. Actual performance is again more closely approximated by the perfect memory case.

Insert Figure 8 about here

⊙ A least squares regression analysis determined the subjects' utilization of available pellets as a function of differing densities. The results are shown in Figure 9. For Group 0-W-S, the mean y-intercept was -1.88 and the mean slope was 0.36 ($r = 0.55$ between amount available and amount consumed). For Group 0-S-W, the mean y-intercept was 0.44 and the mean slope was 0.50 ($r = 0.58$ between amount available and amount consumed).

Insert Figure 9 about here

Comparison of Pre and Post Conditioning Tests

A comparison of several measures of foraging under the various levels of aversion was predicted to show a number of specific effects, provided the experimental manipulations successfully mimicked the presentation of differentially-ranked prey types. According to optimal foraging theory, as the energetic value of prey decreases, the amount of the prey consumed by the forager should also decrease. As a result, the LOC is expected to increase, while patch residence time should decrease. The fit of the optimal foraging model should remain unchanged, regardless of the value of the food type. Consequently, if aversion conditioning forms a mechanism of diet selection, the same effects should be present when foraging on a prey type across different levels of aversion. Each of the indices of foraging are described separately for ease in presentation.

Fit of the LOC Model.

The correlation between the amount eaten and prey density was taken to be an index of the error variability or "degree of fit" with the linear regression model. The fit of the foraging model should

not vary across the different levels of aversion because animals presumably forage in an optimal manner, regardless of the types of prey available.

The actual analysis was carried out on Fisher's z transformation of the correlation coefficient. It was necessary to transform the correlations into z scores because the sample means are correlated with the sample variances. Unlike the correlation coefficient, Fisher's z is a random variable with a normal distribution and, therefore, tests of hypotheses do not violate the assumption of homogeneity of variance inherent in the F test (Staff of Research and Education Association, 1978).

Initially, t tests of the difference in group means at Phase 2 and Phase 3 were computed to determine if the groups differed significantly on their z scores. Since the groups differed only in the order of aversion level conditioned, there was no reason to expect any systematic differences and the t tests, based on the assumption of a common population variance, merely confirmed this: [$t(5)=-2.55, p>.05, \text{two-tailed}$] for Phase 2, and [$t(5)=0.50, p>.05, \text{two-tailed}$] for Phase 3. Thus, it was judged acceptable to collapse the two groups in order to use a more powerful one-way repeated measures analysis of variance. The analysis revealed results consistent with the earlier prediction: a nonsignificant effect due to aversion level

[$F(2,12)=2.80$, $p>.05$]. In other words, the fit of data to the LOC model of patch use did not change over the different levels of aversion.

Y-Intercept of the Utilization Function.

According to optimal foraging theory, utilization of available prey as a function of food density should produce a linear function with a slope of 1.0 and a y-intercept of $-(LOC)$. The LOC, and its additive inverse, amount eaten, are indices of the amount of resources an animal has taken from its environment. Although the average LOC should be the same for all patches of a particular prey quality, the LOC for patches characterized by low quality prey should be greater than the LOC for patches of high quality prey. Likewise, in the present study, the LOC was expected to increase with increasing level of aversion or, in other words, the y-intercepts of the subjects' functions should become more negative under conditions of increasing aversion.

The t tests of the difference in group means indicated a nonsignificant difference for Phase 2 [$t(5)=1.14$, $p>.05$, two-tailed] and for Phase 3 [$t(5)=1.35$, $p>.05$, two-tailed], which was accepted as justification for collapsing the groups. No significant effect due to aversion levels was found for the y-intercepts [$F(2,12)=1.55$, $p>.05$]. Contrary to the change predicted by the LOC model of foraging, the

y-intercepts did not decrease with increasing levels of aversion to the pellets.

Slope of the Utilization Function.

The slope of the least squares regression line represents an index of the amount of resources an animal has removed from the environment in relation to the density of the resources. According to optimal foraging theory, the slope of the function should equal 1.0, regardless of the type of prey present in the habitat. Likewise, in the present study, the slopes of the subjects' functions should remain at 1.0 under all levels of aversion.

t tests of the difference between group means were nonsignificant for Phase 2 [$t(5)=-1.40$, $p>.05$, two-tailed] and for Phase 3 [$t(5)=1.15$, $p>.05$, two-tailed], and the groups were collapsed for the analysis of variance. As expected, any variance due to subjects was not significant [$F(6,12)=1.18$, $p>.05$]. This test was assumed to be unbiased because Tukey's test of additivity (Tukey, 1949) indicated there was no subject by aversion level interaction [$F(1,11)=0.33$, $p>.05$].

The test of the effect due to aversion level was significant [$F(2,12)=8.60$, $p<.005$], even when assuming extreme heterogeneity of variance (at a probability level of 0.05) (Box, 1954). An estimate of the relative effect of the aversion conditioning manipulation was 41% of the total variance in the treatment population. A

set of three contrasts were used to detect the significant sources of variation, with the per comparison error rate adjusted to maintain an overall error rate for the set at a probability level of 0.05. Only the largest contrast, which compared the no aversion mean of 0.81 with the strong aversion mean of 0.45 was significant. [$F(1,12)=16.71, p<.005$]. The remaining two contrasts, the no aversion versus the weak aversion and the weak aversion versus the strong aversion, were not significant [$F(1,12)=7.02, p>.017$] and [$F(1,12)=2.07, p>.017$], respectively. Thus, contrary to the original predictions, the slopes of the individual foraging functions did not remain at 1.0 but, rather, decreased with increasing levels of aversion. Figure 10 shows a comparison of the utilization functions across the three aversion levels for each individual subject.

Insert Figure 10 about here

Patch Residence Time.

The final hypothesis tested was whether time spent in the patches decreased with increasing aversion levels. Although patch residence time is not necessarily a direct index of foraging because it can also reflect non-foraging activities, Mellgren et al. (1984) reported that, in general, residence time increased with

increasing prey density and decreased with decreasing E/h ratio. Similarly, in the present study, it was predicted that residence times should be greater for 20-pellet patches than 10-pellet patches and that these times should decrease with increasing levels of aversion.

Tests comparing the group means on residence time during Phase 2 and 3 were computed separately for each of the two prey densities, in case the groups responded differentially to density. For the low density patches, mean residence time did not differ significantly in Phase 2 [$t(5)=-1.45$, $p>.05$, two-tailed] or in Phase 3 [$t(5)=0.02$, $p>.05$, two-tailed]. Similarly, for the high density patches, the groups did not differ in residence time for Phase 2 [$t(5)=-1.56$, $p>.05$, two-tailed] or Phase 3 [$t(5)=0.35$, $p>.05$, two-tailed]. Based on the nonsignificant differences, the groups were collapsed for a two-factor analysis of residence time and prey density. Assuming a nonadditive model, both prey density [$F(1,6)=71.36$, $p<.001$] and level of aversion [$F(2,12)=14.32$, $p<.001$] were highly significant sources of variance. Furthermore, the interaction of prey density and aversion level was significant [$F(2,12)=8.31$, $p<.01$]. The interaction effect is shown in Figure 11.

Insert Figure 11 about here

Three sets of contrasts were computed to detect differences among subset means. One set of contrasts compared aversion condition means at the low prey density level. For the 10-pellet patches, residence time did not differ significantly for the comparison of no aversion with strong aversion [$F(1,12)=1.01, p>.017$], no aversion with weak aversion [$F(1,12)=0.62, p>.017$], or weak aversion with strong aversion [$F(1,12)=0.00, p>.017$]. Similarly, for the high density patches, the comparison of no aversion with strong aversion was not significant [$F(1,12)=5.30, p>.017$], nor were the comparisons of no aversion with weak aversion [$F(1,12)=2.62, p>.017$] or weak aversion with strong aversion [$F(1,12)=0.05, p>.017$]. Finally, the third set of contrasts compared mean residence times across the two prey densities for each level of aversion separately. Residence times did not differ significantly between the high and low prey densities with no aversion [$F(1,6)=1.28, p>.017$], with a weak aversion [$F(1,6)=0.39, p>.017$], or with a strong aversion [$F(1,6)=0.11, p>.017$].

Overall, residence time was greater for the high density patches than the low density patches, although contrasts of the means were not sufficiently powerful to

detect the exact location of any differences. As predicted, patch residence time decreased with increasing aversion to the pellets, but a significant interaction effect indicates that the decrease was more pronounced for time spent in the high density patches.

Number of Patch Visits.

Although the previous analyses were sufficient to test the major hypotheses of the study, the data collected permitted the extraction of additional indices of foraging. One such measure is the number of patch visits made during a session. It is difficult to make a theoretical prediction of whether the number of visits to each patch should vary across aversion levels because the MVT assumes that return visits to a patch are not made. The rats in this study did tend to make several return visits and the number of visits in a session appeared to decrease across the levels of aversion, as is shown in Figure 12.

Insert Figure 12 about here

The t tests comparing group means on average number of patch visits per session were not significant for Phase 2 [$t(5)=-1.41$, $p>.05$, two-tailed] or for Phase 3 [$t(5)=-0.20$, $p>.05$, two-tailed], and the groups were collapsed. A marginally significant effect due to subjects was detected [$F(6,12)=3.99$, $p<.05$], which

merely suggests there was individual variation in the number of patches visited by the different subjects. Tukey's test of additivity was nonsignificant [$F(1,11)=1.96, p>.05$], which meant the data were additive and the F test of the subject effect was unbiased.

The variation due to aversion levels was significant [$F(2,12)=6.46, p<.025$] and an estimate of the relative effect was approximately 21% of the total variance. The set of contrasts revealed a significant difference only in the number of patch visits in the no aversion (a mean of 10.5 visits) versus the strong aversion condition (a mean of 6.0 visits) [$F(1,12)=12.84, p<.005$]. The no aversion versus the weak aversion and the weak aversion versus the strong aversion comparisons were not significant [$F(1,12)=2.37, p>.017$] and [$F(1,12)=4.18, p>.017$], respectively. Thus, the number of return visits to patches during a session decreased with increasing levels of aversion.

Rate of Return.

A final indication of foraging extracted from the data was a rate of return measure. As both residence time and amount eaten decreased across the levels of aversion, the question arises whether changes in foraging efficiency occurred. Dividing amount eaten by residence time yields a rate of return measure. The difference in group means was not significant for Phase

2 [$t(5)=0.05$, $p>.05$, two-tailed] but for Phase 3, a group difference in mean rate of return was highly significant [$t(5)=5.98$, $p<.002$, two-tailed].

Consequently, the groups were not collapsed and the analysis, using the method of unweighted means, revealed that aversion level was not a significant source of variance [$F(2,10)=3.07$, $p>.05$]. However, there was a significant effect due to groups [$F(1,5)=10.80$, $p<.025$] and a significant interaction of groups with level of aversion [$F(2,10)=5.40$, $p<.05$]. The interaction effect is shown in Figure 13. A visual inspection of the graph reflects the results of the initial t tests that the groups primarily differed in the rate of return obtained during Phase 3. Perhaps the combination of being tested with a strong aversion following the second conditioning had a more powerful effect on rate of return than either a strong aversion following the first conditioning or a weak aversion following the second conditioning. If so, it is puzzling why the O-W-S order would affect only the rate of return and not the previous measures of foraging.

Insert Figure 13 about here

IV. DISCUSSION

The experiment presented in this report was designed to assess the role of taste aversion learning as a mechanism for diet selection. It was expected that the foraging patterns of animals observed under various levels of aversion would obey the same laws as those derived for prey types of differing quality. Thus, four specific hypotheses, corresponding to four measures of foraging, were generated from the LOC model of patch use. The fit of the behavioral data to the model did not change across levels of aversion, but an examination of the utilization of available food as a function of differing densities indicated that the specific predictions of the LOC model were not met. The slope of the utilization function was predicted to be 1.0 in all phases of the experiment, while the y-intercept was expected to decrease with increasing aversion to the food. In the present experiment, the slopes of the utilization functions decreased with increasing aversion, while the y-intercepts remained unchanged. Thus, the subjects showed a tendency to decrease consumption of the pellets across levels of aversion but the reduction was not in accord with the optimal solution generated by the LOC model. An analysis of patch residence time indicated that this fourth measure of foraging also decreased with increasing aversion but, contrary to the original prediction, the effect was greater for the high density patches. In addition, the number of patch visits during a session decreased as a result of the

aversion conditioning. The effect of aversion on rate of return is not entirely clear, since the rate of return obtained by one group tended to decrease, while for the other group, the measure remained unchanged. In summary, with increased aversion to the pellets, patch visits, patch residence time, and pellet consumption decreased. Since these changes were not entirely in accord with the predictions of the LOC model, the original hypotheses were not supported.

Are the experimental results to be taken as evidence that rats forage suboptimally when tested with varying levels of aversion to a prey type? Before concluding this, certain alternative possibilities need to be considered. There may have been limitations in the design of the experiment. For instance, it is feasible that the measurement of aversion level used in the study was not sufficiently sensitive. A general trend observed in the consumption rate across extinction days suggests that over the first few days following the injections (a mean of 9.1 days for Conditioning 1) the rats characteristically ate only one or two pellets a day. Subsequent to this period, consumption rate tended to increase dramatically, with the rats usually reaching criterion within a day or two. Unfortunately, it is not readily apparent how this complication could be avoided. If the extinction criteria were set to lower levels, it is likely that any systematic changes in foraging would be too difficult to detect amid

the "noise" caused by subject variability.

The deviations from optimality reported by Mellgren et al. (1984) under conditions of small interpatch distance point to a second possible limitation in the design of the experiment. Mellgren et al. (1984) found substantial deviations between the behavioral data and the optimal solution generated from the LOC model at low travel costs. As cost increased, foraging patterns moved closer to optimality. The cost of travelling between patches is a measure of the amount of energy a forager must expend in order to obtain food. In the Mellgren et al. (1984) study, deviations from optimality were observed under conditions of low energy expenditure in relation to gain. Similarly, in the present experiment, deviations occurred following the replacement of standard pellets with sucrose pellets during the preliminary training. Switching from a low E/h prey type to a relatively higher E/h type can be viewed as an increase in energy gain, while the energy expended through travel and handling remained unchanged. Thus, with a similar alteration in the ratio of expenditure to gain, the suboptimal patterns observed by Mellgren et al. (1984) may have also complicated the present analyses.

A theoretical explanation of such deviations from the optimal solution is provided by Real's (1980) fitness-variance model of activity allocation. Real hypothesized that under conditions of fitness uncertainty, a forager should initially be conservative because familiar

behaviors result in a greater contribution to fitness per unit of activity than exploratory behaviors. However, once the animal's minimal energy requirements are met, it is often more adaptive to diversify behavior. Specifically, as more time and/or energy becomes available for foraging, an animal should be willing to take greater risks in its behavior and tend to deviate from the optimal solution.

Since the hypotheses tested were generated from the LOC model of patch use, an extension of Charnov's MVT, it may be enlightening to assess how well the theory's constraining assumptions were met in the present study. For example, in order for the LOC model to be applicable to the foraging simulation, it is necessary to assume that the foraging room is viewed as an entire habitat containing discrete patches of food. It is possible that the rats behaved as if the room was one large patch, with food unevenly distributed within. While it would be exceedingly difficult to determine if the assumption of the theorem is valid, certain findings in the data provide suggestive evidence. For instance, the efficient search paths indicate that the rats were easily able to discriminate the four patches of food. Furthermore, the foraging patterns observed during the preliminary training matched very closely with the optimal solution generated by the LOC model. Thus, it is likely that the rats did forage as if the room were a habitat containing four discrete food patches.

A second concern that arises when interpreting the results of the present study is the obvious violation of the constraint of no return visits to a patch. In its current state, the MVT assumes perfect memory with no return visits. If no memory for previously visited patches were assumed, the forager would behave as if the habitat contained an infinite number of patches with a multitude of densities, depending on the amount of previous foraging. Under such conditions, derivation of the optimal foraging pattern would be overwhelmingly complex. The efficient search paths displayed by the rats in the present study indicate that an assumption of perfect memory is much more realistic than an assumption of no memory for already visited sites. This inference also has support from studies of spatial memory, in which it has been shown that rats are capable of remembering up to 32 spatial locations (Olton, 1978). Thus, it seems reasonable to conclude that, at least for this species, the incorporation of return visits into the MVT would produce only slight changes in the predicted optimal foraging patterns. Nevertheless, the extension of the MVT to situations which violate the assumption of single patch visits is necessary and poses an interesting problem for theorists.

The finding that the utilization function slopes tended to decrease with increasing aversion to the pellets suggests a final interpretation of the experimental results.

According to the LOC model, when the slope is 1.0, a

constant amount of food is left in each of the patches, regardless of initial prey density. But if the slope is not 1.0, then the amount left in each patch is not a constant and the animal is not foraging optimally. Mellgren et al. (1984) provide a formula for estimating the optimal LOC for each patch of a habitat:

$$LOC = \frac{R - P}{N}$$

where N is the number of patches, R is the total prey available per bout, and P is the mean number of prey obtained per bout. The mean prey obtained per bout is calculated over all patches in the habitat and all foraging bouts under a particular level of aversion. When optimal LOCs are estimated from the data of the present experiment, a consistent trend of overutilization of the 10-pellet patches and underutilization of the 20-pellet patches exists for each subject. Further evidence of this deviation from optimality comes from an analysis of the actual amounts left in the patches. The interaction of prey density with aversion level was found to be a highly significant source of variance [$F(2,12)=7.29, p<.008$]. This interaction effect, shown in Figure 14, suggests that not only were the left-over-amounts significantly different for the two prey density values, but also the left-over increased more across level of aversion for the high density patches than the low density patches. For the low density patches, the mean left-over-amount increased from 3.2 with no aversion, to 4.4 with a weak aversion, and finally, to 6.2 with a strong

aversion. In contrast, for the high density patches, the mean left-over-amount increased from 5.2 with no aversion, to 8.9 with a weak aversion, and to 11.5 with a strong aversion. Thus, while the subjects did leave more pellets with increasing aversion, the left-over-amount was not a constant across all patches and the magnitude of the increase was not the same for both prey density values.

With unequal prey density conditions, Mellgren et al. (1984) also reported the overutilization of low density patches and underutilization of high density patches. These researchers attributed the tendency to overutilize patches as being due to the rats "sampling" from the environment. If the density of prey in a patch cannot be determined by direct sensory cues, a forager must estimate patch quality with the amount obtained at the start of a patch visit. In other words, the forager attempts to maximize energy intake over the total foraging time by sacrificing short-term gain and acquiring information about the relative quality of the patches. The primary result of using such a strategy is that a forager would, on average, exploit patches to a greater extent than predicted by optimality models because optimal foraging theory assumes that foragers maximize rate of food intake at every moment in time.

Krebs, Kacelnik, and Taylor (1978) tested for the existence of sampling behavior by observing great tits hopping on perches for food delivered on variable-ratio schedules. With two perches concurrently available, the

birds initially distributed the number of hops on each perch roughly equally, followed by a period of pure exploitation of the schedule associated with the higher reward rate. The length of time invested in sampling the two schedules varied directly with the length of the session. With long sessions, the birds spent a considerable amount of time sampling to ensure that only the richer schedule would be exploited. With shorter sessions, though, the birds sacrificed less from the maximum intake rate but also increased the probability of making a mistake and choosing the poorer schedule. Thus, the birds in the Krebs et al. (1978) study behaved as if they were acquiring information during the sampling period to achieve a longer-term optimum.

In the present foraging simulation, initial sampling from the patches would be necessary to discriminate high density from low density patches because density location was switched with every session. An inspection of the patch residence time data suggests this initial period of sampling may have occurred. The rats consistently displayed a tendency to visit one or two patches for very brief periods (under one minute), before spending considerable time in each patch (usually 2-3 minutes per visit). Furthermore, in several cases, the optimal LOCs were estimated to be values which exceeded the initial amount available from the low density patches. Under such conditions, the LOC model would predict these patches would not have been foraged in at all because the rate of return is already lower than the average

rate of return of the habitat (refer to Patch C of Figure 1). Yet in every instance, at least one or two pellets were taken from each 10-pellet patch. Thus, it appears feasible that the rats in the present study were engaging in a short period of sampling at the beginning of each session.

The incorporation of a sample-then-exploit strategy into optimal foraging theory has been restricted to very simple models that predict how the forager ought to estimate the quality of a patch (e.g. Lima, 1984, 1985; McNamara, 1982; Oaten, 1977). Taking a somewhat different approach, Iwasa, Higashi, and Yamamura (1981) have tried to establish the utility of specific foraging strategies under various prey distribution conditions. They compared the immediate maximization strategy with two alternatives: a fixed-time rule, which predicts that a forager will search for a fixed period of time in each patch before leaving, and a fixed-number rule, which predicts that a forager will leave a patch after a fixed number of prey have been consumed. In a habitat where a high density patches cannot be immediately distinguished from low density patches, such as in the foraging room, a pure maximization strategy only provides the greatest rate of return when the between-patch variance in prey abundance is large. Since the distribution they examined involved patches of either zero or 10 items of food, the fixed-number strategy was automatically ruled out.

A potentially more informative approach would have been to contrast combinations of the three strategies because a

sample-then-exploit strategy is most closely approximated by an integration of the fixed-number and immediate maximization rules. A pure fixed-number strategy would produce a utilization function with a slope of 0, while a pure maximization strategy would produce a slope of 1.0. A combination of the two rules would predict foraging patterns more akin to those observed in the study. Thus, the particular pattern of results obtained may be due to the occurrence of an initial period of sampling in each session combined with the design limitation of only having two prey density values. With the optimal time allocation to the low density patches equalling zero on several occasions, the utilization function would not be expected to have a slope of 1.0 because the low density patches should not have been exploited.

In dealing with the underutilization of high density patches, Mellgren et al. (1984) suggest that errors in the judgement of time spent foraging may have been the cause. With patches containing large amounts of food, the total time spent in a patch would include more time for nonforaging activities than with patches containing small amounts of food. Consequently, the forager's internal clock would be biased toward reading too much time relative to the actual time spent foraging and the forager would underestimate the rate of return and leave too soon. On the other hand, a more parsimonious explanation would be that underutilization is also a consequence of sampling because

the forager must sacrifice some of the maximum intake rate available. In other words, if an initial period of sampling occurs, then underutilization of high density patches is a necessary repercussion. Obviously, the most efficient forager must strike an optimum balance between exploration and exploitation of the environment.

In conclusion, the results of the present experiment appear compatible with the notion that foragers do not necessarily use an immediate maximization strategy when foraging. The incorporation of a sample-then-exploit strategy into the LOC model would likely generate predictions that describe the observed foraging patterns more accurately than a model that assumes a maximization rule. If the assumption that animals forage purely to minimize effort relative to payoff is invalid, then the results of the study cannot be used as a basis for determining the role of taste aversion learning as a mechanism for diet selection. Before a mechanism for discriminating food types can be identified, further research must be directed toward establishing the exact nature of the foraging strategy(s) used by the species under study. Elucidation of the various foraging strategies and the proximal rules that permit their use will no doubt be an important aspect of future research in the development of models of foraging behavior.

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APPENDIX 1

Table I.

Experimental design and order for each group.

Group	Phase 1	Conditioning 1	Phase 2	Conditioning 2	Phase 3
0-W-S	8 Foraging Sessions	Extinction to 80%	4 Foraging Sessions	Extinction to 20%	4 Foraging Sessions
0-S-W	8 Foraging Sessions	Extinction to 20%	4 Foraging Sessions	Extinction to 80%	4 Foraging Sessions

Table II.

Schedule of foraging and conditioning for each subject. The first four subjects represent Group O-S-W, while the last three subjects are Group O-W-S. (F = Foraging Days, C = Conditioning Days, E = Extinction Days, R = Rest Days)

Subject	Phase 1	Conditioning 1	Phase 2	Conditioning 2	Phase 3
R1	8F	2C/12E	4F/5R	2C/14E	4F
R3	8F	2C/10E	4F/7R	2C/14E	4F
R4	8F	2C/13E	4F/4R	2C/45E	4F
R6	8F	2C/12E	4F/5R	2C/19E	4F
R2	8F	2C/21E	4F/18R	2C/5E	4F
R5	8F	2C/27E	4F/12R	2C/26E	4F
R7	8F	2C/10E	4F/29R	2C/4E	4F

Table III.

Measures of foraging behavior as a function of aversion level.

Aversion Level	Behavioral Measure			
	Average amount eaten	No. patches visited	Residence time (in min) 10 item patch 20 item patch	Rate of return (pellets/min)
No aversion	43.0	10.5	7.07 10.12	2.4
Weak aversion	34.1	8.2	5.63 7.72	2.7
Strong aversion	23.1	6.7	5.10 6.13	1.9

Note. The data from Phase 2 and 3 were collapsed across groups for the weak and strong aversion levels.

APPENDIX 2

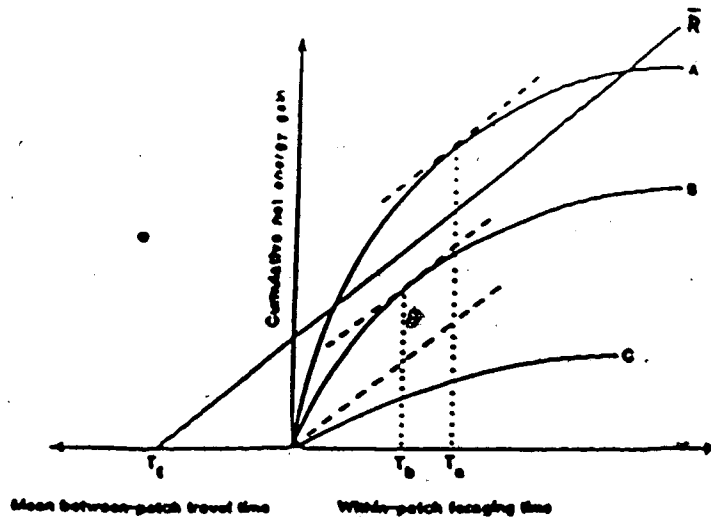


Figure 1. The marginal value theorem for time allocation to a set of patches. The curves labelled A, B, and C plot the instantaneous marginal capture rates for three different patches during a foraging bout. The line of slope \bar{R} represents the average capture rate for the entire set of patches, including time spent traveling between patches (T_0). The optimal time allocation to each patch can be determined by constructing the highest line tangent to the return rate curve for that patch that is parallel to \bar{R} (the broken lines). A line from this point of tangency perpendicular to the time axis intersects this axis at the optimal time allocation for that patch (dotted lines to T_a and T_b). A patch whose return rate curve does not pass above the mean return rate curve (e.g. Patch C) should not be utilized, since the point of tangency is at the origin and the optimal time allocation would be zero. Note. From "Anthropological Applications of Optimal Foraging Theory: A Critical Review" by E. A. Smith, 1983, Current Anthropology, 24, p. 632. Copyright 1983 by the Wenner-Gren Foundation for Anthropological Research. Reprinted by permission.

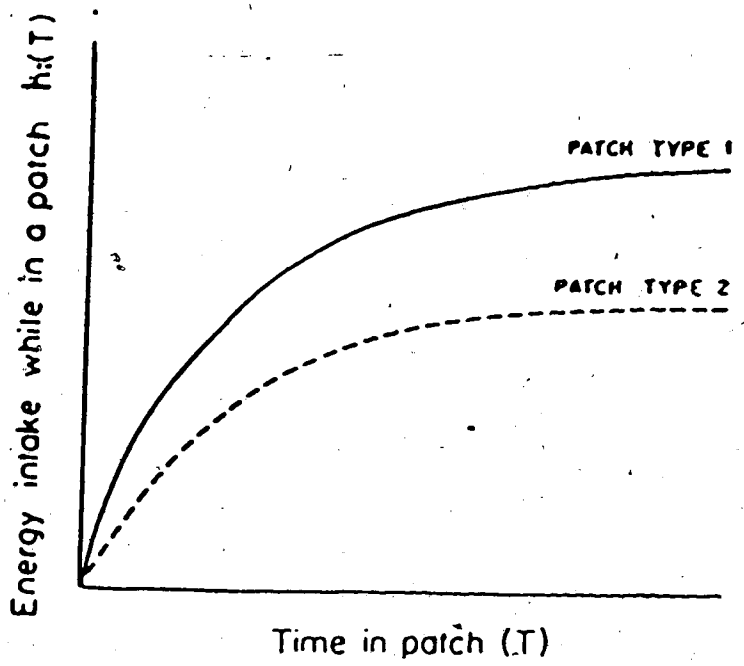


Figure 2. The energy intake for time (T) spent in a patch of type i is given by $h_i(T)$. The function is assumed to rise to an asymptote. Note. From "Optimal Foraging, the Marginal Value Theorem" by E. L. Charnov, 1976, Theoretical Population Biology, 9, p. 130. Copyright 1976 by Academic Press, Inc. Reprinted by permission.

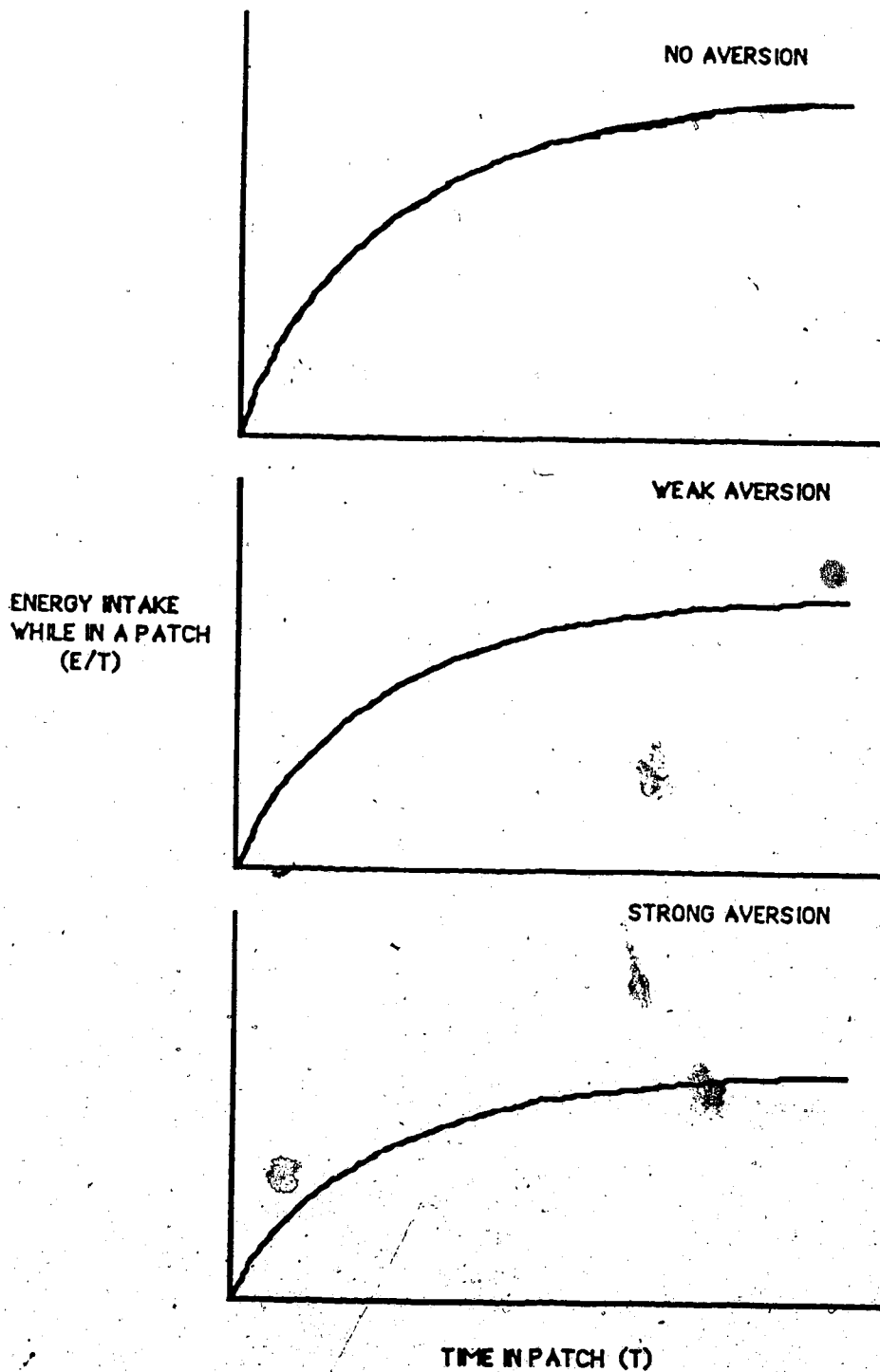


Figure 3. The relative changes predicted to occur in the energy-intake-over-time function of a prey type, under different levels of conditioned aversion. The form of the function is assumed to remain the same while the height of the asymptote is assumed to lower.

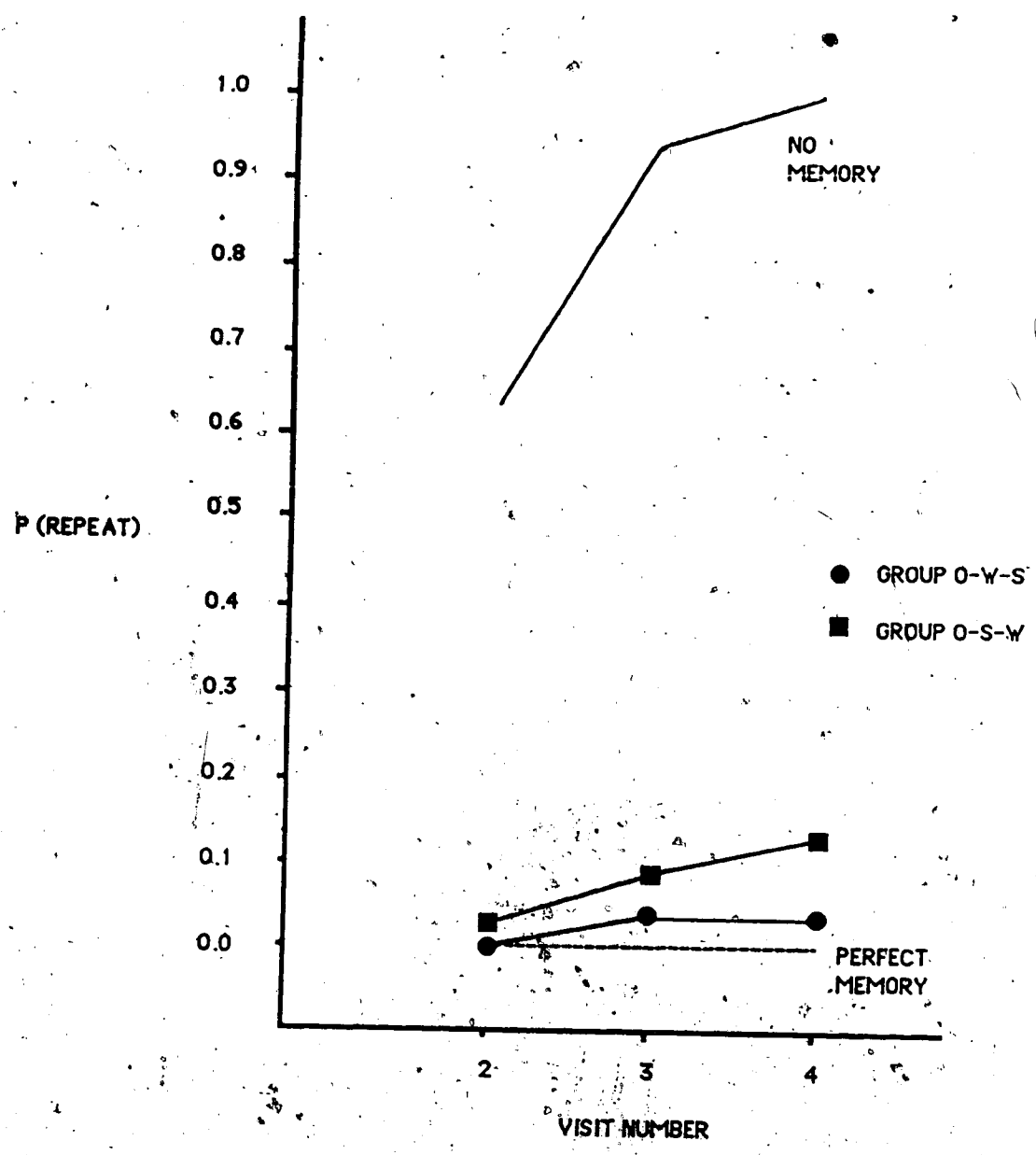


Figure 4. Probability of repeating a visit to an already visited patch as a function of visit number during Phase 1.

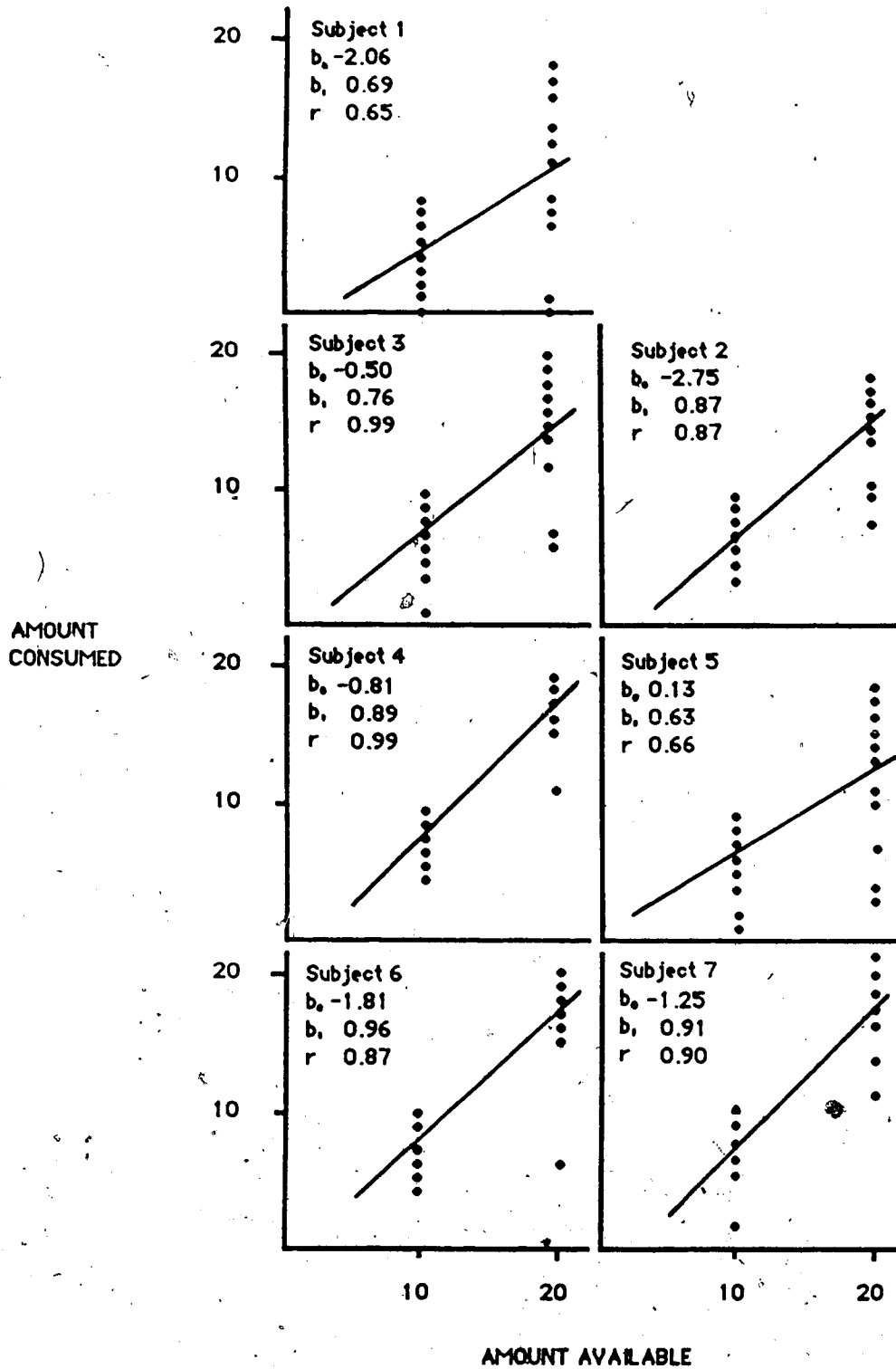


Figure 5. Utilization of available prey as a function of prey density for Phase 1. The solid line is the least-squares regression.

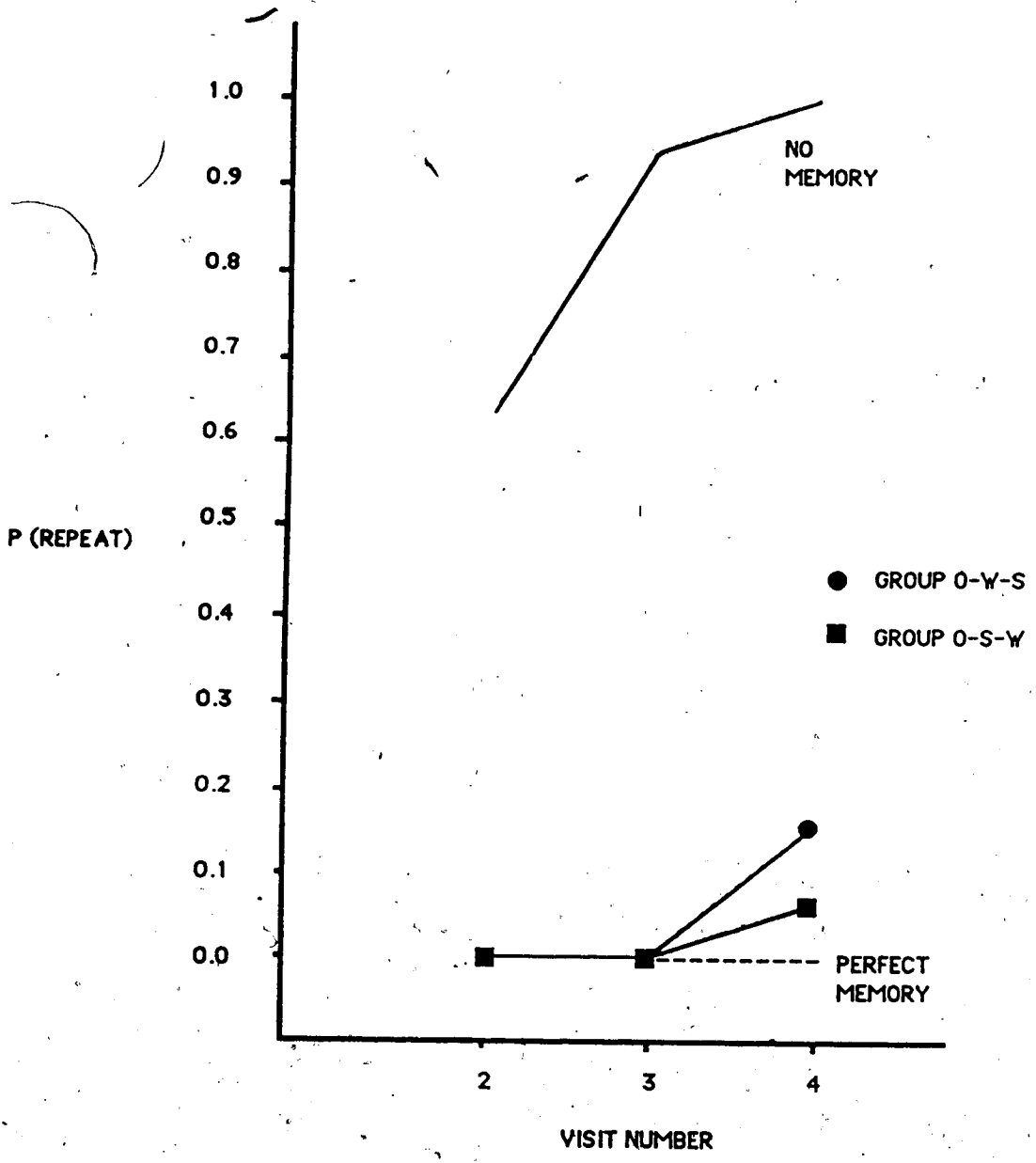


Figure 6. Probability of repeating a visit to an already visited patch as a function of visit number during Phase 2.

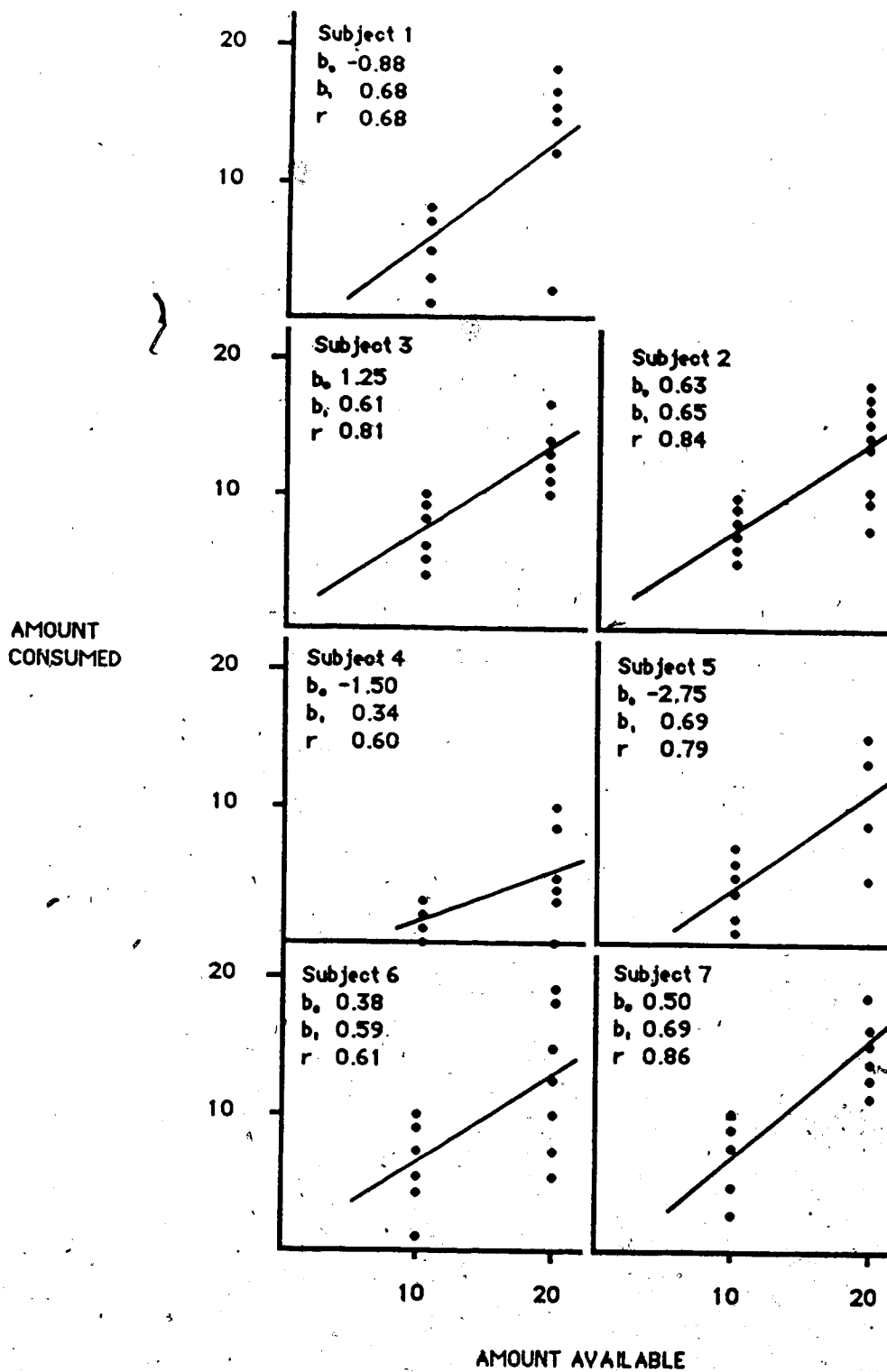


Figure 7. Utilization of available prey as a function of prey density for Phase 2. The solid line is the least squares regression.

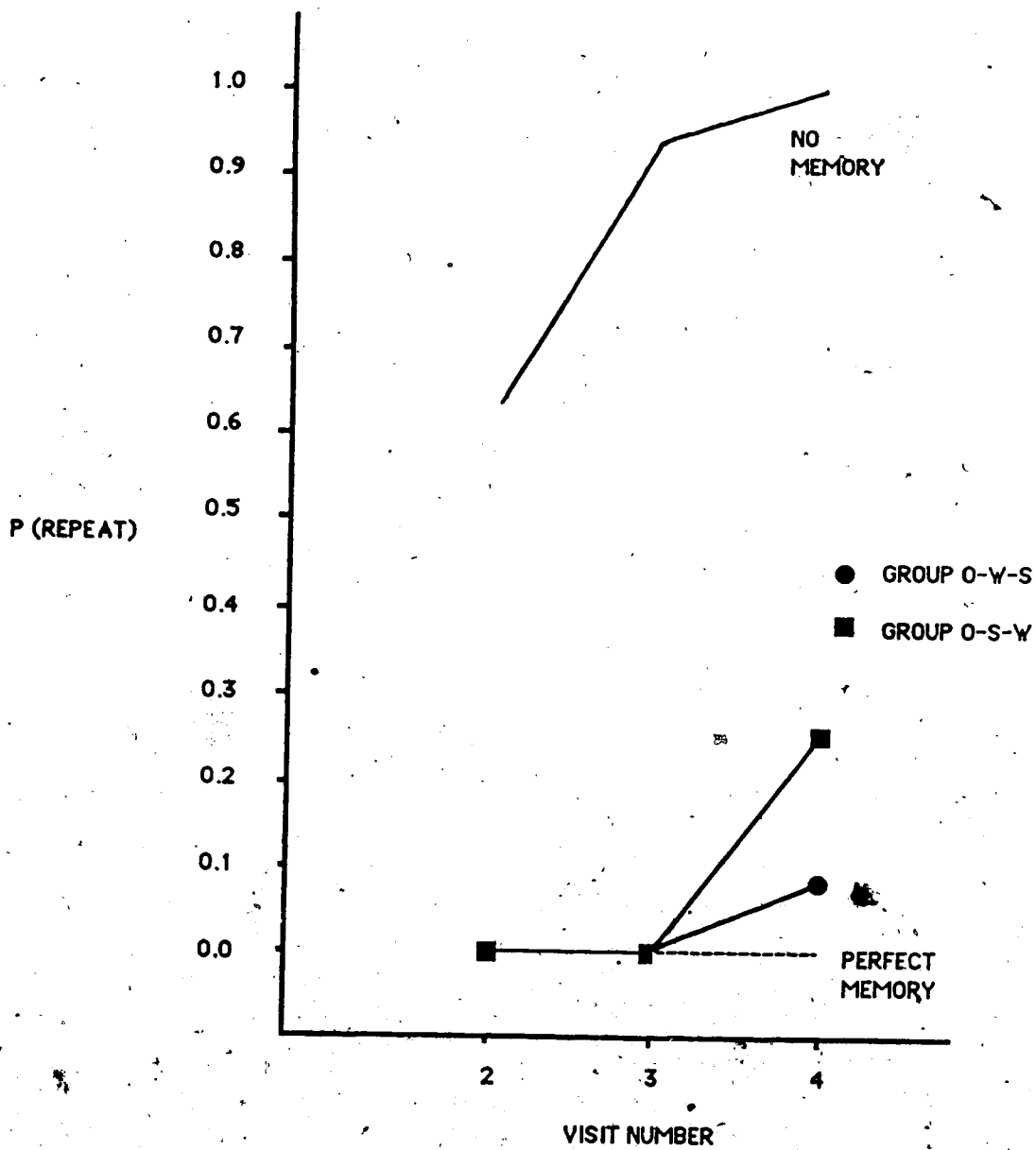


Figure 8. Probability of repeating a visit to an already visited patch as a function of visit number during Phase 3.

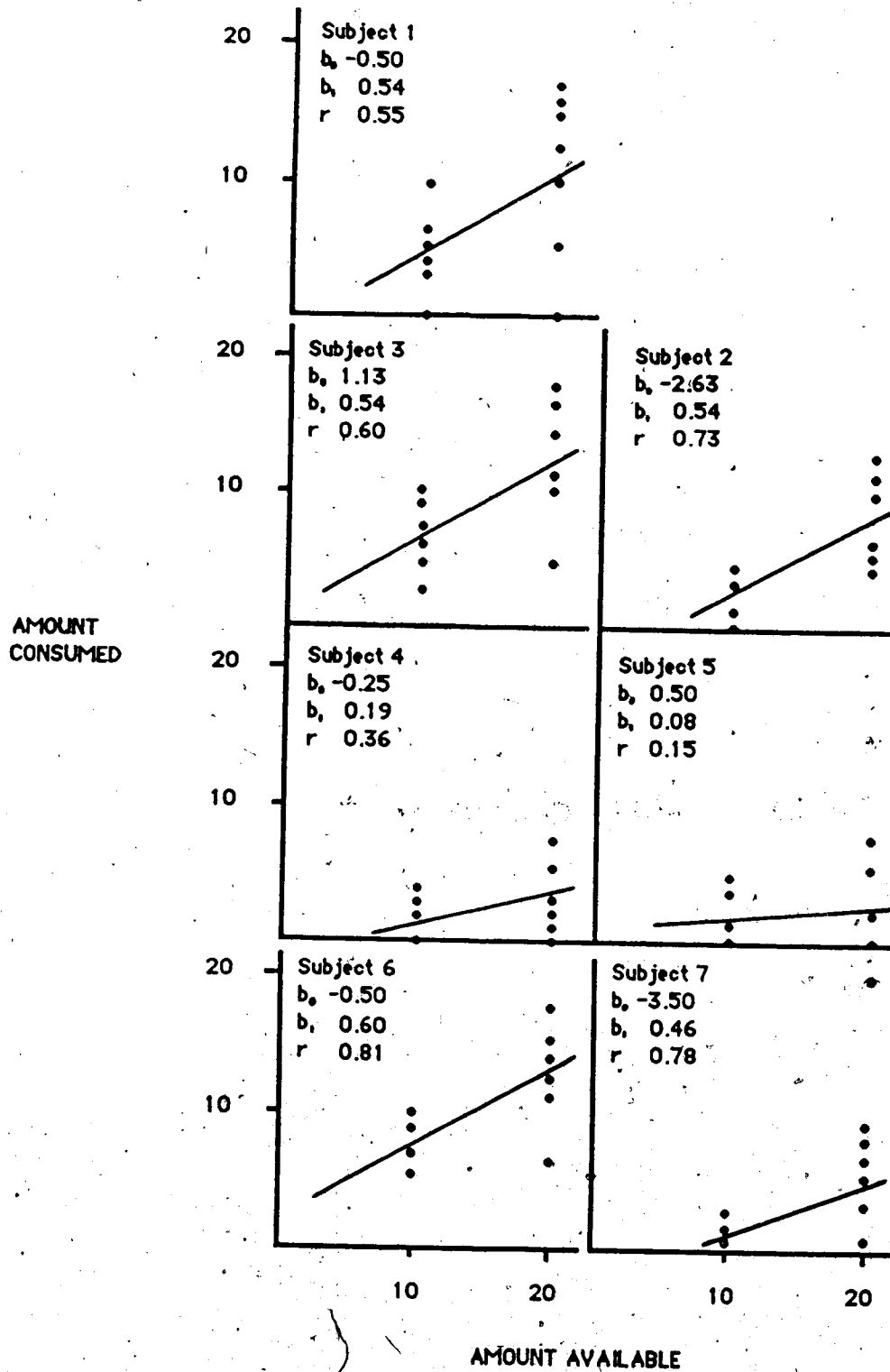


Figure 9. Utilization of available prey as a function of prey density for Phase 3. The solid line is the least squares regression.

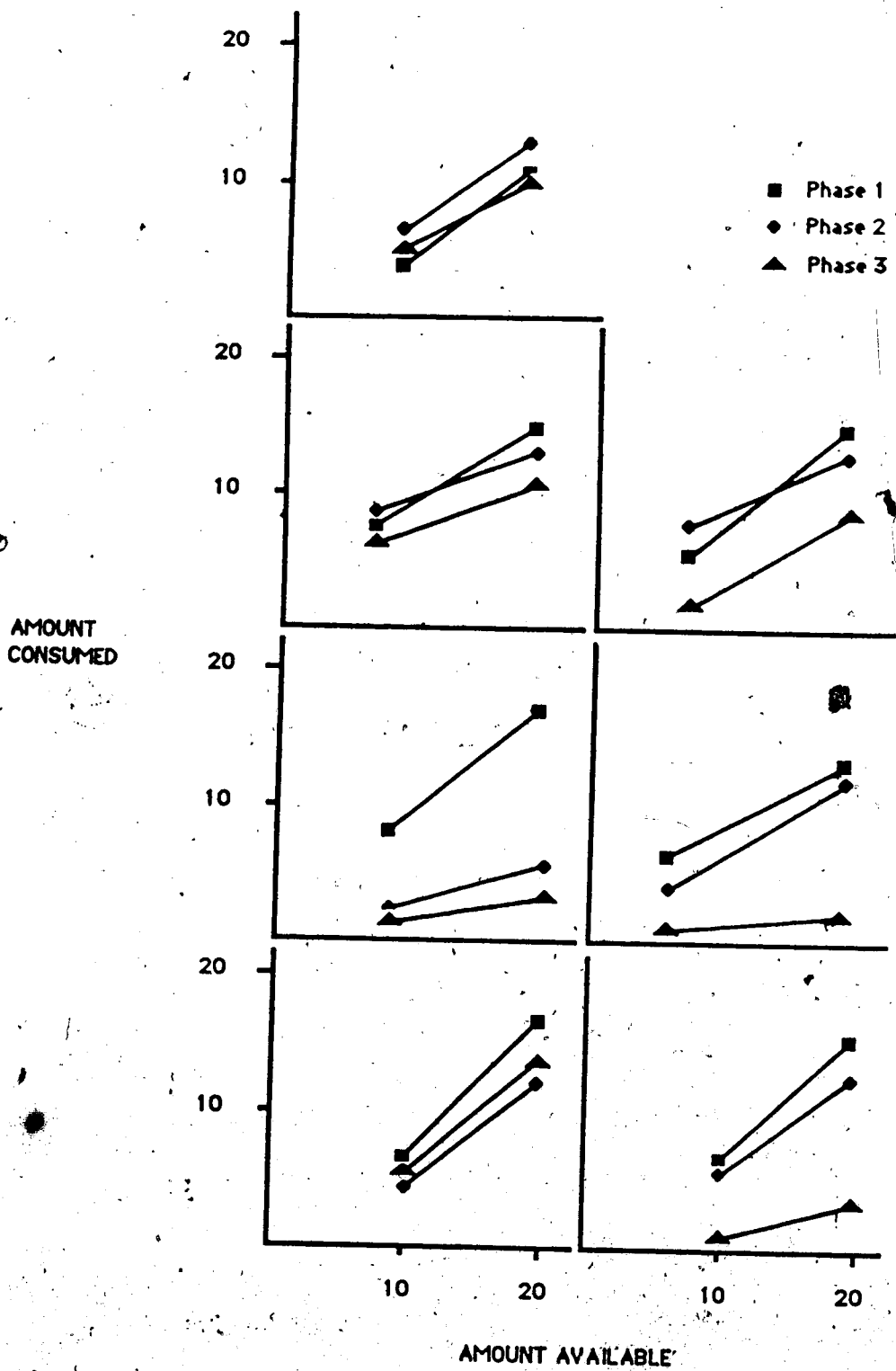


Figure 10. Patch utilization regression lines for the three levels of aversion.

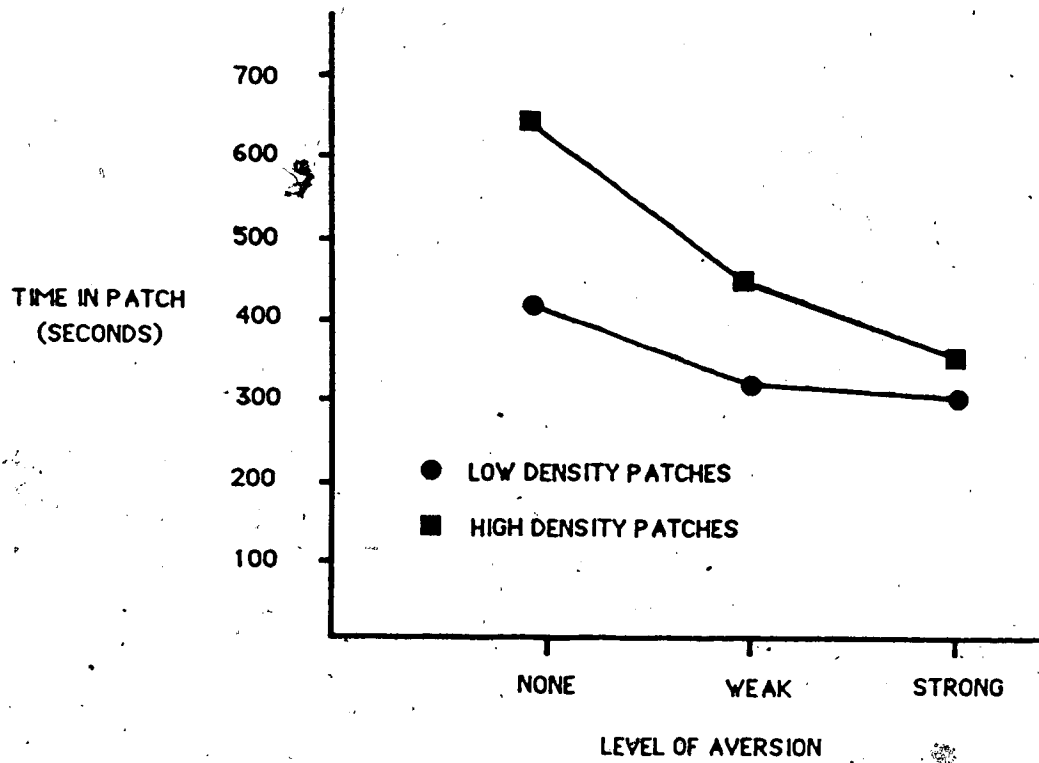


Figure 11. Mean patch residence time for each prey density across levels of aversion.

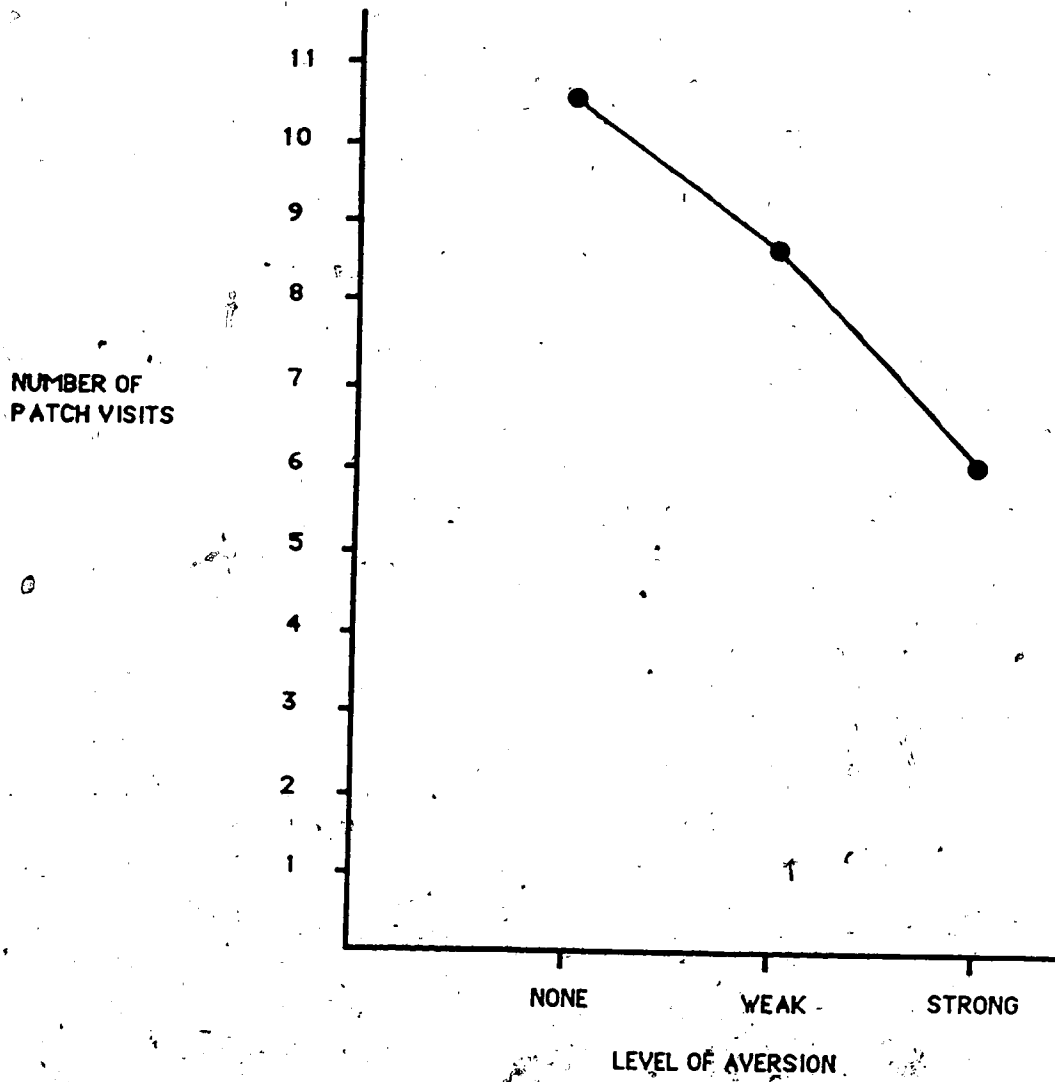


Figure 12. Mean number of patch visits for the different levels of aversion.

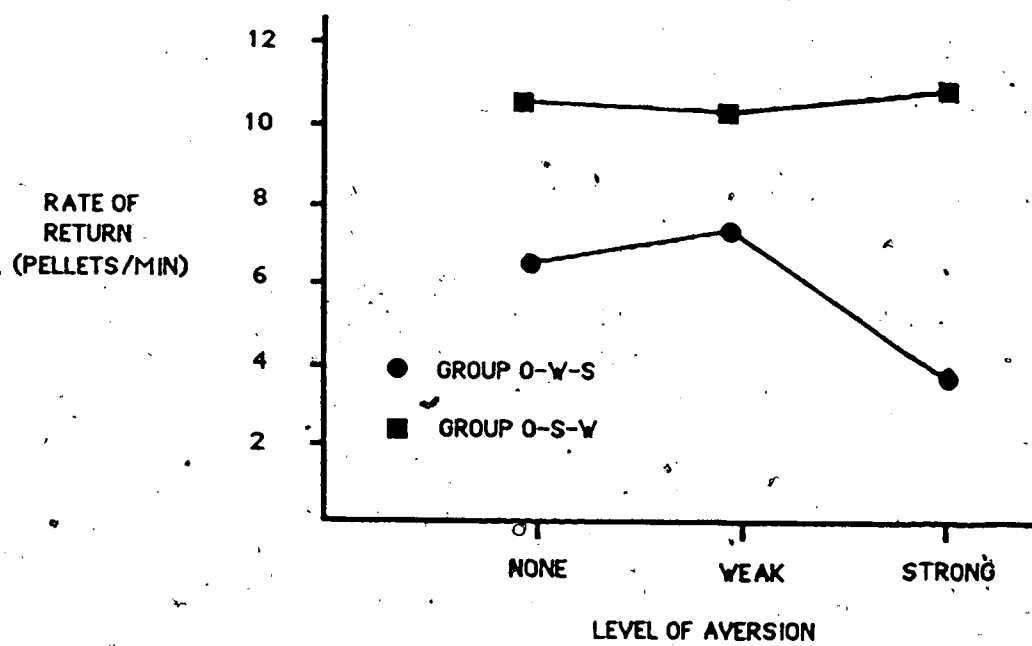


Figure 13. Rate of return in pellets obtained per minute for each group across aversion levels.

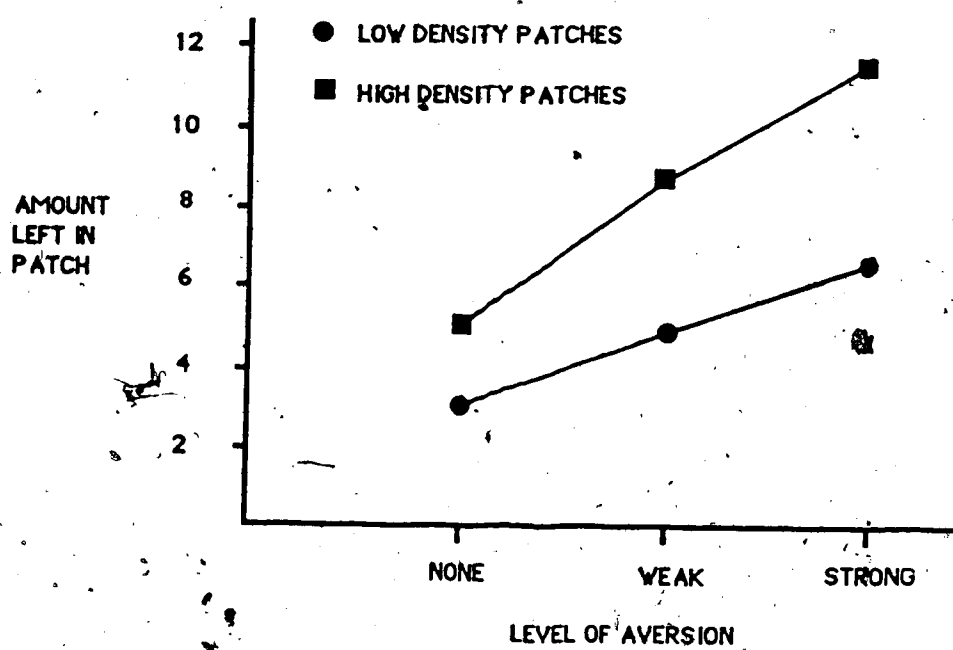


Figure 14. Mean amount left in patches for each prey density across levels of aversion.