DISCRIMINATION LEARNING IN A FORAGING SITUATION

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Rats were allowed to forage in a simulated natural environment made up of eight food sources (patches) each containing a fixed number of pellets. Two of the eight contained an extra supply of peanuts. The peanut patches were signaled by an olfactory/visual cue located at the bottom of the ladder leading to the patch. In successive phases the number of sessions per day, height of the patches, and availability of peanuts were manipulated. Subjects showed evidence of discrimination learning under these conditions, although the degree of discriminatory behavior varied as a function of environmental manipulations. Assessment of behavior within foraging sessions showed that subjects systematically changed their patterns of utilization of patches across time. Sampling or exploration, as well as food reinforcement, seem implicated in these results.

Key words: foraging, discrimination learning, natural environment, choice, optimal behavior, sampling, exploration, rats

Discussions of the interactions of behavioral ecology and psychological learning principles have become common in the literature (e.g., Fantino & Abarca, 1985; Kamil, 1983; Kamil & Roitblat, 1985; Kamil & Yoerg, 1982; Lea, 1981; Pulliam, 1981; Shettleworth, 1984). These discussions usually have assumed that learning principles discovered in the psychologist's laboratory will have relevance for understanding foraging behavior in nature. To date there have been few studies attempting to assess directly the occurrence of learning in foraging situations (for some exceptions see Pietrewicz & Kamil, 1981; Rashotte, O'Connell, & Djuric, 1987).

In the present experiment we asked, "Will the forager learn to use cues that are remote from a patch to discriminate the quality of the patch?" The importance of the concepts of discrimination learning and stimulus control to animal learning psychology is unquestionable (e.g., Mackintosh, 1977; Rilling, 1977; Terrace, 1966). Therefore we decided to use a discriminative cue to study the acquisition of stimulus control based upon its signal value for higher quality patches. We agree with others (Baum, 1983; Collier, 1983; Collier & Rovee-Collier, 1981; Johnston, 1981) that learning phenomena should be studied in ex-

perimental situations resembling the natural environment.

Rats were given a foraging problem in which eight food sources (patches) were available simultaneously in a room, similar to the procedure used by Mellgren, Misasi, and Brown (1984). The main variable of interest in this experiment was the rats' ability to discriminate two patches containing greater amounts of food than the other patches. In the foraging situation we assume that an optimal forager will discover the relationship between environmental cues and the availability of different foods. We chose to use a visual/olfactory cue as the discriminative stimulus for signaling the availability of higher valued patches under the assumption that a functionally similar cue would be expected to exist in the natural environment.

The patches consisted of vinyl boxes placed on ledges at varying heights from the floor. Each patch could be reached by climbing a ladder made by driving nails part way into a pole placed vertically (floor to ceiling) in the experimental room. The patches had food buried in sand, the less favorable alternative (LFA) containing six pellets of a cereal-grain food and the more favorable alternative (MFA) containing six pellets and six unshelled peanuts (three nuts per shell). There were six LFAs and two MFAs in each foraging session. The MFAs were made discriminable from the LFAs by placing an olfactory/visual cue at the bottom of the ladder to each MFA and the same olfactory cue in each MFA patch. The

The authors wish to express their gratitude to Jill Devenport, Stephen Long, Lenny Roberts, Diana Trice, and Susan Wootner for assistance in conducting the experiment. Requests for reprints may be sent to Roger L. Mellgren, Department of Psychology, University of Texas at Arlington, Arlington, Texas 76019-0528.

spatial location of the MFAs was not predictable from one session to the next and could only be discriminated by the cue. The order of patch visits, duration of visits (residence time), travel time between patches, and other behavior were recorded. Environmental manipulations included the duration of foraging sessions, travel costs (varying heights of patches), and a shift in quality of the MFA. We assumed that the subjects would learn the relationship between the odor cue and the availability of peanuts in these patches. Our previous experiments have shown that the more restrictive the environmental conditions, the greater the likelihood that the subject will behave according to optimality principles (Mellgren, 1982; Mellgren & Brown, 1987; Mellgren et al., 1984). For example, Mellgren et al. (1984) found that rats' behavior in the present apparatus conformed very closely to optimality when travel between the patches was made difficult by moving the patches to 2.1 m from the floor. In contrast, the rats' behavior failed to conform to the optimal model when the patches were 0.3 m from the floor.

In the present experiment the manipulations described above were instituted to determine whether, and to what degree, learning about the odor cue had occurred. The multiple measures of behavior also provide a descriptive study of foraging under conditions that resemble those found in nature.

METHOD

Subjects

Three male hooded rats of the Long-Evans strain (*Rattus norvegicus*), 120 days old at the start of the experiment, were used as subjects. During the experiment they lived in the experimental room in ventilated wooden nest boxes (26.5 cm by 24 cm by 28 cm) provided with bedding material, each located in a different corner of the room. Their diet was composed of what they obtained during foraging sessions (i.e., a "closed economy"; Hursh, 1980) except in the last phase of the experiment, as described below. Water was available *ad libitum* through a water bottle mounted on the outside of each nest box with the spout protruding to the inside.

Apparatus

The laboratory room that served as the experimental space measured 5.80 m by 3.32 m

by 2.44 m. Eight patches consisting of vinyl boxes (27.5 cm by 27.5 cm by 15 cm) contained food buried in approximately 4 cm of sand. Travel to the patches was made difficult by placing them on a ledge attached to a vertical pole (3.5 cm by 8.5 cm). The height of the ledge could be adjusted from 0.3 m to 2.1 m above the floor in 0.3-m units. Steel nails (9 cm long) were partially driven into one of the narrow sides of each pole to provide a ladder for climbing. The location of each pole-patch is shown in Figure 1. The experimenter observed the subjects from a swivel chair positioned in the center of the room. All sessions were conducted under dim illumination.

Procedure

All subjects had extensive experience in the experimental room, having served in a previous foraging experiment. This experience included exposure to peanuts and Purina Startina® pellets at various densities in the patches and manipulation of patch height. In the present experiment, subjects were first given eight sessions of pretraining in which two of the patches were marked with a distinctive odor. This experience allowed the rats to overcome initial neophobic reactions to the presence of the odor. Patches were marked by lightly spraying two cotton balls with a commercially made room air freshener. The cotton balls were then taped to plastic disks, which were hung on the poles at a height of 20 cm above the floor of the room. The plastic disks were used in an attempt to prevent the odor from being absorbed by the wooden poles. In addition, a cotton ball treated with the same air freshener was taped to the edge of each corresponding patch. The same two vinyl boxes always served as the marked patches to ensure the odor would remain localized to those boxes. During pretraining, both odor-marked patches contained seven unshelled peanuts (three nuts per shell, 21 in total) and six pellets of Purina Startina® weighing an average of 0.2 g each. The six unmarked patches each contained one unshelled peanut (three nuts per shell) and six Startina pellets. All patches were positioned 1.2 m above the floor of the room. Each subject received two 30-min foraging sessions beginning at approximately 8:00 a.m. and 8:00 p.m. each day. Subjects were weighed before being released from their nest boxes for a foraging session. At the end of a session, the subject was removed from the patch and placed in its nest

box, or, in some cases, ran back into its box when the session was over. The door to the nest box remained open during the foraging sessions to allow access to water. While 1 subject foraged, the other subjects were confined to their nest boxes. The order in which subjects were studied was counterbalanced across sessions.

In all phases of the experiment one odor-marked patch was located near a corner of the room and the other along a wall during each session. We have found that patches in the corner are visited more frequently than those along the wall, although the utilization of food in the patches does not vary as a function of the corner-wall distinction (Mellgren & Brown, 1987). The location of odor-marked patches was varied between sessions in a counterbalanced sequence across each phase for a particular subject and was different for each subject within a session. Thus, the subject was unable to predict the location of the odor-marked patches for each session, but one was always in a corner and one along a wall.

The experiment was comprised of four phases. Phase 1 was identical to pretraining except that the amount of food available in the patches was reduced. During this phase both odor-marked patches contained three unshelled peanuts and six pellets of *Startina*. Unmarked patches contained six *Startina* pellets but no peanuts. Phase 1 consisted of 24 sessions.

In Phase 2 foraging sessions were reduced from two 30-min sessions per day to one 30-min session per day (beginning at 8:00 a.m.). Patch magnitudes remained the same as the previous phase. Phase 2 consisted of 16 sessions.

During Phase 3 patch height alternated between 1.2-m and 2.1-m positions in blocks of four sessions. Subjects first received four consecutive sessions with all patches at 2.1 m followed by four sessions with all patches at 1.2 m. This pattern was repeated for the next eight sessions, thus comprising a total of 16 sessions. In all other respects Phase 3 was the same as Phase 2.

In Phase 4, an extinction procedure was instituted in which no peanuts were available in the odor-marked patches but the odor cues were still present for the two patches. All patches contained six *Startina* pellets, and patch height remained constant at 1.2 m. Because peanuts were removed from patches in this

Fig. 1. A floor plan of the experimental room.

phase, and they were an important source of calories in the rats' diet, the animals were provided with a supplemental feeding of 6 g of Purina Lab Chow® 30 min to 2 hr following each session to maintain a reasonably stable body weight and motivation level. Phase 4 consisted of 16 sessions.

The experimenter recorded the order of patch visits, the amount of time a subject spent in each patch (residence time), the time taken to travel from one patch to another (travel time), and visits to the nest box. The number of peanuts and/or *Startina* pellets eaten was determined by sifting the contents of each patch through a wire screen at the end of the session.

RESULTS AND DISCUSSION

The results of the experiment are divided into two sections for ease of exposition. In the first section consideration will be given to between-session effects: Those effects that characterize the behavior of the subject for the total session and comparisons of this behavior between the different conditions of each phase. In the second section we will consider within-session effects; a focus on the order and structure of behavior during individual foraging sessions. A significant statistical result means that the probability of obtaining the stated effect was .05 or better.

Between-Session Effects

Figure 2 shows the theoretical and empirical cumulative probabilities of visiting both of the MFA odor-cue patches as a function of visit number for Phase 1. We assume that the subjects preferred peanuts to *Startina* pellets, an assumption well supported by preference tests with both food types freely available (Misasi,

Fig. 2. The theoretical and empirical probabilities of visiting both MFA patches as a function of visit number for Phase 1. Subject 1 is designated by open circles, Subject 2 by closed circles, and Subject 3 by asterisks.

1983). We also assume that the existence of a highly preferred food in discriminable locations should influence patch choice. For example, the delay-reduction hypothesis (Fantino, 1987; Fantino & Abarca, 1985) applied to patch selection predicts that odor-marked patches would be visited early in the session. Because there were two odor-marked patches containing peanuts, we evaluated the subjects' preference for these patches by comparing the observed probability of visiting both odor patches by Visit 2, 3, 4, 5, 6, 7 or 8 to a theoretical probability distribution generated under the assumption of a random sampling of patches without replacement. Therefore, the "theoretical" line represents a subject with perfect memory for previously visited patches (sampling without replacement) but not influenced by the odor cue (random choice of unsampled patches).

To encourage the subjects to learn the relationship between the odor cue and patch quality, the total amount of food available in the habitat was reduced in Phase 1 compared to pretraining conditions. During these 24 sessions the subjects showed little evidence of the acquisition of a preference for the MFAs as shown in Figure 2. The Kolmogorov-Smirnov test for goodness of fit (Sokal & Rohlf, 1969) indicated that each subject's observed probability of visiting both MFAs did not differ significantly from the theoretical expectancy (all $D_s < .32$) across Phase 1. This finding is surprising if we consider an analogous situation in an instrumental learning context. Spear (1964), for example, used a T-maze apparatus

in which the MFA contained four 45-mg food pellets on all trials and the LFA contained one, two, or four pellets on 26%, 50%, or 100% of the trials for different groups of subjects. All groups quickly learned to choose the MFA on virtually all of the choice trials. Similar results are reported by Logan (1968).

To evaluate the utilization of the food available in the two different patch types for Phase 1, an analysis of variance was conducted on time spent in patches and number of pellets consumed. This analysis confirmed that the subjects spent more time foraging in the MFA patches (426.06 s) compared to the LFAs (149.25 s), $F(1, 2) = 82.63$, but there were no differences in number of *Startina* pellets eaten in the two patch types $F(1, 2) = .89$ (mean number consumed = 2.98 for MFAs and 2.93 for LFAs). The longer time spent in the MFAs thus seems to reflect the handling and consumption time for peanuts because the number of pellets eaten in MFA and LFA patches did not vary significantly across foraging sessions.

Based on the order of choice data from Phase 1, there is no evidence that the subjects had learned the significance of the odor cues. However, it is possible that their performance was an underestimate of the learning that had occurred. The failure to visit MFAs at greater than chance probability may not indicate a failure of discrimination learning, but rather a performance effect. Therefore, the number of sessions per day was reduced from two to one in an attempt to influence performance. Presumably this constraint would encourage the subjects to visit the MFAs earlier in each session if they had learned the relationship between the odor cue and patch quality.

In Phase 2 only one 30-min foraging session was given every 24 hr (at 8:00 a.m.). The immediate effect was to increase the probability of visiting both MFAs earlier in the sequence of visits (see Figure 3). An evaluation of goodness of fit between each subject's observed probability of visiting both MFAs as a function of visit number and chance performance indicated that both Subject 1 and Subject 3 significantly differed from the chance expectancy ($D_s = .64$ and $.51$, respectively). Subject 2, on the other hand, failed to visit both MFAs at greater than chance probability ($D < .3$) although his behavior is clearly in the same direction as the other 2 subjects. Thus,

Fig. 3. The theoretical and empirical probabilities of visiting both MFA patches as a function of visit number for Phase 2. Subject 1 is designated by open circles, Subject 2 by closed circles, and Subject 3 by asterisks.

reducing session duration in Phase 2 increased the probability of visiting both MFAs during the early choices of a session.

Analysis of time spent in patches and pellets eaten again showed greater time spent in the MFA patches (403.2 s) than in the LFA (109.7 s), $F(1, 2) = 55.57$. Unlike Phase 1, this difference is not completely accounted for by handling and consumption of peanuts because the subjects also ate significantly more pellets from the MFA (2.97) than the LFA (1.94) patches, $F(1, 2) = 82.02$.

It is interesting to note that a forager searching for two (or more) prey types of different value may adopt one of several possible strategies. The different strategies reflect the extent to which the less valuable prey types will be taken. A "search image" analysis (Pietrewicz & Kamil, 1981; Tinbergen, 1960) suggests that a highly valued or preferred prey will cause the forager to tune its perceptual apparatus to improve detection of the valued prey and thereby reduce the detectability of other prey items. This hypothesis predicts that fewer pellets would be eaten in the patches containing peanuts. However, such tuning is only necessary when the valued prey is cryptic. Because it is unlikely that peanuts are cryptic, a search image is probably not appropriate for this situation. A second possibility is that the presence of peanuts does not influence the number of pellets eaten, perhaps because the subject allocates time to searching for peanuts and pellets independently of each other. Thus prey item y encountered while searching for prey item x would be ignored. This seems to be a

Fig. 4. The theoretical and empirical probabilities of visiting both MFA patches as a function of visit number for Phase 3. Subject 1 is designated by open circles, Subject 2 by closed circles, and Subject 3 by asterisks.

rather inefficient strategy, although factors such as digestibility of the prey items (i.e., a dry food pellet might be difficult to eat at certain times so it is ignored in favor of a peanut) may favor an "independent search" strategy. A third possibility is that the subject uses an "opportunistic strategy" in which, as it searches for and finds the peanuts, it also encounters and eats more pellets relative to patches where no peanuts are present. The opportunistic strategy seems to be supported by the Phase 2 data.

In Phase 3 the height of the patches was increased to 2.1 m for two 4-day periods (the first and third blocks of four sessions in this phase). This manipulation has been shown to affect the fit of performance with predictions derived from an optimality model of foraging under similar conditions (Mellgren et al., 1984) and also to reduce the number of patches visited. If fewer patches are visited, it might be expected that early visits to the MFAs would increase.

The probability of visiting both MFAs as a function of visit number was evaluated by considering the 2.1-m and 1.2-m patch heights separately (see Figure 4). At 2.1 m all subjects visited both MFAs significantly earlier than would be expected under the hypothesis that patches were visited randomly without replacement (smallest $D = .52$). However, at the 1.2-m patch height only Subjects 1 and 2 visited both MFAs significantly earlier than chance.

All subjects visited significantly fewer

Fig. 5. The theoretical and empirical probabilities of visiting both MFA patches as a function of visit number for Phase 4. Subject 1 is designated by open circles, Subject 2 by closed circles, and Subject 3 by asterisks.

patches when they were at the 2.1-m height than when they were at the 1.2-m height. At 1.2 m, Subjects 1, 2, and 3 averaged 5, 4.9, and 7.2 patch session per session, respectively, whereas at 2.1 m they averaged 3, 2.9, and 6 visits per session ($t_2 = 6.59$). Interestingly, Subject 3 failed to show a significant deviation from chance in the order-of-visits measure at 1.2 m, and he visited the most patches of all subjects during this phase. This finding is consistent with the hypothesis that the fewer the number of patches visited in a session, the more likely that the subject will visit the MFAs early in the foraging session.

Analysis of variance of the time-in-patch data with patch height and MFA-LFA as factors confirmed that subjects still spent significantly more time in the MFA than the LFA, $F(1, 2) = 30.24$, and although time-in-patch was greater at 2.1 m than at 1.2 m for both the MFAs (535.15 s to 418.04 s) and LFAs (118.58 s to 107.23 s), the main effect for patch height was not significant, $F(1, 2) = 6.79$, $p = .13$. The number of pellets eaten was greater for MFA patches than LFAs, $F(1, 2) = 32.68$, consistent with the opportunistic strategy (eat all prey encountered) hypothesized for Phase 2. The mean number of pellets eaten increased when patch height was 2.1 m in the LFAs (2.67 to 3.05), but decreased for the MFA (3.94 to 3.50); however, these effects of patch height and its interaction with MFA-LFA were not statistically significant.

In Phase 4 the peanuts were removed from the MFAs. The immediate effect was an in-

crease in the frequency of early visits to the former MFAs. In fact, 2 subjects chose the odor-cued patches as their first two visits for several sessions. Because the subjects changed their pattern of choices across Phase 4 as they learned that the odor-cued patches no longer contained peanuts, we evaluated performance during the first eight sessions and the second eight sessions separately (see Figure 5). During the first eight sessions of Phase 4, all subjects visited both of the former MFAs earlier than would be expected by chance (smallest $D = .65$). However, during the second eight sessions, only Subjects 2 and 3 continued to visit the odor-marked patches significantly earlier than chance expectancy.

Removing the higher quality reinforcer had the effect of facilitating responses directed toward its signal. Vigor of responding, as measured by running speeds in a straight alley, has been shown to be increased by the absence of food in a place where it is expected (Amsel & Roussel, 1952). This "frustration effect" is usually thought of as an invigorating motivational effect due to the absence of a reinforcement. In the foraging situation, the effect of reduced quality of available food might be similar to the frustration effect. Consistent with the invigorating effect, there was an abrupt increase in patch revisits. A total of 85 revisits to patches occurred within sessions during Phase 4 and 48 of the revisits were to the odor-marked patches. In comparison, during Phase 2 there were only 11 revisits, eight of them being to the odor-marked patches. (We use Phase 2 for comparison because experimental conditions were identical to Phase 4 except for the removal of peanuts in Phase 4.) The mean number of patches visited during a foraging session was also greater in Phase 4 than in Phase 2 (8.7 and 5.3, respectively) consistent with the invigorating effect of the absence of an expected high-quality food. One interesting difference between frustration studies in more traditional contexts and the effect of frustration in the foraging context is that the traditional work has evaluated frustration by measuring the subject's tendency to escape from a location associated with frustration (e.g., Daly, 1969, 1974), but in the present context the presumably frustrated subject showed an increase in the total number of approaches to the location associated with frustration.

Consideration of the behavior of subjects

Fig. 6. The number of visits to MFAs in the first two choices of a session plotted as a function of four-session blocks. Subject 1 is designated by open circles, Subject 2 by closed circles, and Subject 3 by asterisks. The line represents the mean of subjects across sessions.

once they had entered the former MFAs provides additional evidence that their responding was invigorated by removal of the peanuts. In Phase 4, subjects consumed significantly more pellets in the odor-marked patches $F(1, 2) = 20.53$, but did not spend significantly more time in these patches $F(1, 2) = 1.67$, compared to non-odor-marked patches. Because rate of return (pellets consumed per minute) is greater in the former MFAs, it suggests that the animals were searching more vigorously in the odor-marked patches relative to unmarked patches.

To compare changes in behavior across the different phases (different conditions) of the experiment and because there are numerous ways of indexing choice of the MFAs, an alternative choice measure was derived. For this purpose we tabulated the frequency of visiting the MFA patches in the first two visits of each session. Assuming random sampling with replacement, the chance probability of either of the first two choices of a session being to one of the odor-marked patches is .25, so we expect two such choices within a block of four sessions. The assumption that sampling with replacement occurs also tends to make the "chance value" of two choices in eight an overestimate, because subjects never revisited a just-visited patch on the second patch visit. Thus, the likelihood of a visit to an odor-marked patch is not two in eight after one such patch has been visited, but rather one in seven.

The results of this analysis are shown in Figure 6. The solid line in the figure represents the means for the 3 subjects, and the symbols

represent individual subjects constituting the means. These results broadly support the conclusions from previous patch choice analyses.

From halfway through Phase 1, the mean visits to MFAs in the first two trials exceeded the chance value of two per session block consistently. Decreasing the number of available foraging sessions from two per day to one (Phase 1 to Phase 2) increased the probability that the odor-signaled patches containing a preferred food would be visited sooner in the session, although this effect could be seen as the continuation of gradual learning occurring towards the end of Phase 1. However, increasing the height of the patches from 1.2 m to 2.1 m (within Phase 3) had no obvious effect on the subjects' tendency to visit the MFAs early in the session. The most dramatic effect on order of visits was produced by the removal of peanuts (extinction) from the MFAs (Phase 4). A more detailed analysis of within-session behavior should be useful in providing a clearer understanding of the mechanisms determining order of patch visits and other foraging behavior in this situation.

Within-Session Effects

At the start of a foraging session the subject frequently made a quick trip along the walls of the room before climbing to a patch. We also noticed a tendency for the rat to leave patches more quickly at the start of a foraging session than later in the session. Therefore we decided to undertake some exploratory analyses (Tukey, 1977) on the nature of patch use within a session. The analyses are based on

Table 1

Measures of patch utilization for MFA patches.

Phase	Order of visit to MFA	
	First	Second
1	402.81	469.29
	5.39	5.43
	3.03	3.05
2	307.31	499.77
	4.51	5.41
	2.48	2.85
4	114.15	156.85
	3.63	4.57

Note. The first number in each cell is mean residence time, the second number is mean peanuts consumed, and the third number is mean pellets consumed.

Phases 1, 2, and 4 because there were only eight sessions of Phase 3 data under constant conditions, whereas there were at least 16 sessions for the other phases. The conclusions reached based on the analyses of these three phases would not be altered by including Phase 3.

For the two MFA patches, the patch residence times were analyzed by including data from only those sessions in which both patches were visited and then obtaining a mean for each phase (see Table 1). These data were analyzed using a dependent t test and confirmed our impression that the rats spent significantly less time in the first MFA visited than the second, $t(2) = 4.36, 24.21, 5.90$, for Phases 1, 2, and 4, respectively. Although there was a significant tendency to show longer residence times in the second visited MFA, utilization of the available food was not as strongly influenced by order of visit. The mean number of peanuts eaten in Phases 1 and 2 (there were no peanuts present in Phase 4) was greater for the second patch visited than the first, but the difference was significant only for Phase 2, $t(2) = 7.05$. The mean number of pellets eaten was also numerically greater for the second visited MFA than the first but the differences were not significant for any of the phases, $ts(2) = .04, 1.56, 3.28$. Table 1 shows the mean number of peanuts and pellets eaten in each phase.

The change in residence time across visits to the LFAs was evaluated by dividing each session into early, middle, and late patch visits. The residence times for the first two LFAs

Table 2

Measures of patch utilization for LFA patches.

Phase	Order of visit to LFA		
	Early	Middle	Late
1	127.0 _a	163.51 _b	167.52 _b
	2.77 _a	2.97 _a	3.19 _a
2	73.14 _a	107.55 _b	143.22 _c
	1.54 _a	1.89 _a	2.16 _a
4	83.92 _a	128.28 _b	161.25 _c
	2.73 _a	3.16 _a	3.43 _a

Note. The first number in each cell is mean residence time, and the second number is mean pellets consumed. Means with different subscripts (within a phase) differ significantly at $p < .05$.

visited constituted the early visits. Middle visits were the third and fourth LFAs visited, and the late visits were all visits after the fourth. This procedure resulted in an approximately equal number of observations for each category. The results of the statistical analyses are analogous to the MFA results; shorter residence times earlier in the foraging session, longer residence times later. A repeated measures, one-way ANOVA showed that there were significant differences in residence times in all phases, $F(2, 4) = 16.78, 20.06, \text{ and } 28.09$, for Phases 1, 2, and 4, respectively. A similar analysis of the number of pellets consumed as a function of whether the visit occurred during the early, middle, or late portion of the sessions showed that subjects tended to consume fewer pellets from patches visited early in the session and more pellets from late patch visits. However, this effect did not reach an acceptable level of significance (all $F_s < 1$). Table 2 presents the mean residence times and pellets eaten for the three phases.

Several reasons can be suggested as to why the subjects should show a pattern of increasing residence times to equal value patches within the foraging session. Motivation level might be hypothesized to be responsible. As the subject becomes satiated, he is less likely to be motivated to search vigorously for food and therefore must stay longer in each patch to realize the same gain as when he was more highly motivated. This motivational explanation is clearly ad hoc, although it is potentially testable. For example, subjects could be fed before the start of the session with the expectation that they would increase residence

times to the first visited patches but not change the amount consumed in them relative to a no-preneeding condition.

Another possibility is that the subjects may have learned that the environment contained a finite number of available patches. By their own behavior the rats produced a habitat that monotonically decreased in quality with each patch visited. A lean habitat should produce longer residence times than a rich habitat, according to the marginal value theorem of optimal foraging theory (e.g., Krebs, 1978), and therefore as the habitat is depleted, residence times should increase. If the number of patches available were increased dramatically so that an individual forager's activities had little effect on the overall quality of the habitat, the pattern of increasing residence times would not be expected according to this explanation, a testable possibility.

The finding that residence times across a session increase while the number of pellets consumed does not change significantly leads us to raise the question, "What is the appropriate measure of patch utilization?" The two answers to this question are (a) time spent in the patch and (b) the amount of food obtained from the patch. Under the assumption that the forager spends all its time foraging when in the patch, the two answers are equivalent. However, our data strongly suggest that the rat is doing something other than just foraging while in a patch. The type of activities receiving time allocation from a resident forager might include monitoring the environment for potential predators, competitors, or mates. We also observed our subjects grooming frequently during foraging sessions. Under the influence of Charnov's (1976) seminal work in deriving the marginal value theorem, theoretical developments have tended to favor time as the measure of patch utilization (e.g., Cowie, 1977; Iwasa, Higashi, & Yamamura 1981; McNair, 1982). We have used amount consumed-amount left over (the LOC model; Mellgren et al., 1984) as a measure of patch utilization. It is likely that both residence-time models and amount-of-food obtained models (e.g., Green, 1980) are compatible when the forager does nothing but forage in a patch, but one type of model may be more appropriate than another in particular situations.

Finally, the basic assumption of optimal for-

aging theory is that a subject will behave in such a way as to maximize inclusive fitness. The time needed to achieve optimization may transcend the time spent in one foraging bout. To be efficient in utilizing the food available in a habitat, it is necessary to gather information about the habitat. The process usually invoked to account for information gathering is *sampling* (see Kamil & Roitblat, 1985, for a review of some of the ways the concept of sampling has been used in the foraging literature). Unlike *reinforcement*, which may be characterized as a mechanism for reducing the variability of performance (e.g., Staddon & Simmelhag, 1971), sampling may be characterized as a mechanism for increasing the variability of performance (Devenport, 1983). Both mechanisms are important for adaptive behavior. The finding that the two MFA patches were visited more reliably early in the session after the peanuts had been removed than when they were available is consistent with the importance of gathering information to the foraging subject (in this case, information about the sudden decrease in habitat quality).

What has been called sampling in the foraging literature traditionally has been called *exploratory behavior* in the psychological literature (e.g., Berlyne, 1960; Russell, 1983). This research seems to have been overlooked by those investigators currently interested in foraging. Recently, the study of exploratory behavior has broken from the original concerns of its relationship to drive reduction, and contemporary work has become directly relevant to issues of foraging behavior. Inglis (1983), for example, has developed a cognitive theory of exploratory behavior that begins with the basic assumption "... that gathering information is the dominant behavioral activity for any animal living in a stochastic environment" (p. 272). The integration of theory and data on exploratory behavior may be useful in elucidating current conceptions of sampling as a component of foraging behavior.

In summary, the analysis of foraging behavior in the simulated natural environment indicates that discrimination learning occurs, but that performance, as measured by order of choice of the discriminated patches, varies with environment conditions. The distinction between learning and performance (e.g., Tolman & Honzik, 1930) is well known to be-

havioral psychologists but perhaps less well understood by behavioral ecologists (e.g., Mellgren, 1985; Shettleworth, in press). Foraging is a situation in which such a distinction is particularly important, because the forager may be concerned with more than one characteristic of the environment and therefore may not demonstrate, through performance, all that has been learned.

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Received February 24, 1988
Final acceptance July 21, 1988