

FORAGING IN A SIMULATED NATURAL ENVIRONMENT: THERE'S A RAT LOOSE IN THE LAB

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Rats were required to earn their food in a large room having nine boxes placed in it, each of which contained food buried in sand. In different phases of the experiment the amount of time allowed for foraging, the amount of food available in each food patch, and the location of the different available amounts were varied. The rats exhaustively sampled all patches each session but seemed to have fairly strong preferences for certain locations over others. If position preferences were for patches containing small amounts of food, the sensitivity to amount available was increased so that when location was compensated for, a pattern of optimal foraging was evident. The importance of environmental constraints in producing optimal behavior and the relation of the observed behavior to laboratory findings are discussed.

Key words: foraging, amount of food, optimal behavior, seminatural environment, rats

In the past few years psychologists interested in animal behavior have become much less myopic in their outlook on what constitutes the appropriate procedure(s) and theoretical framework(s) for understanding behavior. On the theoretical side, economic models have been used to explain schedule effects (e.g., Allison, Miller, & Wozny, 1979; Hursh, 1980). Another related view is that learned behavior represents adaptation to environmental constraints on the basis of a homeostatic mechanism (e.g., Staddon, 1979). The influence of ecological and ethological theories of foraging behavior (e.g., Lea, 1979) has also served to broaden our theoretical perspective. On the procedural side, there has been a new appreciation for the "naturalness" of behavior and how the constraints of a learning situation affect naturally occurring activities (e.g., Shettleworth, 1975). To promote the idea of studying natural behavior, several researchers have also advocated the use of learning situations that require the animal to spend a significant amount of time (if not all the time) in the situation and work for all the daily food and/or water it will receive during this time (e.g.,

Collier, Hirsch, & Kanarek, 1977). These theoretical and procedural innovations are not independent but are mutually interdependent and compatible, promising a new look for animal psychology.

The present experiment represents an attempt to develop a procedure along the lines of a more natural or representative environment and procedure. It has the characteristics of a natural situation, but maintains some of the important controlled aspects of laboratory studies. This was done by allowing the rat to forage for its food in a large room containing nine food sources, or patches, and two water bottles. The patches consisted of boxes containing sand that had food buried in it. The room itself was in total disarray, with tables, chairs, and desks laid on their sides making it difficult for a human to move around in the room. With the contents of each patch being known and only one subject foraging at a time a quantitative test of optimal foraging theory (e.g., Krebs, 1978) is possible. In particular, this theory claims that a predator will capture prey in a patch so as to maximize the rate of return relative to the whole environment. In the present experiment the amount of food available in each patch was varied and the total amount was known. In the natural environment these parameters must often be guessed and are subject to fluctuation due to factors beyond the experimenter's control (e.g., weather, seasonal changes, other predators, etc.)

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In the present experiment, the optimal foraging behavior is a function of the amount of food available in each patch. Consider the following situation where there are four food patches each containing a different number of prey: 10, 7, 4, and 1 prey, respectively. If we know the total number of prey captured by the forager is 12, then how should the optimal forager utilize the different patches? First it is assumed that average time between successive captures of prey items is inversely related to the number currently available. That is, a prey item will be found sooner if there are 10 available than if there are only 9. Second, it is assumed that the cost of searching for prey within a patch is relatively greater than the cost of traveling from one patch to another. If it was not costly to search and handle prey within a patch, as might be the case if soft pellets were available in a cup, then the predator should simply eat everything available before moving on to the next patch. Similarly, if the environment was very rich, meaning each patch had a very high density of prey available, the cost of traveling between patches would increase relative to the cost of staying in a patch since in a rich environment the cost of searching for prey is less than in a poor environment. Under these assumptions the optimal predator will act to minimize the time spent searching within a patch since such searching is the main cost in the situation. In the hypothetical example above the total number of prey obtained is known to be 12, and the predator therefore should have captured 7 from the 10 prey patch, 4 from the 7 prey patch, 1 from the 4 prey patch and 0 from the 1 prey patch. In this fashion the predator will have depleted each patch to 3 prey items available (except for the 1 prey patch, of course). A strategy that resulted in reducing a given patch below the 3 prey level is nonoptimal because it involves greater costs than the optimal.

The form of the optimal solution to predation in a patchy environment depends on the nature of the environment and constraints of the predator. For example, in the above prediction it was assumed that the cost (measured in some appropriate currency such as time or energy expended) of searching for prey within a patch was greater than the cost of traveling from one patch to another. Suppose that restrictions on travel were imposed. There might be either physical barricades between patches

or the danger of becoming the prey of some other predator when traveling in the exposed areas between patches. In this case the optimal strategy would be to deplete each patch utilized to a greater degree than in the previous example since the cost of doing so is less than the cost of traveling to a new patch. Schoener (1971) discusses these and other cases and provides a mathematical formulation of the various possibilities.

In the present experiment 9 patches were made available, each containing differing numbers of prey items during the experimental phases. It was assumed that the cost of travel was less than the cost of searching within a patch (the first case discussed above). The optimal strategy would then be to reduce all patches to a given level, that level being determined by the total amount of food to be harvested and the distribution of food between patches. To simplify matters, the amount of food available was systematically varied in increments of 3 and 5 pellets per patch for the two subjects. This results in the optimal strategy being expressed as a linear relationship between amount available and amount eaten. This prediction is also consistent with the idea that the predator has a cutoff time for successive prey captures, and once this cutoff time is reached without finding a prey item the predator "gives up" and moves to a new patch (Charnov, 1976).

METHOD

Subjects

Two male hooded rats of the Long-Evans strain approximately 100 days old at the start of the experiment were obtained from Blue Spruce Farms, Altamont, N.Y.

Apparatus

A large windowless classroom and several smaller rooms, used for experimental psychology classes during the academic year, were used as the experimental apparatus. A floor plan and dimensions of the room are shown in Figure 1. The patches were rubberized boxes 27.5 by 27.5 by 15 cm deep, filled with 3.71 liters (4.7 kg) of sand that was obtained from a local river bed. This volume of sand resulted in a depth of approximately 4 cm in each patch. During the time the subjects were in the apparatus no lights were on, although some illumi-

nation was caused by the gap under the two doors of the main classroom. Food pellets were Purina Hog Startina pellets with a mean weight of .119 g each. These pellets are very firm and will not crumble from the weight of a rat or by being handled. Two small water bottles were located in the apparatus as shown in Figure 1, and each contained 100 ml of water when a subject was placed in the room.

Procedure

Both rats had extensive experience with foraging for food buried in sand prior to the start of this experiment, having served in one of M. W. Olson's dissertation experiments (Olson, Note 1).

Phase 1 lasted for nine sessions, each 12 hours long for each subject. For the first five sessions 15 pellets were available in each patch and 20 pellets for the next session. There was a break of 10 days for extraexperimental reasons, followed by the last three sessions of this phase with 20 pellets in each patch. The rats were changed, food eaten was measured, patches were stocked, etc., at 9 a.m. and 9 p.m.

Phase 2 lasted for six sessions with different numbers of pellets available in each patch, as shown in Table 1. An attempt was made to counterbalance small and large amounts by location between the two subjects, but any true counterbalancing would have required many more subjects. Foraging periods continued to last for 12 hours during this phase.

Phase 3 lasted for 15 sessions and was identical to Phase 2, except the rats were allowed only one hour of foraging time per session. Rat 9 foraged from 9 to 10 a.m. and Rat 10 foraged from 9 to 10 p.m.

Phase 4 lasted for 9 sessions of one hour duration. Number of pellets available in each patch was rotated so that each amount was represented once in each patch. This was accomplished by shifting the number of pellets for a particular patch to the next highest number patch and Patch 9 shifted to Patch 1. Thus, for Rat 9 on the first day of this phase, Patch 1 had 12 pellets in it, Patch 2 had 27 pellets, Patch 3 had 9 pellets, and so on. On the ninth session the amounts were as they were during Phases 2 and 3.

The sand from all patches was periodically mixed together and redistributed to prevent possible odor effects from differentially influencing the rat's behavior. No food was given to

the rats in their homecages during the course of the experiment, except for the occasional feedings during Phases 3 and 4 at the time when the other rat was foraging. Such feedings occurred when a subject's weight dropped below 80% of its ad lib weight (during the 10-day break of Phase 1 food was available ad lib). Water was continually available in the home cage.

Data recorded were number of pellets eaten, number of feces, and evidence of urine for each patch. This was accomplished by sifting the sand after each session. Amount of urine was quantified by rating the amount of coagulated sand on a 1 to 10 scale. Amount of water drunk from each water bottle was measured and the weight of the rat at the start and finish of a session was also recorded. A note was made concerning the rat's location in the apparatus at the time the experimenter entered at the end of a session.

RESULTS AND DISCUSSION

The data will be viewed in two different (but not exclusive) ways. First a theoretically neutral, descriptive account will be given, and then the relation of these data to optimality theory will be evaluated.

Descriptive Account

The subjects rapidly learned the location of the nine food patches. On the first foraging session, Rat 9 visited and ate from seven of the nine patches and ate from all of them on the second session. Rat 10 ate from six of the nine on the first session, and the others, except for Patch 9 which was closest to the front door, on

Table 1

Amount of food (number of pellets) available in each patch for the five phases of the experiment.

Patch Number	Experimental Phase			Rotation	
	1	2,3			4
		S9	S10		
1	15,20	27	16		
2	15,20	9	41		
3	15,20	30	6		
4	15,20	21	1		
5	15,20	24	26		
6	15,20	15	11		
7	15,20	6	36		
8	15,20	18	21		
9	15,20	12	31		

the second session. It was not until the fifth session that Rat 10 ate from patch nine.

Although there were numerous occasions when food was not taken from a patch, it was almost always the case that every patch was visited and some indication was present of foraging having taken place, since the surface of each patch was smoothed-over at the start of a foraging session, and disturbances due to digging in the sand were quite obvious. After the second session of Phase 1, Subject 9 visited 99.1% of available patches throughout the remaining phases, and Subject 10 visited 97.7% of the patches.

Phases 1 and 2 involved 12-hour foraging periods and that amount of time allowed the subjects to deplete almost completely all

patches each session. Recorded occurrences of feces and urine were restricted to the patches, with only one exception. Both rats adopted a "home" in the rear corner of the large room. The home was in the area where books would be placed under a desk chair which was on its back on the floor. Rat 9 was first found in the home on the second session of Phase 1 and was subsequently found there frequently (five of six sessions during Phase 2). Rat 10 was found in the same location on the fifth and sixth sessions of Phase 2. Feces and urine were also found in this location, but unlike that found in the patches, it was not removed. Presumably, the odors left by Rat 9 induced Rat 10 to adopt the same home. During subsequent phases there was less consistency in where the

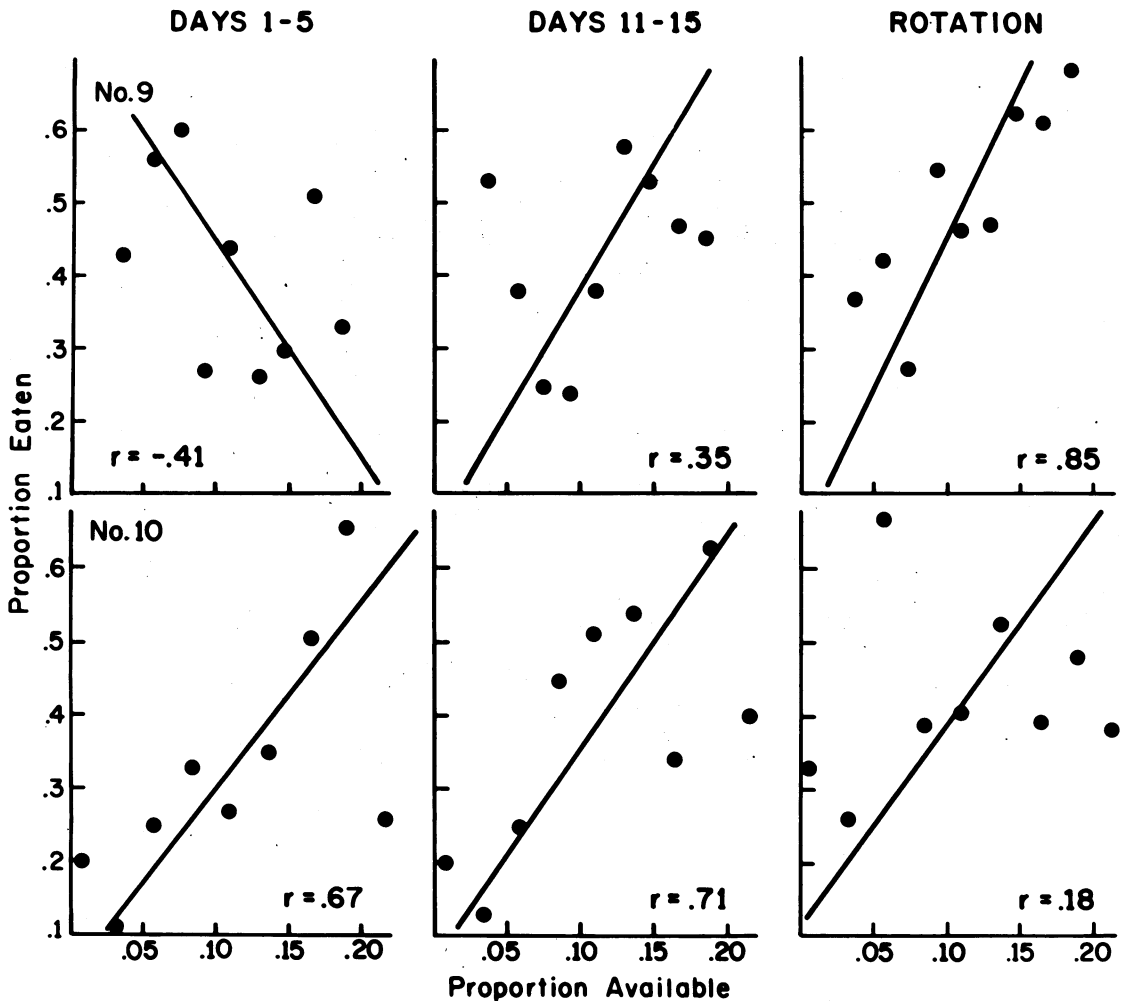


Fig. 2. The proportion of food available in the environment plotted against the actual proportion of food eaten that came from that patch during the first and last five days of constant patch locations and all nine days with food availability rotated through all locations.

rats were found, presumably because the foraging periods were restricted to one hour in these phases. It is interesting that during the phases with one-hour foraging sessions, when the session terminated with the rat in the open (i.e., not in a patch), it often ran to the home.

In order to evaluate the effect of having differing densities of food available in each patch, several correlation coefficients (Pearson's r) were computed. These correlations are used as a descriptive device to indicate the degree of relationship between patch densities and patch utilization. Scattergrams and regression lines for the correlations are shown in Figure 2. A correlation between the proportion of total food available in a particular patch and the proportion of food actually eaten in that patch was computed for each rat on the average data of the first five days of Phase 3. For Subject 9 this correlation was $-.41$, indicating that this subject ate proportionately less from higher density patches than from lower density patches. However, for Subject 10 the same correlation was $+.66$. We interpret this to mean that the placement of patches for Subject 9 was contrary to its preferences for location at the start of this phase, but they were consistent for Subject 10. Evidence that Subject 9 changed its preferences for patches comes from the correlation computed between proportion available and proportion eaten over the average of the last five days of Phase 3. Now the correlation was $+.35$ for Rat 9 and $+.71$ for Rat 10. This suggests that Rat 9 adjusted its foraging pattern to reflect more closely the relative availability of food, but Rat 10, since it already had a preference for the more dense patches, showed little change.

Data from Phase 4 support the hypothesis that Rat 9 was forced to readjust its preference for patch location by being more sensitive to patch density, but Rat 10 was not. During Phase 4 the density of food available in each patch was systematically varied so that each density occurred once in each location. Correlations were again computed for amount available and amount eaten so that a subject sensitive to patch density should show a positive correlation, but one insensitive to density and concerned (primarily) with location should show a low correlation. The correlation was $.85$ for Rat 9 and $.18$ for Rat 10. These findings are consistent with the hypothesis that Rat 9 adjusted its foraging pattern because the

density-location relationship originally experienced in Phase 3 was inefficient. The efficiency of foraging could be increased by Rat 9 through increased sensitivity to patch density. Rat 10 had preestablished preferences for patch locations that also happened to be some of the more dense patches, so it would be expected that little pressure was put on this subject to increase his foraging efficiency and responsiveness to patch density differences.

Although there were two water sources available in the foraging environment, surprisingly little water was consumed. Generally no more than 10 ml was consumed from either bottle, with the average amount being between 6 and 7 ml per session during the 12-hour phases and less than 5 ml during the one hour phases.

Optimal Foraging Theory

According to this theory organisms will act in such a way as to optimize their patterns of foraging to provide the greatest return (energy gain, caloric intake, etc.) with the minimal expenditure (energy expended, exposure to predation, etc.). Most tests of optimality theory have involved unifactor manipulations in the sense that only one aspect of the test situation was varied to test predictions of the theory. Size of prey or other aspects of the prey have been the favorite standard for testing the theory (e.g., Krebs, 1978), although occasionally travel time between patches has been used. The method employed in the present experiment was designed to be similarly unifactor, with the density of prey in a patch being the variable of interest.

Figure 3 shows the prediction of optimal foraging theory in relation to the density of prey on the final five days of Phase 3 (one hour foraging sessions, constant patch-density locations). The predictions were derived by the method outlined in the introductory part of this report. This method involves taking the total number of pellets consumed by each subject and determining the optimal pattern of patch utilization under the assumption of increasing costs of searching with decreasing prey availability and relatively greater costs for searching within a patch relative to travel between patches. The fit of data and theory is not overly impressive.

The deviations from predicted behavior are systematic and similar for each subject. Those patches containing low densities of prey are

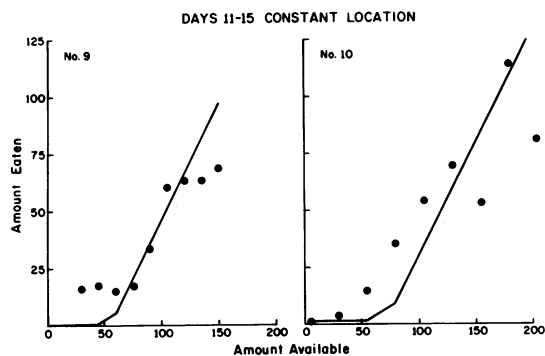


Fig. 3. Predictions of Optimal Foraging Theory (solid lines) for amount eaten as a function of the amount available for the last five days of constant patch locations.

overutilized and those containing high densities are underutilized. This behavior indicates that the subjects are too conservative relative to optimality theory. The subjects do not exploit the high density patches to the degree that optimality theory predicts and instead, sample from lower density patches, overexploiting them. Changing the assumption concerning relative costs of searching within a patch and travel between patches will not help the fit. If travel between patches was actually more costly than originally assumed, the slope of the predicted line in Figures 3 and 4 would be increased and the intercept would be shifted to the right, making the fit even worse. It is interesting that there is a parallel phenomenon in research on decision making by humans. Our species underutilizes the diagnostic value of information relative to the optimal (Bayes Theorem in this case), showing a more conservative pattern of behavior than is optimal (e.g., Edwards, Lindman, & Phillips, 1965).

Optimal foraging theory makes nearly identical predictions concerning patch utilization regardless of whether patch densities maintain constant locations from one foraging session to the next, or if the locations vary in nonsystematic fashion. The only difference between these two situations is the fact that when patch densities vary in location, it will take some time for the subject to discover the rate of return in a particular location, thereby increasing the probability that a low density patch will be overforaged relative to the condition where patch densities and their locations remain constant. Figure 4 shows the predictions of optimal foraging theory and the outcome

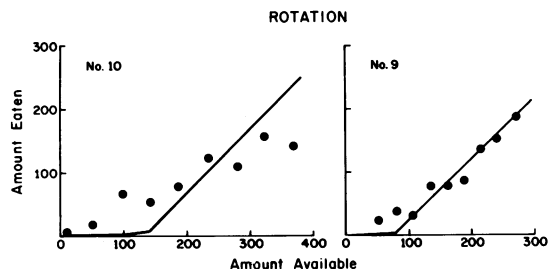


Fig. 4. Predictions of Optimal Foraging Theory (solid lines) for amount eaten as a function of the amount available for the nine days of patch densities rotated among patch locations.

of Phase 4 of the experiment (densities rotated among all patch locations). Although Rat 10 shows essentially the same pattern of deviation from what optimal foraging theory predicts—also evident in the previous phase of constant patch-density locations—(overutilizes low density, underutilizes high density), Rat 9 shows fairly impressive agreement with the predictions of the theory. Excluding the two lowest density patches, a chi-square goodness-of-fit procedure indicated that the predicted and observed number of prey eaten were not significantly different ($\chi^2(6) = 12.47, p > .05$).

The finding that Rat 9 was consistent with predictions from optimal foraging theory also supports the earlier argument that Rat 9 was forced to be more sensitive to patch densities than Rat 10 because of the mismatch between Rat 9's initial patch preferences and what was available in those patches. By being forced to be more sensitive to the contents of a patch, Subject 9 shows an optimal pattern of foraging, but Subject 10 does not. It appears then that optimal foraging is not a necessary result of biological programming, but depends on how such programming interacts with environmental constraints for its occurrence.

The main results of the experiment may be summarized as follows: (1) rats are exhaustive samplers of their potential food sources. Both rats showed evidence of visiting virtually every patch available on each session. (2) Rats tend toward conservatism in the sense of preferring a particular location for foraging over what is available in that location, except when preferred locations contain very small amounts of food. (3) When the environment is structured so that preferred locations do not contain rich food sources, there appears to be increased sen-

sitivity to the richness of the food source. When location is subsequently not a factor, there is optimization of the utilization of differentially rich food sources. It is also interesting that at least one subject showed more efficient behavior in a changing environment than a constant one. This may reflect the fact that more than one kind of learning is called for in an environment as complex as the one used in this experiment. Learning about where food sources are and learning about the nature of the food sources and how to obtain the food they contain may be relatively independent processes. Such different components of foraging are more dramatically evident in other species such as birds which fly to a beach area and then walk on the beach probing the sand with their beaks for worms (e.g., Goss-Custard, 1977).

In conclusion, the procedure described in this experiment is an effective method for evaluating the operation of variables that have been shown to affect behavior in the lab and the interaction of such variables in a situation that is more complex than is normally studied in the lab but maintains sufficient control and precision to allow for meaningful conclusions about environmental constraints that govern behavior.

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