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In two experiments conducted in an eight-arm radial maze, food pellets were delivered in the arms according to interval schedules of reinforcement. The behavior of rats in this situation was well-described by the generalized matching law; that is, there was a linear relationship between log behavior ratios and log pellet ratios. The slopes of these functions, an index of sensitivity to reinforcement frequency, were greatest for nose pokes, intermediate for time spent in an arm, and least for arm entries. Addition of a 10-second changeover delay eliminated the slope differentials between nose pokes and time spent by reducing the slopes of the nose poke functions. These results suggest that different aspects of foraging are differentially sensitive to reinforcement. Further, the results validate the use of this animal model for the assessment of stress and drug effects on behavior.

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AN EIGHT-ALTERNATIVE CONCURRENT SCHEDULE: FORAGING IN A RADIAL MAZE

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In two experiments conducted in an eight-arm radial maze, food pellets were delivered when a photocell beam was broken at the end of each arm via a nose poke, according to either fixed-interval or random-interval schedules of reinforcement, with each arm providing a different frequency of reinforcement. The behavior of rats exposed to these procedures was well described by the generalized matching law; that is, the relationships between log behavior ratios and log pellet ratios were approximated by linear functions. The slopes of these log-log functions, an index of sensitivity to reinforcement frequency, were greatest for nose pokes, intermediate for time spent in an arm, and least for arm entries. Similar results were obtained with both fixed-interval and random-interval schedules. Addition of a 10-s changeover delay in both experiments eliminated the slope differentials between nose pokes and time spent in an arm by reducing the slopes of the nose-poke functions. These results suggest that different aspects of foraging may be differentially sensitive to reinforcement frequency. With concurrent fixed-interval schedules, the degree of temporal control exerted by individual fixed-interval schedules was directly related to reinforcement frequency.

Key words: concurrent schedules, matching, foraging, interval reinforcement schedules, changeover delay, timing, maze, nose poke, rats

Parallels between food reinforcement in the laboratory and foraging for food in the natural environment have been frequently described (e.g., Baum, 1987; Fantino & Abarca, 1985; Lea, 1979; Mellgren, 1982). Food is not uniformly distributed in the environment; instead, it exists in "patches" in which food is plentiful relative to the overall environment. Examples of patches might be a clump of strawberry plants, a trash can in an urban alley, or a water hole in the desert. As animals consume the food in a patch, it becomes depleted, and another patch must be found. Over time, patches usually become replenished; that is, more berries ripen, or more prey animals come to the water hole to drink. This pattern of foraging may be thought of as a many-component concurrent schedule, in which the depletion-replenishment cycle in each patch defines the schedule of reinforcement in effect for patch seeking. Interval schedules of reinforcement provide a model for this depletion-replenishment cycle, because once a reinforcer has been obtained (i.e., the patch is depleted), a period of time must pass before another reinforcer becomes available (the patch becomes replenished). Concurrent interval schedules thus provide a model for foraging in an environment with multiple patches.

In the natural environment, animals move among patches. In the history of psychology, locomotor behavior of animals has been studied in many different types of mazes. Recently, radial-arm mazes, in which the arms of the maze extend radially from a central platform, have been used for the study of memory processes, brain mechanisms in memory, and drug effects on memory (e.g., Eckerman, Gordon, Edwards, MacPhail, & Gage, 1980; Jarrard, 1980; Levy, Kluge, & Elsmore, 1983; Olton & Samuelson, 1976). Rats are extremely proficient at finding food in a radial-arm maze. For example, if a single pellet of food is placed at the end of each arm, animals quickly learn to find and consume all of the pellets with no, or very few, errors (i.e., entries into previously visited arms), even if they are temporarily removed from the maze during the session before all of the pellets are consumed. The radial-arm maze is thus well suited as a laboratory analogue of the natural environment in which rodents forage for food. Each arm of the maze

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may be thought of as a different patch, and the effects of varying contingencies for procurement of food in each arm may be investigated. Thus, the radial maze provides an opportunity for quantitatively studying foraging within the context of concurrent schedules of reinforcement.

Concurrent-schedule performance has typically been studied in pigeons in two-alternative key-pecking situations (Davison & McCarthy, 1988), although a few experiments with more than two alternatives have been reported (Davison & Hunter, 1976; Miller & Loveland, 1974; Pliskoff & Brown, 1976; Reynolds, 1963). Less frequently, other species and responses have been studied (see Davison & McCarthy, 1988, for a review). The nearly universal finding in these studies is that behavior conforms to the generalized matching law, which states that the ratio of behavior of a given type to other behavior in the situation is proportional to the ratio of reinforcement received by that behavior relative to reinforcement for alternative behavior (Baum, 1974). If it can be shown that this principle applies to the considerably more complex environment provided by a radial maze with many alternative activities and sources of reinforcement, our understanding of both foraging and choice will be enhanced. Thus, the present paper examines the application of the generalized matching law to foraging in the radial maze.

Adapted to the present experiment, the generalized matching law may be mathematically expressed as

$$\log(B_i/B_o) = a \log(R_i/R_o) + \log c,$$

where B_i and R_i are behavior and reinforcement in a given arm of the maze, B_o and R_o are the sum of behavior and reinforcement in all other arms, the proportionality constant a is the slope of the line in log-log coordinates, and c is the y intercept (see Davison & McCarthy, 1988). Thus, B_i/B_o represents the ratio of the behavior occurring in a given arm to the sum of behavior in the other arms, and R_i/R_o represents the ratio of pellets received in an arm to the sum of pellets received in the other arms. The proportionality constant a is a measure of the sensitivity of behavior to reinforcement density, with $a = 1.0$ representing strict matching, values less than 1 representing undermatching, and values greater than 1 representing overmatching. Bias, a systematic deviation from matching that is unrelated to reinforcement density, is measured by c.

In two experiments, eight-alternative concurrent schedules of reinforcement were arranged, with a different value of the schedule programmed for each arm of the maze. These experiments examined the relationships between the ratios of responses, time, and entries in a given arm to the ratio of reinforcement received in that arm for both concurrent fixed-interval (FI) and concurrent random-interval (RI) schedules. In both experiments, the effects of a changeover delay (COD) were also investigated.

EXPERIMENT 1
FI SCHEDULES

Method

Subjects

Six male albino rats were maintained at their preexperimental free-feeding body weights by daily postsession feeding. The weights of the subjects ranged from 470 to 510 g. The subjects were approximately 1 year old at the start of the experiment. They were housed in individual wire cages in which water was freely available. The cages were housed in a room with a 12:12 hr light/dark schedule, with light onset at 6:00 a.m. daily.

Apparatus

Testing occurred in a covered eight-arm radial maze constructed of 6.25-mm polycarbonate plastic (Figure 1). The walls and ceiling of the maze were clear, and the floor was black. The plastic covering the arms and central platform could easily be removed for cleaning and access to the subjects. The arms extended from a central platform (52 cm diameter). Clear plastic guillotine doors at the entrance to each arm could be remotely raised and lowered with a system of strings and pulleys. Each arm was 20 cm wide by 60 cm long by 12.5 cm high. Automatic dispensers for delivering 45-mg food pellets and a food trough (Coulbourn Instruments) were mounted on aluminum panels at the end of each arm. White cue lights were located on the end panels to the right of each food trough. Light sources and photoelectric cells were located in the food trough for detecting nose pokes into the cup, and were located 15 cm from the entrance to

the arm for detecting entries into the arm. A relay mounted outside the end of each arm next to the feeder was operated when the photocell beam was broken to provide response feedback. Metal legs elevated the entire maze 75 cm from the floor. The maze was located in a room with a window on one side (adjacent to Arm 4), an equipment rack on another (adjacent to Arms 2 and 3), and [illegible] office partitions on the remaining two [illegible] rge (20 cm high) white symbols (a + and a △) were mounted on the partitions to mal[illegible] them more discriminable. For identification purposes, arm numbers were assigned in a clockwise fashion, with Arm 1 being the arm closest to the point at which the experimenter entered the room. Programming of the experimental apparatus was accomplished by a PDP® 11 minicomputer operating under the SKED® 11 system for programming behavioral experiments (Snapper & Inglis, 1985).

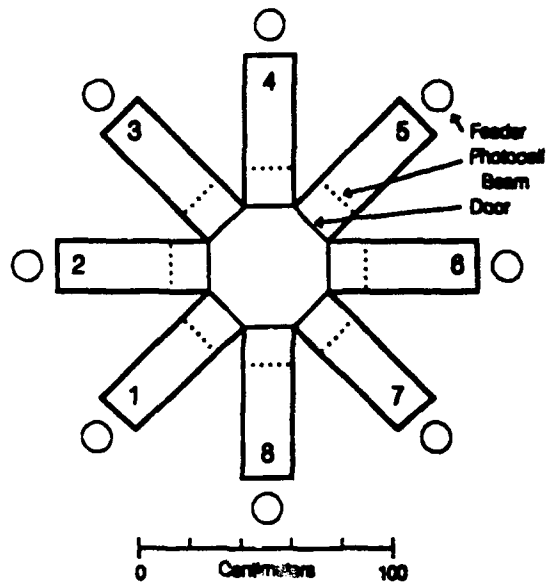

Fig. 1. Schematic diagram of the eight-arm maze. See text for construction details.

Procedure

Initial training. Following training to eat pellets from the food cup at the end of each arm, the rat was allowed to earn pellets in each of the eight arms. This involved confining the animal in an arm by lowering a door at the entrance to the arm. Each interruption of the photocell beam in the food cup (nose poke) produced a single pellet. After about 20 pellets were earned, the animal was moved to another arm; this process continued until 20 pellets were earned in each arm.

Experimental sessions. After initial training, the final procedures were instituted. Prior to the start of the experimental session, the rat was placed in the center of the maze with the doors to all compartments closed. The beginning of the session was signaled by raising the doors to all arms and illuminating the cue lights at the end of each arm. The cue lights remained on until the session was over. Pellets were delivered according to independent FI schedules of reinforcement, in which the FI values were multiples of a series of prime numbers such that delivery of a pellet in one arm never reliably predicted availability of a pellet in another arm. To arrange an overall maximum pellet frequency of approximately 180 pellets per hour, the prime numbers 3, 5, 7, 11, 17, 23, 31, and 41 were multiplied by the constant 18.5 to yield FI values of 55, 92, 129, 203, 314, 425, 574, and 759 s. These values resulted in maximum pellet delivery rates of 65.45, 39.13, 27.90, 17.73, 11.46, 8.47, 6.27, and 4.74 pellets per hour. The FIs were randomly assigned to the arms of the maze, with a different random assignment for each animal. To minimize predictability at the beginning of each session, the timers for each FI were not initialized to zero, but were randomly set to a value, t, within the interval such that $t = r \times \text{FI}$, where r was randomly chosen from the set {.1, .2, . . ., .9}. Sessions were 1 hr in duration, and were conducted at the same time most weekdays. Due to scheduling conflicts, occasional weekdays were skipped. The exact time, in 0.1-s units, and location of each photocell beam break and pellet were recorded, permitting detailed analysis of response rates and patterns.

Sequence of conditions. The initial conditions remained in effect for 51 experimental sessions, at which time there were no systematic changes in any of the dependent variables. In order to assure that the distribution of responses to arms was controlled by the values of the reinforcement schedules in effect in the different arms, in the second condition, the assignment of FIs to arms of the maze was rerandomized for each animal, with the restriction that the FI in any arm could not remain the same. The second condition remained in effect for 39 sessions. Finally, a 10-s change-

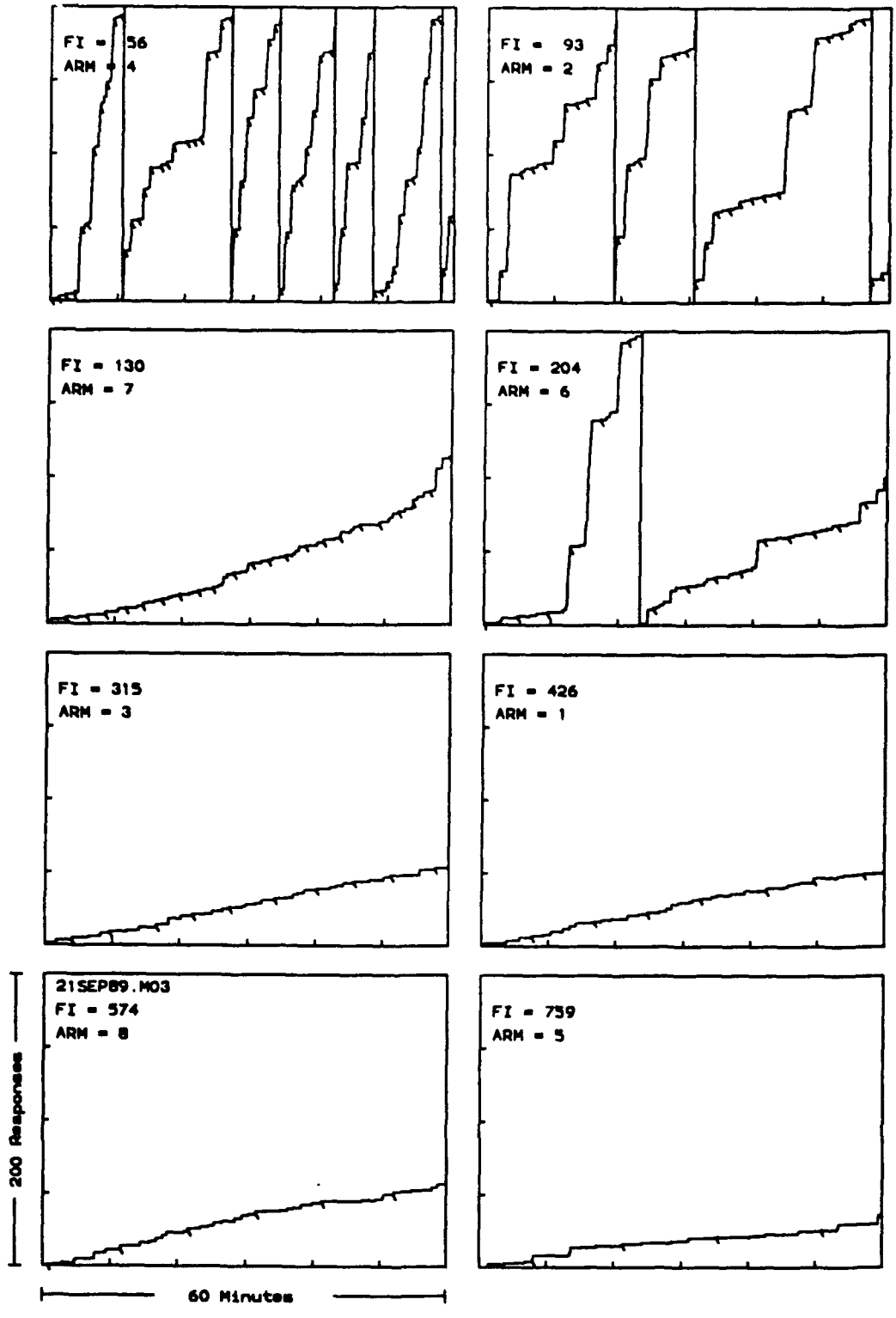

Fig. 2. Cumulative nose-poke records for Rat 3 for each arm of the maze for the last session in Condition 1.

over delay (COD) was instituted to prevent the reinforcement of rapid switching between arms (see Herrnstein, 1961). The COD was implemented by starting an arm-unique timer each time the animal made a nose poke at the end of a given arm. A nose poke in any other arm could not be reinforced until the COD had elapsed in all other arms. Each nose poke reset the COD timer for that arm. This procedure remained in effect for 20 sessions.

Results

All numerical results represent the means of the final five sessions under a given experimental condition. Appendices A, B, and C show individual means for all subjects, by arm, of obtained pellets per hour, nose pokes (responses) per hour, total time per arm, arm entries, responses per entry, time per entry, and quarter-life values (Herrnstein & Morse, 1957) for Conditions 1, 2, and 3 respectively. Arm entries were defined as all occasions upon which at least a single nose poke was made in the feeder at the end of the arm. The number of visits to an arm upon which no nose pokes were recorded was negligible. Visits to arms were timed from the breaking of the photocell beam at the entry of the arm until the beam was broken upon exit. In general, there was a positive relationship between the behavior in a given arm and the frequency of pellets received in that arm.

Condition 1: Initial Training

Figure 2 shows cumulative nose-poke records for the last session on this condition for Rat 3. For simplicity, the terms "lean" and "rich" will be used to refer to arms of the maze with infrequent and frequent reinforcement, respectively. Each panel shows behavior in one arm of the maze, with data from the richest arm at the upper left, and data from the leanest arm at the lower right. Fixed-interval durations (in seconds) and arm numbers are indicated in each frame. In the richer arms, responding was often characterized by postpellet pausing followed by bursts of responding terminated by pellet delivery (i.e., a "typical" FI behavior pattern). Instances of pellet deliveries for a single response were fairly frequent. Behavior in the leaner arms was much more sporadic, with few bursts, although in this session several large response bursts occurred in Arm 6 (FI 204 s). The behavior of this subject was representative of all 6 subjects.

In Figure 3, log response ratio, log time ratio, and log entry ratio are plotted as a function of log pellet ratio in Condition 1 for each subject. Obtained pellet frequencies rather than programmed pellet frequencies were used. In each frame, each point is for a single arm of the maze. The solid line in each frame is the least squares fit to the data. The equation of the line is shown in the frame, as is the proportion of the variance accounted for by the line (r^2). The dotted diagonal line represents strict matching. The data from all subjects were remarkably similar. For responses, shown in the top row, the slope of the line was greater than 1.0 in all cases, indicating that the rats responded more in the rich arms of the maze and less in the lean arms than would be predicted by strict matching. Linear functions described the data reasonably well, accounting for 80% to 95% of the variance. There appeared to be a slight clustering effect, with most of the animals showing a group of five or six points on or near the lower end of the function and two or three points on the higher end. The time functions, shown in the middle row, all had a lower slope than the response functions, indicating slightly less sensitivity to reinforcement density. Again, linear functions accounted for greater than 80% of the variance for all animals. The clustering effect, noted above for responses, was less apparent for the time measure. The bottom row of Figure 3 shows the effects of pellet frequency on entries into an arm. In all cases, the data were well described by linear functions, with slopes substantially lower than for either responses or time. Thus, the behavior of switching between arms appeared to be much less sensitive to reinforcement conditions than behavior (or time) within an arm.

The animals spent very little time in the central platform of the maze. Transition times between arms were measured between the exit beam break in one arm and an entry beam break in a different arm. Average transition times (in seconds) for Rats 1 to 6 were 1.18, 0.98, 1.29, 1.44, 2.02, and 0.77, respectively.

Because the reinforcement schedules in effect in each arm of the maze were FI schedules, it might be expected that responding in each arm would conform to the typical FI pattern

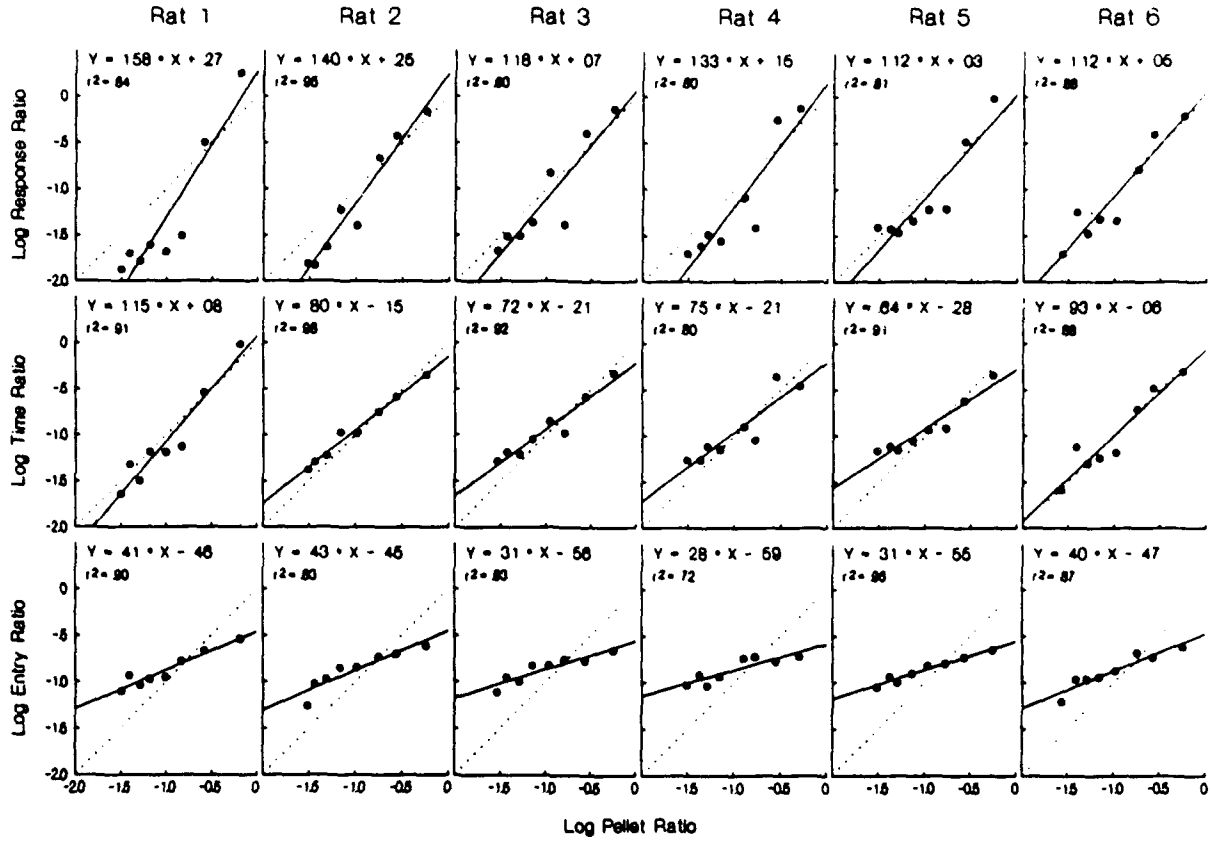

Fig. 3. Matching functions for the eight-component concurrent FI schedule in Condition 1. Log behavior ratios are plotted as a function of log obtained pellet ratios. The top, middle, and bottom rows are for responses, time, and arm entries. Each column is for a separate animal. Solid lines are least squares fits. Dashed lines show perfect matching.

of response, which consists of a pause after each reinforcement followed by continual responding until the next pellet is received in that arm (Ferster & Skinner, 1957). This pattern is clearly evident in the cumulative records shown in the top two frames of Figure 2. Response patterning in FI schedules can be evaluated by the quarter-life measure, which is the average percentage of an FI required to make 25% of the total responses on that FI (Herrnstein & Morse, 1957). Figure 4 shows quarter-life values for each FI for each subject in Condition 1. The dotted horizontal reference line is drawn at 25%, which is the value to be expected if responding is uniformly distributed within the interval. The quarter-life values for all subjects increased with pellet frequency to above 50% in the richest two arms. The quarter-life values for 2 of the subjects, Rats 3 and 6, consistently increased with increasing pellet frequency, whereas the values for the other 4 subjects remained constant over the four leanest arms, increasing only in the richer arms. Rat 1 showed no evidence of temporal patterning in any of the six leanest arms.

Condition 2: Reassignment of Schedule Values

The subjects readily adapted to changed reinforcement densities, with performances approximating those of Condition 1 within 20 sessions. For example, on the average, over 84% of the variance in response matching functions was accounted for by the fifth block of five sessions following reassignment. There was little effect of this manipulation on the matching functions. Figure 5 shows that, compared to Figure 3, the slopes of the response functions were increased for 5 of the 6 animals, indicating an increased sensitivity to reinforcement density. The time functions were indistinguishable from those in Figure 3, and the slopes of the entry functions were decreased slightly for 5 of the 6 animals. Goodness of fit was improved for some of the animals and decreased for others.

The clustering effect was even more appar-

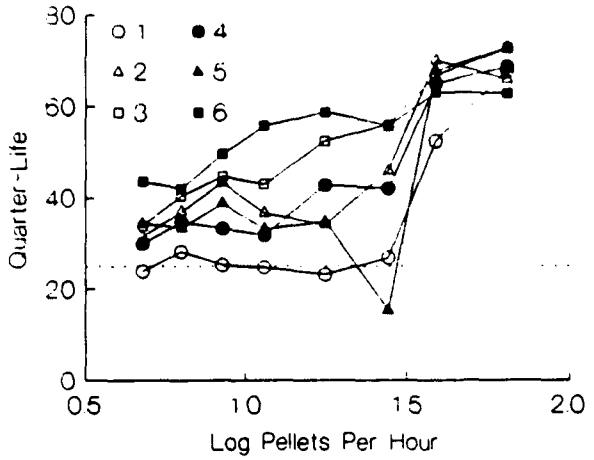

Fig. 4. Quarter life as a function of programmed pellet frequency in Condition 1. Each function is for a different animal. Dashed line at 25% indicates no temporal patterning.

ent for responding in this condition. The rats tended to leave the leaner arms promptly if a pellet was not obtained immediately, and to persist in the richer arms. The average number of nose pokes per entry in the three leanest arms was 2.17 in Condition 1 and 1.79 in Condition 2, whereas in the richest three arms the average numbers of nose pokes per entry were 11.53 and 15.21 for Conditions 1 and 2, respectively.

Condition 3: 10-s Changeover Delay

In all 6 animals, the imposition of a 10-s COD dramatically decreased the sensitivity of responding to reinforcement density. Figure 6 shows that the response ratios of all animals substantially undermatched pellet proportions, with slopes of the functions declining an average of 0.77 (or 55%) from Condition 2 to Condition 3. In most cases, the data continued to be well described by the generalized matching law, with linear functions accounting for greater than 75% of the variance (except for Rat 1, for whom the linear function accounted for only 42% of the variance in responding). The behavior of Rat 1 in the richest three arms was somewhat aberrant, with several of the

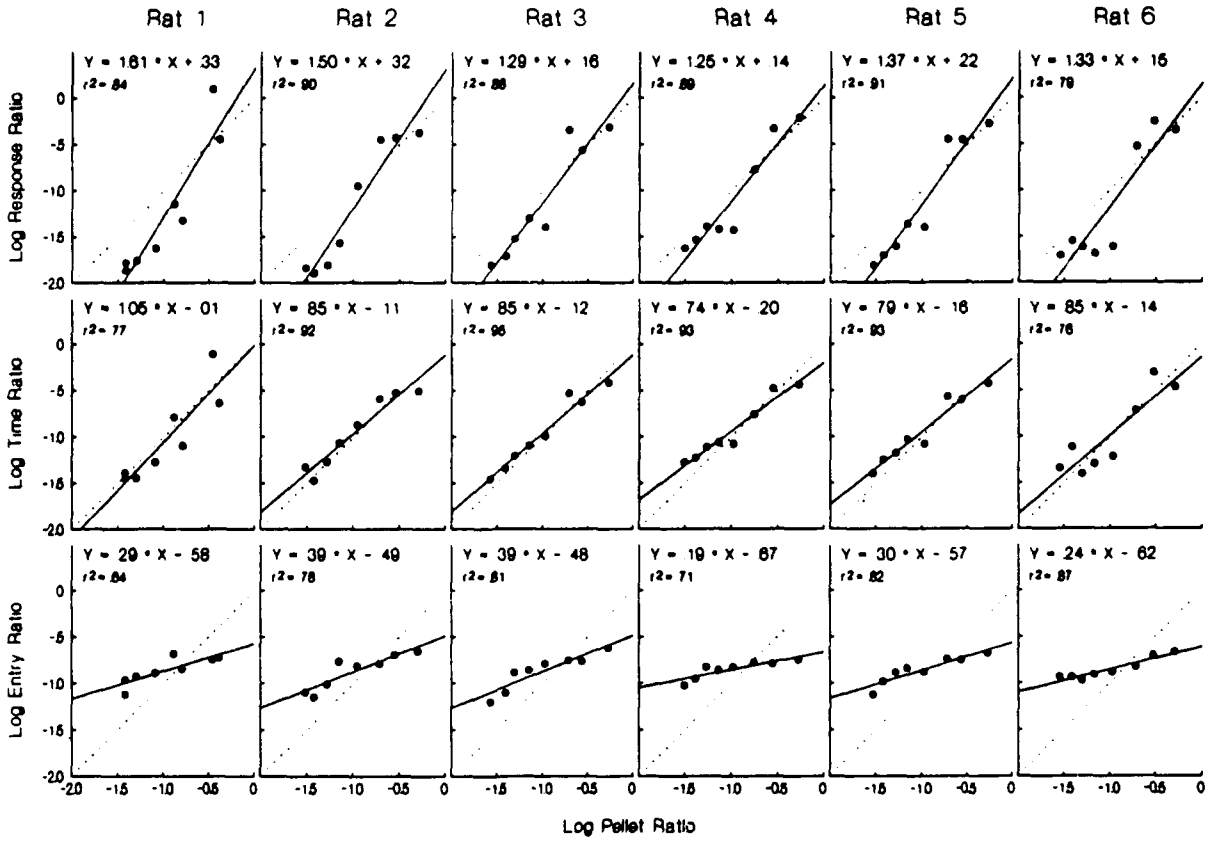

Fig. 5. Matching functions for the eight-component concurrent FI schedule in Condition 2. Log behavior ratios are plotted as a function of log obtained pellet ratios. The top, middle, and bottom rows are for responses, time, and arm entries. Each column is for a separate animal.

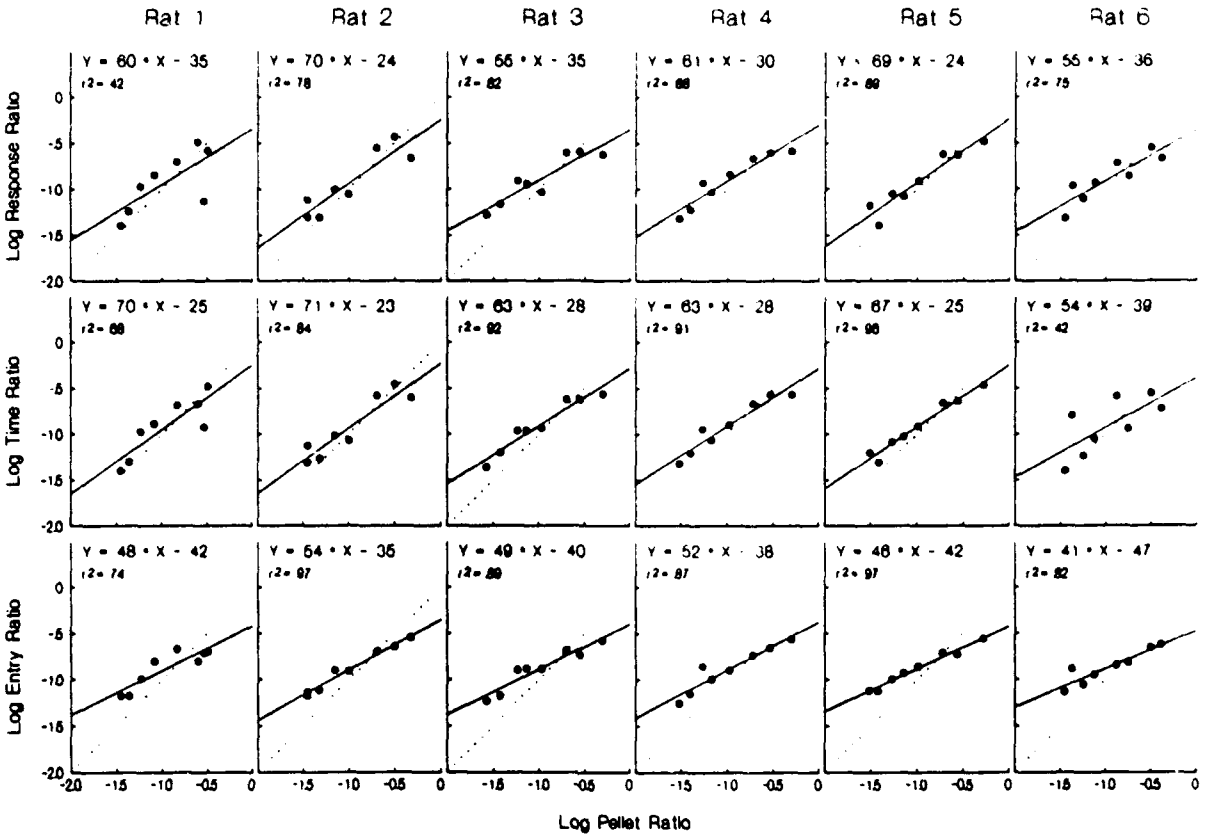

Fig. 6. Matching functions for the eight-component concurrent FI (COD 10 s) schedule in Condition 3. Log behavior ratios are plotted as a function of log obtained pellet ratios. The top, middle, and bottom rows are for responses, time, and arm entries. Each column is for a separate animal.

measures departing from the normal monotonically increasing pattern.

The COD had the desired effect of eliminating the immediate reinforcement of arm switching. The number of arm entries declined by an average of 33% from Condition 2 to Condition 3. Conversely, the number of nose pokes per entry rose about 800%, to an average of 14.3 in the three leanest arms, and by 33%, to 19.8 in the three richest arms. Thus, the observed decrease in sensitivity is accounted for by the disproportionately large increase in responding in the lean arms. The mean time spent in an arm rose dramatically from Condition 2 to Condition 3. Prior to the COD, the animals almost always remained in an arm for less than 10 s per visit to the leanest arms, averaging 5.3 s for the leanest three arms. With the 10-s COD in effect, visit duration increased to an average of 11.6 s for the leanest three arms. In contrast to the non-COD conditions, the subjects tended to spend a higher proportion of their time in an arm responding and less time entering and exiting the arm. Thus, the response and time measures were very similar when the COD was in effect.

EXPERIMENT 2
RI SCHEDULES

Despite the fact that the FI values used in Experiment 1 were chosen to prevent interactions among the schedules, the argument might be made that the fixed FI durations provided temporal discriminative stimuli for switching among the arms of the maze. Thus, to extend the generality of the findings of Experiment 1, the schedules of reinforcement in the individual arms of the maze were changed from FI to RI schedules, and Conditions 2 and 3 of Experiment 1 were replicated. That is, the RI schedules were conducted both with and without a changeover delay.

METHOD

Subjects

Approximately 5 months elapsed between the end of Experiment 1 and the beginning of Experiment 2. Because of time constraints on the use of the apparatus, only 4 subjects could be run in Experiment 2. Four of the subjects from Experiment 1 were randomly selected. During the time between experiments, the subjects were irregularly exposed to the procedures of Condition 2 from Experiment 1 (i.e., FI schedules with no COD). At the start of Experiment 2, the subjects' weights ranged from 500 to 550 g.

Apparatus and Procedure

The apparatus remained the same as that in Experiment 1. The RI schedules were arranged such that every second during the session, a pellet was made available in an arm with a given probability, with the probabilities chosen to approximate the pellet delivery rates from Experiment 1. For the leanest to the richest arms, the probabilities were .001296, .001764, .002401, .003136, .004900, .007744, .010816, and .018225. These probabilities provided maximum pellet delivery rates of 4.67, 6.35, 8.64, 11.29, 17.64, 27.88, 38.94, and 65.61 pellets per hour, for a total of approximately 180 pellets per hour. The association between arms and programmed pellet rates remained as it was in Conditions 2 and 3 of Experiment 1. For example, if Arm 3 had been the richest arm for an animal at the end of Experiment 1, it remained so in Experiment 2. Sessions continued to be 1 hr in duration. In the first phase of this experiment, which lasted 20 sessions, there was no COD, and in the second phase, which lasted 15 sessions, a 10-s COD was instituted.

RESULTS

Cumulative records for Rat 4 for the last session without a COD are shown in Figure 7. The break-and-run pattern seen with FI schedules was much less evident under the RI schedules, although occasional long bursts of responding occurred, particularly in the richer arms.

As in the first experiment, numerical results represent the means of the last five sessions under a given condition. Appendices D and E present the data by arm for each animal. All of the essential quantitative results of Experiment 1 were replicated. In the first phase of this experiment, shown in Figure 8, the order of sensitivity of the dependent variables to reinforcement was the same as in Conditions 1 and 2 of the first experiment, with responses most sensitive, followed by time in an arm and arm entries. The data are well described by the generalized matching law, except for the time and response measures for Rat 6. This subject spent an excessive amount of time in the next-to-lowest-frequency arm.

Effects of the 10-s COD, shown in Figure 9, were similar, although less dramatic than in Experiment 1. The slope of the response ratio functions was decreased for all animals by an average of 0.42 (or 35%), and for 3 of the 4 animals, the response ratio and time ratio functions became indistinguishable. Baum (1982) suggested that, when changeover delays are used, behavior during the COD should be excluded from analysis. The dashed lines in the top row of Figure 9 were plotted excluding responses during the COD and show that although the slopes were slightly increased, this exclusion made little difference. The time and entry ratio functions, shown in the bottom two rows, were essentially unchanged by the imposition of the COD.

DISCUSSION

The present experiments extend the quantitative analysis of choice to situations involving eight concurrent-interval schedules of reinforcement. The generalized matching law provides an acceptable description of the animals' behavior in these experiments. All three dependent variables—responses in an arm, time spent in an arm, and entries to an arm—were sensitive in differing degrees to the rate of reinforcement in each arm. In the absence of a COD, responding was the most sensitive to reinforcement density, time was intermediate, and arm entry was least sensitive. Addition of a COD eliminated most of the differences between allocations of responding and time. In all conditions, arm entry was the least sensitive to reinforcement density.

Effects of the COD were complex. The fact that the COD reduced sensitivity to reinforcement for responding and time is contrary to the usual effect of a changeover delay, which is to increase sensitivity to reinforcement

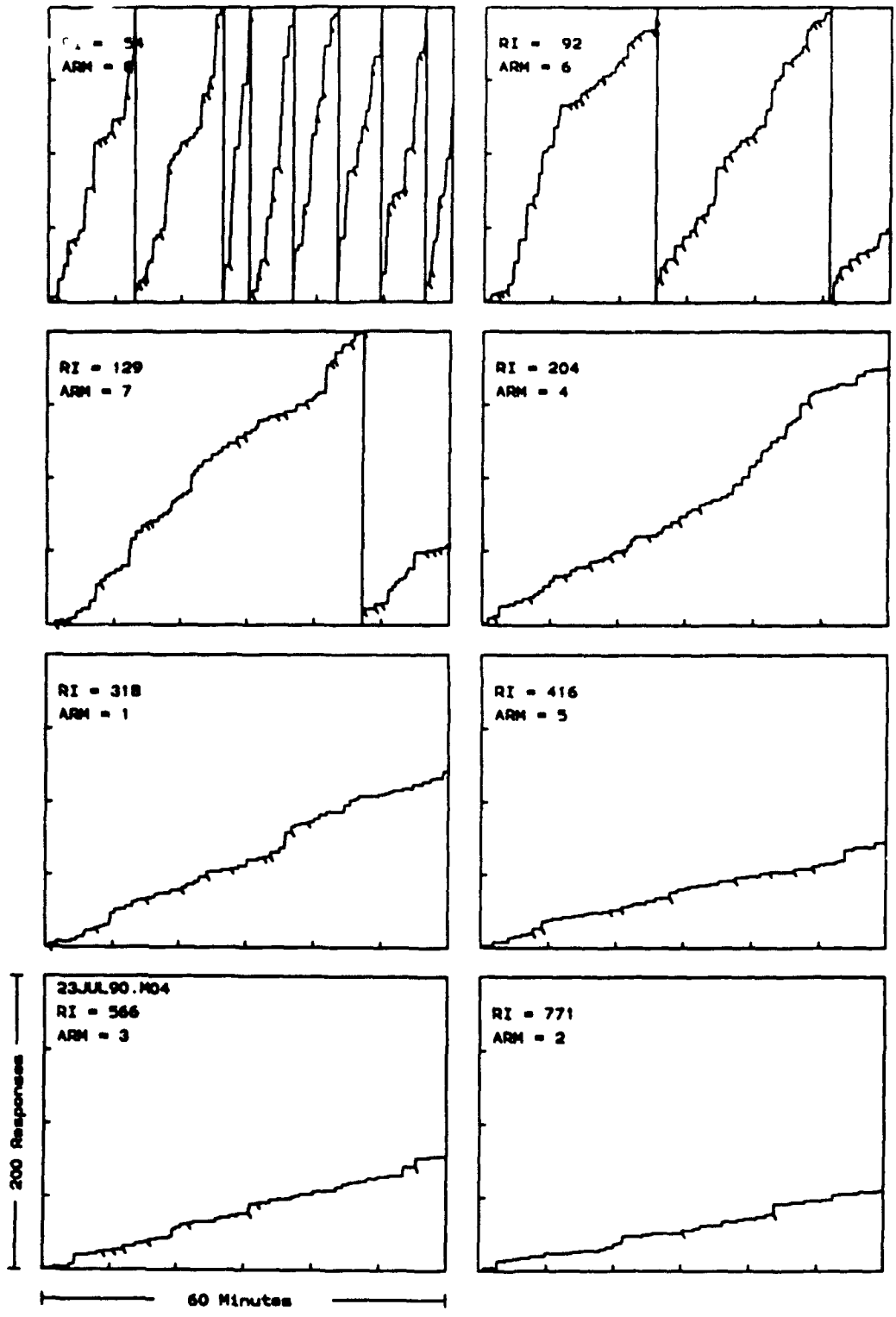

Fig. 7. Cumulative nose-poke records for Rat 4 for each arm of the maze for the last session in Condition 1 of Experiment 2.

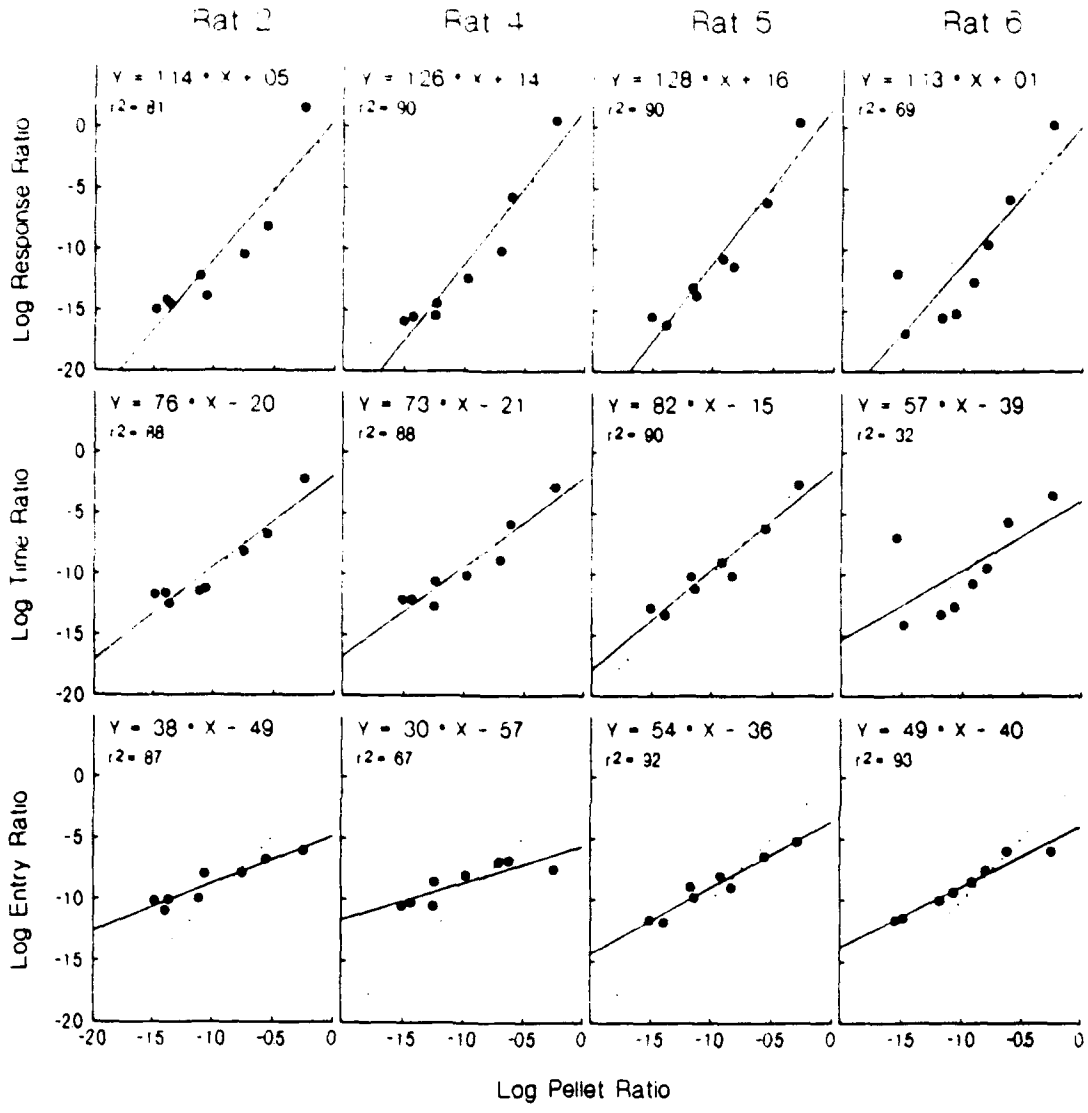

Fig. 8. Matching functions for the eight-component concurrent RI schedule in Condition 1 of Experiment 2. Log behavior ratios are plotted as a function of log obtained pellet ratios. The top, middle, and bottom rows are for responses, time, and arm entries. Each column is for a separate animal.

(Baum, 1974; Shull & Pliskoff, 1967), although Scown (1983, cited in Davison & McCarthy, 1988, p. 82) found little effect on sensitivity of COD variations from 2 to 15 s, with all CODs producing greater sensitivity than a no-COD condition. In most cases in which CODs have been employed, undermatching prevailed prior to their introduction. In the present experiments, all subjects showed overmatching for responses in the absence of a COD. When the COD was introduced, the major effect was to reduce the sensitivity of responding to reinforcement, in fact changing it to undermatching. The undermatching seen in the time functions was either exaggerated (Experiment 1) or unchanged (Experiment 2) by the COD. Finally, in both experiments, the slopes of the entry functions were increased by the COD.

Baum (1982) showed that addition of a travel requirement between alternatives increased sensitivity to reinforcement. Travel time was clearly also a factor in the present study, because there was a minimum of 120 cm to travel between alternatives. However, it is impossible to evaluate this factor, because the size of the maze was not manipulated in this study. It is likely that addition of a COD to the already sizable requirement for switching between arms is a quite different manipulation than it

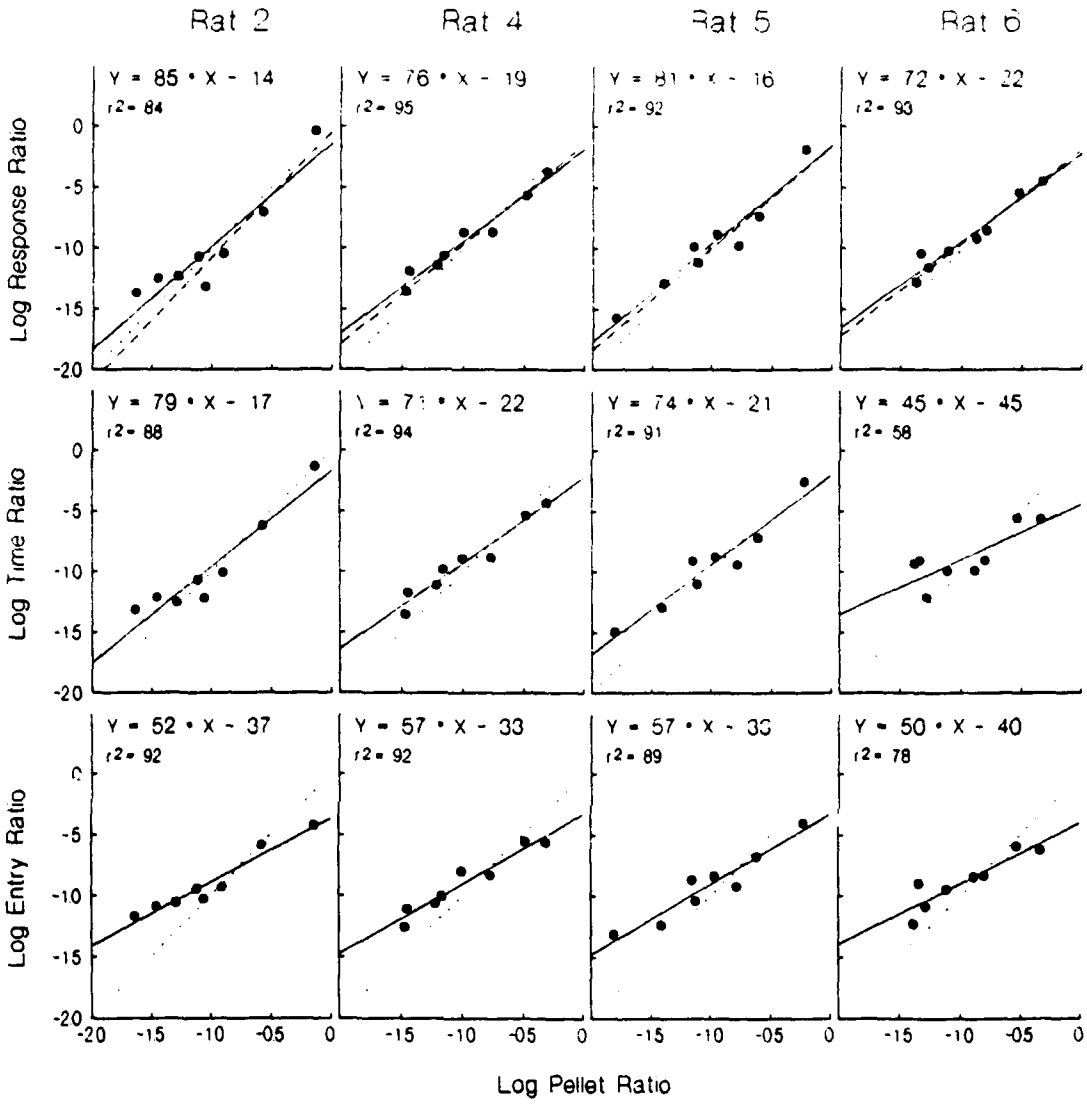

Fig. 9. Matching functions for the eight-component concurrent RI (COD 10 s) schedule in Condition 2 of Experiment 2. Log behavior ratios are plotted as a function of log obtained pellet ratios. Dashed lines in top row show least squares fits calculated after omitting responses during the 10-s COD. The top, middle, and bottom rows are for responses, time, and arm entries. Each column is for a separate animal.

would be in the absence of the travel requirement.

Surprisingly, in Experiment 1, a substantial degree of temporal control, as measured by quarter-life values (Figure 4), was exerted by the FI schedules. Temporal control was positively related to reinforcement density in all subjects. This stands in contrast to the finding that temporal control, as measured by post-reinforcement pause (PRP) or breakpoint (BP), is independent of FI duration. That is, in singly presented FIs, PRP and BP are a constant proportion of FI duration (Dukich & Lee, 1973; Schneider, 1969). Thus, the concurrent presentation of FIs in the present experiment degraded temporal control in direct relation to FI duration.

The present data are consistent with an interpretation of foraging behavior that postulates two functionally different components of foraging—search for a patch of food and procurement of the food within a patch (Mellgren & Elsmore, 1991). The radial maze used in the present experiments provides clear-cut definitions of search and procurement, with search being entries into the arms of the maze, and procurement being behavior within an arm of the maze (responses, time). The generalized

matching law provides a means of quantifying these aspects of foraging and investigating their properties. The present data show that procurement in this situation, whether measured by time in an arm or nose pokes at the end of the arm, is much more sensitive to reinforcement frequency than is search behavior. The data do, however, question the adequacy of the search/procurement dichotomy, because different aspects of procurement—responses and time—were differentially affected by the COD. Thus, the details of the reinforcement schedule in effect within a patch determine how behavior occurs within that patch.

Perhaps the most remarkable aspect of the data presented here is the degree to which the behavior of the animals in this complex laboratory analogue of foraging is adequately described by the generalized matching law. Although there are numerous theories regarding molecular mechanisms controlling foraging behavior, including optimal foraging (Charnov, 1976), the delay-reduction hypothesis (Fantino & Abarca, 1985), and momentary maximizing (Hinson & Staddon, 1983), no attempt is made here to address questions of mechanism. If the analogy to foraging in the wild is valid, the present data strongly support the view that, at a molar level, animals in the wild allocate behavior according to well-established principles of choice.

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APPENDIX A

Condition 1: initial exposure.

Rat	Programmed pellet rate (pellets per hour)							
	4.74	6.27	8.47	11.46	17.73	27.90	39.13	65.45
Obtained pellets per hour								
1	4.4	5.4	7.0	8.8	12.8	18.4	29.6	56.4
2	4.6	5.4	7.2	10.0	14.6	23.4	33.4	56.6
3	4.4	5.6	7.6	10.4	15.4	21.6	34.0	56.4
4	3.8	5.2	6.2	8.4	14.4	18.4	28.2	42.6
5	4.4	6.0	7.2	10.2	14.6	21.6	32.0	53.4
6	4.2	6.0	7.8	10.4	15.2	24.4	33.8	57.8
Nose pokes per hour								
1	26.0	38.4	31.8	47.0	40.0	59.0	473.4	1,254.8
2	47.0	45.0	70.0	171.6	119.0	542.8	838.4	1,249.4
3	47.2	66.2	68.2	93.6	290.2	87.4	645.6	951.6
4	32.0	39.2	52.2	44.4	124.2	60.8	588.4	702.6
5	65.2	62.4	57.0	75.4	98.6	100.2	429.8	849.4
6	74.0	204.2	121.6	172.0	166.0	534.0	1,065.0	1,440.2
Total time per arm (s)								
1	74.0	150.6	101.4	201.6	201.8	229.4	742.0	1,617.2
2	128.8	155.0	180.4	307.6	303.3	483.8	661.0	997.2
3	141.4	174.2	166.6	238.0	352.2	273.2	600.2	916.8
4	128.8	130.0	180.0	166.6	280.8	208.2	762.6	649.6
5	153.2	170.0	155.4	193.6	247.4	255.8	461.2	742.2
6	76.2	214.2	144.0	165.2	187.4	491.2	744.2	1,001.8
Entries per arm								
1	17.0	24.2	19.4	22.2	23.2	33.0	41.0	51.8
2	15.4	25.6	28.6	36.6	37.3	46.6	49.4	58.2
3	26.4	37.0	33.8	48.0	48.4	55.2	53.6	66.4
4	25.0	31.4	24.6	30.2	45.0	46.6	42.0	46.6
5	33.0	41.4	36.8	45.0	53.0	55.6	63.8	73.7
6	23.8	40.0	40.0	42.0	48.2	70.4	63.8	79.2
Nose pokes per entry								
1	1.75	1.60	1.66	2.12	1.70	1.80	12.54	24.02
2	3.34	1.72	2.48	4.76	3.73	11.62	16.96	21.32
3	1.82	1.78	2.02	1.94	6.04	1.60	12.40	14.34
4	1.32	1.32	2.16	1.52	2.78	1.36	12.58	14.94
5	1.94	1.48	1.56	1.70	1.86	1.80	6.70	11.50
6	3.24	4.94	2.98	3.92	3.36	7.50	16.16	18.32
Time per entry (s)								
1	4.35	6.22	5.28	9.38	8.72	7.04	18.88	30.98
2	8.54	6.16	6.38	8.48	8.13	10.38	13.42	17.20
3	5.58	4.64	4.94	4.94	7.30	4.94	11.34	13.82
4	5.16	4.24	7.82	5.26	6.38	4.58	16.98	13.88
5	4.68	4.02	4.22	4.38	4.66	4.62	7.22	10.04
6	3.22	5.26	3.72	3.92	3.80	6.94	11.52	12.76
Quarter life								
1	23.9	28.2	25.3	24.8	23.2	26.9	52.4	67.7
2	31.5	37.0	43.4	36.7	34.1	45.9	70.0	65.8
3	33.9	40.4	44.7	43.0	52.4	56.0	66.8	72.7
4	30.0	34.7	33.3	31.8	42.8	42.1	65.0	68.6
5	34.3	33.4	38.8	33.2	34.8	15.4	67.7	72.8
6	43.6	42.0	49.6	55.8	58.7	55.7	63.0	62.8

APPENDIX B

Condition 2: arm reassignment.

Rat	Programmed pellet rate (pellets per hour)							
	4.74	6.27	8.47	11.46	17.73	27.90	39.13	65.45
Obtained pellets per hour								
1	4.0	4.0	5.2	8.2	12.6	15.2	28.4	32.0
2	4.4	5.4	7.4	9.8	14.8	24.2	33.0	50.2
3	4.0	5.8	7.2	10.2	14.8	25.0	33.0	53.8
4	4.6	6.0	7.8	10.4	14.6	23.0	33.6	53.2
5	4.4	5.6	7.6	10.0	14.8	24.6	33.2	54.2
6	4.2	5.6	7.2	9.6	14.6	24.4	35.0	51.4
Nose pokes per hour								
1	30.8	25.6	32.4	43.8	127.6	86.4	1,056.4	501.6
2	46.0	40.4	49.0	84.0	324.6	844.0	876.0	956.4
3	32.0	40.0	61.2	99.6	81.2	654.4	452.4	686.6
4	51.0	62.2	86.0	79.8	79.2	313.8	698.6	834.6
5	39.6	50.8	62.6	107.0	99.6	684.2	677.6	895.8
6	59.6	84.8	72.6	62.4	73.8	707.4	1,099.2	956.2
Total time per arm (s)								
1	123.8	109.2	109.2	159.4	444.0	235.0	1,386.8	593.0
2	145.4	105.0	163.8	254.4	383.2	658.2	737.2	766.6
3	102.2	132.0	176.6	225.2	278.8	688.0	580.2	835.4
4	154.0	172.2	219.2	245.4	236.8	454.8	760.8	818.6
5	107.0	148.2	174.0	238.0	213.8	593.4	555.6	760.0
6	136.8	224.0	118.4	150.8	179.2	503.6	1,033.8	802.0
Entries per arm								
1	16.2	11.6	17.6	18.8	28.4	20.6	25.2	26.2
2	22.2	19.8	26.6	43.6	39.8	41.8	50.4	54.4
3	19.2	23.6	37.2	39.2	45.2	48.6	47.6	62.4
4	35.6	41.2	53.2	49.8	53.6	58.8	57.4	62.4
5	27.6	37.2	45.2	49.6	45.8	60.6	59.0	68.2
6	36.2	36.2	33.4	38.2	40.2	45.0	57.4	61.8
Nose pokes per entry								
1	2.00	2.28	1.80	2.36	4.50	4.02	42.98	19.18
2	2.26	2.00	1.84	1.94	8.22	20.84	18.14	17.56
3	1.64	1.68	1.66	2.54	1.78	13.48	9.70	10.88
4	1.40	1.50	1.62	1.60	1.42	5.60	12.08	13.14
5	1.42	1.36	1.38	2.14	2.18	11.46	11.46	13.02
6	1.66	2.34	2.30	1.62	1.84	15.32	19.14	15.94
Time per entry (s)								
1	7.86	9.32	6.12	8.98	16.06	11.64	57.60	22.62
2	7.02	5.42	6.38	5.90	9.80	16.20	15.08	14.20
3	5.40	5.68	4.80	5.76	6.24	14.20	12.38	13.40
4	4.24	4.20	4.16	4.92	4.42	7.98	13.20	13.06
5	3.90	4.04	3.86	4.80	4.70	9.90	9.40	11.12
6	3.82	6.14	3.60	3.90	4.44	10.94	17.96	13.36
Quarter life								
1	29.6	13.0	24.5	13.5	33.0	27.0	56.3	41.9
2	47.8	34.7	27.1	44.6	58.9	68.3	68.0	66.0
3	39.4	38.7	49.3	51.7	54.4	75.1	75.0	75.9
4	31.0	34.6	37.1	41.0	39.7	58.7	67.1	71.0
5	31.1	31.9	36.6	48.0	40.4	65.5	73.1	73.9
6	39.2	48.7	41.2	49.5	46.8	65.2	63.9	62.8

APPENDIX C

Condition 3: COD 10 s.

Rat	Programmed pellet rate (pellets per hour)							
	4.74	6.27	8.47	11.46	17.73	27.90	39.13	65.45
Obtained pellets per hour								
1	3.6	4.4	5.8	8.0	13.4	21.0	25.6	8
2	4.8	4.8	6.4	9.2	12.8	23.6	33.8	2
3	3.6	5.0	7.6	9.4	13.4	23.0	30.2	2
4	4.0	5.2	7.0	8.6	13.0	21.8	31.2	46.2
5	4.2	5.2	7.2	9.4	13.2	22.6	30.6	49.0
6	4.2	5.0	6.6	8.6	14.4	18.6	29.6	35.8
Nose pokes per hour								
1	128.0	180.0	319.6	415.2	549.2	814.0	691.4	228.6
2	263.8	176.0	174.2	336.6	300.8	814.0	1,005.4	663.8
3	160.0	206.4	349.4	324.2	271.0	634.8	646.8	614.6
4	151.4	187.2	348.4	284.0	421.8	590.6	664.6	682.6
5	234.2	146.4	307.6	290.8	414.8	726.0	715.6	938.4
6	180.0	381.2	285.2	413.0	627.4	474.4	862.6	693.0
Total time per arm (s)								
1	121.0	150.4	303.6	363.6	541.8	560.0	788.8	335.8
2	230.8	154.0	170.2	290.2	259.2	686.6	856.4	659.4
3	132.2	188.4	310.4	309.6	331.0	609.0	607.2	682.4
4	139.4	179.2	313.4	245.2	346.0	545.2	655.8	651.2
5	174.6	138.4	223.4	253.6	322.0	532.0	549.6	754.4
6	119.2	428.2	170.4	254.8	637.8	318.6	677.0	492.6
Entries per arm								
1	9.2	9.2	13.6	20.0	25.8	20.0	24.6	23.8
2	14.2	13.0	14.8	23.0	22.8	34.4	38.2	45.8
3	12.4	14.0	25.2	26.0	25.8	38.0	35.0	46.8
4	12.4	15.6	29.0	21.8	26.6	36.8	43.0	50.8
5	16.6	16.4	21.4	24.6	28.4	38.0	36.6	50.8
6	13.0	22.0	15.4	19.2	23.8	25.2	34.4	36.6
Nose pokes per entry								
1	13.76	18.22	21.40	20.44	21.26	41.04	27.88	9.38
2	18.42	13.46	11.48	14.40	13.28	24.32	26.40	14.44
3	12.60	14.44	13.90	12.30	10.32	16.58	18.16	13.06
4	11.88	11.12	11.94	13.04	14.94	15.94	15.50	13.48
5	14.06	8.64	13.72	11.64	14.24	18.92	19.60	18.38
6	13.56	17.82	17.82	21.50	26.80	18.40	25.36	18.98
Time per entry (s)								
1	13.52	17.14	21.00	17.96	21.18	27.62	32.74	14.00
2	16.14	11.92	11.54	12.58	11.44	20.28	22.48	14.42
3	10.54	13.28	12.34	11.96	12.84	15.98	17.30	14.58
4	11.06	10.38	10.80	11.30	12.64	14.74	15.32	12.94
5	10.68	8.30	10.32	10.40	11.36	14.14	15.22	14.94
6	8.98	19.24	10.88	13.28	27.04	12.46	19.96	13.52
Quarter life								
1	41.3	51.4	53.0	52.4	58.8	55.5	45.3	18.7
2	51.2	57.1	66.1	52.1	72.0	64.4	69.7	69.1
3	45.6	48.2	61.2	60.0	65.7	69.0	74.0	64.5
4	53.7	55.6	52.3	62.1	67.1	67.6	73.4	73.0
5	53.3	56.2	57.6	62.9	63.3	66.2	72.8	64.3
6	50.3	52.7	54.4	64.5	62.0	63.0	62.8	39.6

APPENDIX D

Random interval, no COD.

Rat	Programmed pellet rate (pellets per hour)							
	4.67	6.35	8.64	11.29	17.64	27.88	38.94	65.61
Obtained pellets per hour								
2	4.6	6.0	5.6	10.4	11.6	21.8	31.6	52.2
4	4.4	5.2	7.8	8.0	14.0	24.4	28.6	53.4
5	4.6	6.0	9.8	10.4	16.6	19.8	33.2	52.2
6	4.8	4.2	9.4	12.0	16.6	21.0	29.4	55.2
Nose pokes per hour								
2	77.0	84.6	91.0	141.2	98.0	206.4	329.8	1,466.6
4	68.0	74.2	75.8	94.0	148.0	240.6	577.0	1,444.2
5	55.8	48.0	93.4	80.8	157.8	137.2	397.8	1,060.6
6	57.6	170.2	76.8	82.8	146.8	283.4	585.8	1,454.8
Total time per arm (s)								
2	203.4	172.6	208.0	216.0	226.2	425.8	560.2	1,206.4
4	174.4	175.2	154.4	241.8	268.4	348.2	616.4	1,029.6
5	140.4	123.6	243.6	196.7	312.2	247.2	535.0	985.0
6	114.0	513.6	138.0	158.2	238.8	311.0	653.2	942.4
Entries per arm								
2	32.8	33.6	27.8	34.2	51.6	52.6	64.8	74.4
4	34.6	36.6	34.4	51.8	57.8	71.2	72.6	63.6
5	30.4	29.2	53.8	45.0	64.0	53.2	87.6	109.4
6	34.2	32.8	46.4	53.0	63.4	76.2	102.8	102.6
Nose pokes per entry								
2	2.36	2.54	3.40	4.98	1.92	3.94	5.10	20.58
4	1.94	2.12	2.20	1.80	2.56	3.36	8.12	29.98
5	1.78	1.64	1.72	1.92	2.46	2.60	4.54	9.80
6	1.68	5.22	1.64	1.58	2.32	3.74	5.72	14.22
Time per entry (s)								
2	6.40	5.16	7.66	6.36	4.38	8.10	8.60	16.72
4	4.96	5.08	4.52	4.70	4.70	4.90	8.62	17.50
5	4.52	4.24	4.52	4.40	4.82	4.70	6.08	9.08
6	3.28	15.72	2.96	2.98	3.78	4.12	6.36	9.24

APPENDIX E

Random interval, COD 10 s.

Rat	Programmed pellet rate (pellets per hour)							
	4.67	6.35	8.64	11.29	17.64	27.88	38.94	65.61
Obtained pellets per hour								
2	2.4	3.6	5.2	7.6	8.6	11.8	22.4	44.8
4	3.8	4.0	6.6	7.4	10.4	16.8	28.6	38.0
5	1.8	4.4	7.8	8.4	11.6	16.8	23.2	44.2
6	4.0	4.4	5.0	7.2	11.6	13.8	23.0	32.0
Nose pokes per hour								
2	169.4	221.6	229.2	326.4	190.4	342.8	683.2	1,972.4
4	184.0	263.6	295.6	346.6	520.4	520.2	936.2	1,305.6
5	117.4	219.8	421.4	318.4	521.0	430.6	702.4	1,771.8
6	217.6	363.8	284.0	382.8	471.6	540.8	971.6	1,151.6
Total time per arm (s)								
2	146.6	183.6	167.4	251.2	181.6	283.6	612.0	1,338.4
4	129.8	191.8	219.0	286.8	347.8	351.8	686.4	823.4
5	95.6	147.4	336.6	225.4	364.2	317.4	494.2	1,091.4
6	322.0	341.8	179.2	286.4	287.8	341.2	669.2	660.2
Entries per arm								
2	9.4	11.2	12.0	15.2	12.8	15.6	30.6	40.6
4	11.0	15.2	16.6	18.8	28.6	27.0	45.4	45.0
5	9.0	10.6	23.2	16.2	24.8	20.8	33.8	55.0
6	9.2	18.6	12.6	16.8	20.8	21.2	33.6	31.8
Nose pokes per entry								
2	18.22	19.42	19.08	21.32	14.62	21.16	22.46	49.42
4	16.70	16.98	17.74	18.74	18.38	19.48	20.70	29.34
5	13.36	20.36	18.06	19.72	21.24	20.86	20.88	32.20
6	23.60	19.56	22.70	22.68	22.74	25.54	29.16	36.14
Time per entry (s)								
2	15.44	16.28	13.96	16.50	14.06	18.34	20.16	33.60
4	11.76	12.64	13.14	15.54	12.20	13.28	15.18	18.52
5	10.70	13.86	14.48	13.90	14.72	15.32	14.62	19.80
6	34.48	17.84	14.36	17.08	14.06	16.20	20.28	20.94

Accesion For
NTIS CRA&I
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Unannounced
Justification
By
Distribution /
Availability Codes
Dist | Avail and / or Special
A-1 | 20