

*PROCUREMENT TIME AS A DETERMINANT OF
MEAL FREQUENCY AND MEAL DURATION*

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Foraging involves the expenditure of both time and effort in the acquisition of food; animals typically modify their meal patterns so as to reduce these expenditures or costs. The contribution of time, as compared with effort, to the overall cost perceived by an animal is not known. We investigated the effect of foraging time as a cost independent of effort by measuring the meal patterns of rats living in a laboratory foraging simulation in which they earned all their daily intake. They pressed a bar once to initiate an interval (procurement interval) leading to the presentation of a large cup of food from which they could eat a meal of any size. As the length of the interval increased from 1 s to 46 hr, meal frequency decreased regularly. Meal size increased in a compensatory fashion, and total daily intake was conserved through an interval of 23 hr. The changes in meal frequency occurred because of changes in the rat's latency to bar press after each meal. The functions relating meal frequency and size to the procurement interval were of the same shape as those seen when cost is the completion of a bar-press requirement, which entails the expenditure of both effort and time. When the bar-press requirement was increased to 10, meal frequency was reduced, but time and effort did not appear to simply add together in the rat's perception of cost. These data reveal that time is perceived to be a cost by rats foraging in this laboratory environment. These results suggest that the time parameters of foraging are different from those of consumption.

Key words: foraging, currency, time cost, free feeding, reinforcement delay, rats

A central problem for any theory of optimal foraging is the specification of the "currency." Currency is the dimension of foraging cost (e.g., time or energy) to which the animal attends. Moreover, it is the metric used to compare alternative foraging strategies. According to classic foraging theory, foraging decisions should maximize profitability, defined as the net energy gained per unit time. This definition suggests at least two possible currencies: effort and time (Schoener, 1971, 1987). Classic models (Emlen, 1966; MacArthur & Pianka, 1966; Schoener, 1971) assumed that time spent foraging was primary; therefore, foraging time should be minimized by an optimally foraging animal.

Collier (1983) and his colleagues (Collier, Hirsch, & Kanarek, 1977; Collier & Johnson, 1990; Collier & Rovee-Collier, 1981) have shown that as the number of bar presses or wheel turns required to procure unrestricted access to food increases, meal frequency decreases, and meal duration and meal size in-

crease in a compensatory fashion, conserving daily intake. The reduction in meal frequency has been interpreted to be a tactic that reduces foraging cost, because the procurement cost is paid less often. There are at least three possible cost currencies that may be responsible for these observed changes in meal patterns: (a) effort (i.e., the physical work expended in completing individual responses of a ratio requirement or the cumulative physical work expended across the ratio requirement), (b) numerosity (i.e., the number of responses), and (c) time. The rate at which rats bar press (i.e., approximately 30 bar presses per minute) or run in a wheel (i.e., approximately 15 turns per minute) during procurement is unaffected by the size of the response requirement; thus, time, effort, and numerosity have been confounded in these studies (Collier, Kaufman, Kanarek, & Fagen, 1978).

The present study investigated time alone as a foraging cost. We manipulated procurement time independently of numerosity and effort by withdrawing the bar following a single response and imposing a delay between the instrumental response and access to a cup of food. At the end of the meal the cup was withdrawn and the bar was reinserted. If time is a currency of foraging cost, then as the pro-

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urement time increases, meal frequency should decrease and meal size should increase to maintain daily intake.

METHOD

Subjects and Apparatus

Six male 8-week-old Sprague-Dawley rats were individually housed in double-sized stainless steel cages (41 cm by 23 cm by 19 cm) located in a temperature-controlled room (22 °C) with lights on from 8:00 a.m. to 8:00 p.m. daily. The rats lived in these cages continuously, except for a daily maintenance period of approximately 60 min starting at 9:15 a.m. during which they were weighed, food and water were replenished, and the apparatus was cleaned and tested.

Each cage was equipped with a running wheel, a 100-ml drinking tube, and a feeder tunnel giving access to a food cup filled each day with 160 g of Purina® ground rat chow. A cam-operated arm moved the food cup up to and away from the mouth of the feeder tunnel. Each feeder tunnel was fitted with an opaque Plexiglas door that covered the mouth of the tunnel when the cup was moved away from the mouth, preventing the animal from reaching the food. A retractable T-shaped bar (BCS, Inc.) was located next to the feeder tunnel. A response required 0.35 N applied through a throw of 15 mm. A microswitch monitored wheel turns, and a photocell monitored the presence of the rat in the feeder tunnel.

Procedure

The rats were trained to eat from the food cup for 3 days, during which the food cup was alternately raised and lowered for 30-min intervals. Baseline feeding patterns were then recorded with the food cup continuously raised for 10 days, giving the rat free access to food. The bar was absent during this training phase. The bar was then installed, and access to the food was contingent on completion of one bar press. Immediately following the bar press, the bar was withdrawn, and the procurement interval began. The length of the interval was the procurement cost. At the end of the interval, the food cup was raised and the rat could eat a meal of any size. A meal was defined as at least one feeder tunnel entry while the cup was raised; a meal ended

when the rat remained out of the feeder tunnel for 10 consecutive minutes. At that time, the food cup was lowered and the bar was extended. This meal-ending criterion was established according to log survivorship functions of interfeeding intervals (Collier, Johnson, CyBulski, & McHale, 1990). To begin another meal, the rat again needed to complete the bar-press requirement and wait for the procurement interval to elapse. If the rat procured access to the food cup but did not enter the tunnel, the cup was lowered after 10 min.

There were two experimental phases. In Phase 1, the bar-press requirement was one throughout. The procurement interval began at 0 s, was increased to 5 s, and then was doubled progressively up to 163,840 s (about 46 hr), for a total of 17 procurement intervals. For ease of data presentation, the interval lengths will be referred to in minutes or hours that approximate their actual length. The intervals were first presented in ascending order; then every fourth interval (0 min, 0.33 min, 3 min, 21 min, 3 hr, 23 hr, and 46 hr) was presented again in ascending order. These intervals correspond to the time rats have actually spent completing ratio requirements ranging from 1 to 10,240 in previous studies in our laboratory. For example, rats take approximately 3 min to complete a ratio of 80, 20 min to complete a ratio of 640, and 6 hr to complete a ratio of 10,240. These seven intervals were then presented in a random order. Each rat was exposed to a different random order. In Phase 2, the bar-press requirement was increased from 1 to 10 to allow measurement of the bar-press rate, and four intervals (0 min, 3 min, 21 min, and 23 hr) were presented in a random order. Each interval was in effect for 7 days or until there had been no obvious trend in any behavioral measure and no loss of body weight for at least 6 days. If a rat's weight dropped below 80% of its previously stable weight on any schedule, the rat's data were not included in the analysis for that schedule and it was not exposed to longer schedules.

Data Analysis

The 1st day of any schedule was not used in the analysis. Once body weight and daily food intake were stable, the next 6 days of exposure to a schedule were analyzed. Some

days were excluded due to occasional equipment failures. We recorded daily food intake and meal frequency and calculated average meal size. For each meal we recorded "meal time" (the total time that the food cup was raised, excluding the 10-min meal-ending criterion period) and "eating time" (the cumulative time that the rat was in the feeder tunnel while the cup was raised). The average consumption rate (in grams per minute) was calculated as daily intake divided by daily eating time. The intermeal interval was divided into two parts: the bar-press latency (the time from the withdrawal of the food cup at the end of a meal until the rat pressed the bar for the next meal) and the procurement interval (the time from the bar press until the cup came up). Although the food cup was lowered and out of the rat's reach during intermeal intervals, the rat could still enter the feeder tunnel at any time. These feeder tunnel entries outside of meals were recorded as "tunnel activity." The distributions of wheel running and tunnel activity were analyzed with respect to the bar press and arrival of the food cup.

In Phase 2, the local bar-press rate was calculated as total number of bar presses separated by 30 s or less divided by the sum of the interresponse intervals between those bar presses. The occurrence of wheel running and tunnel activity during the interval between the first and tenth bar presses and during an equivalent interval preceding the first bar press was compared.

The effect of procurement interval length was evaluated using one-way analysis of variance (ANOVA) for repeated measures with $\alpha = .05$ and post hoc Newman-Keuls tests. Each phase was analyzed separately. In Phase 1, some intervals were presented more than once. For these intervals, the data first were analyzed separately for each exposure. Because there were no statistically significant differences between exposures (i.e., no change in performance), the values shown here are means over all exposures. Data were also analyzed separately for the light and dark phases of the diurnal cycle, but, because the effects were the same in both phases, the values presented are means over the entire 23-hr period. For clarity of presentation, the figures show only data from the seven selected intervals that were presented more than

once. Rat 5 fell below the weight-loss criterion and did not complete the 23-hr and 46-hr conditions.

RESULTS

For all rats, daily number of meals (Figure 1) was a linear, decreasing function of the log procurement interval, Phase 1: $F(4, 20) = 9.04$, $p < .05$; Phase 2: $F(2, 10) = 30.5$, $p < .05$. However, in Phase 2, when the bar-press requirement was 10, the rats took an average of only 5.5 meals at a procurement interval of zero, in contrast to the mean of 9.5 meals per day they took in Phase 1, and the rate of decrease in meal frequency across the procurement intervals was slower in Phase 2.

Meal length (Figure 2) increased as a function of increasing procurement interval, Phase 1: $F(4, 20) = 31.9$, $p < .05$; Phase 2: $F(2, 10) = 8.05$, $p < .05$. Throughout the 23-hr procurement interval, the increase in meal duration compensated for the decrease in meal frequency, and daily meal time was constant.

Similarly, the amount of food consumed per meal (Figure 3) increased as the procurement interval increased up to 23 hr, Phase 1: $F(4, 20) = 36.1$, $p < .05$; Phase 2: $F(2, 10) = 18.8$, $p < .05$. At this point, the rats were eating an average of about 23 g per meal, and meals lasted approximately 53 min. Meals were no larger at the 46-hr interval. The consumption rate remained constant over the shorter procurement intervals but started to decrease at the 6-hr interval, Phase 1: $F(7, 32) = 17.4$, $p < .05$; Phase 2: $F(3, 14) = 30.26$, $p < .05$ (Figure 4).

Daily food intake (Figure 5) was conserved throughout the 23-hr procurement interval during Phase 1, and the rats showed normal growth. However, at the 46-hr procurement interval, daily meal time was reduced by 35% and daily intake was reduced by 60% to an average of 10 g per day. Body weight also fell at the 46-hr procurement interval to about 90% of the previously stable weight. This new weight level was stable throughout the 46-hr condition. In Phase 2, daily intake was conserved until the 23-hr interval, when it was maintained at 15 g.

The intermeal interval (Figure 6) lengthened as the procurement interval increased, Phase 1: $F(4, 20) = 31.6$, $p < .05$; Phase 2:

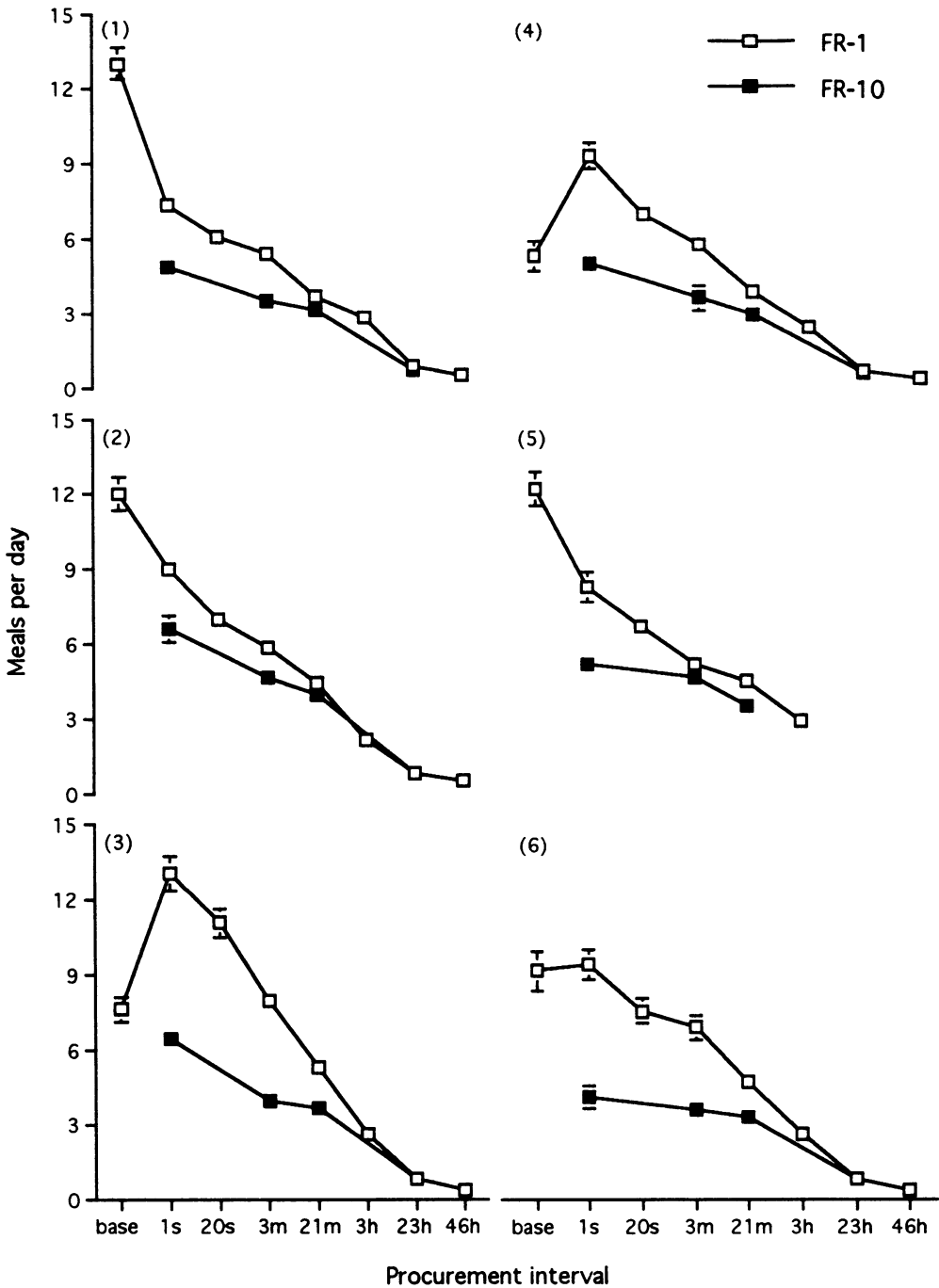


Fig. 1. Meals per day as a function of the procurement interval (shown on an approximate log scale) for each rat when the bar-press requirement was 1 (Phase 1) and 10 (Phase 2). The "base" condition represents data recorded when food was continuously available. Error bars are the standard error of the mean. The designation "1 s" on the x axis actually represents the 0-s procurement delay.

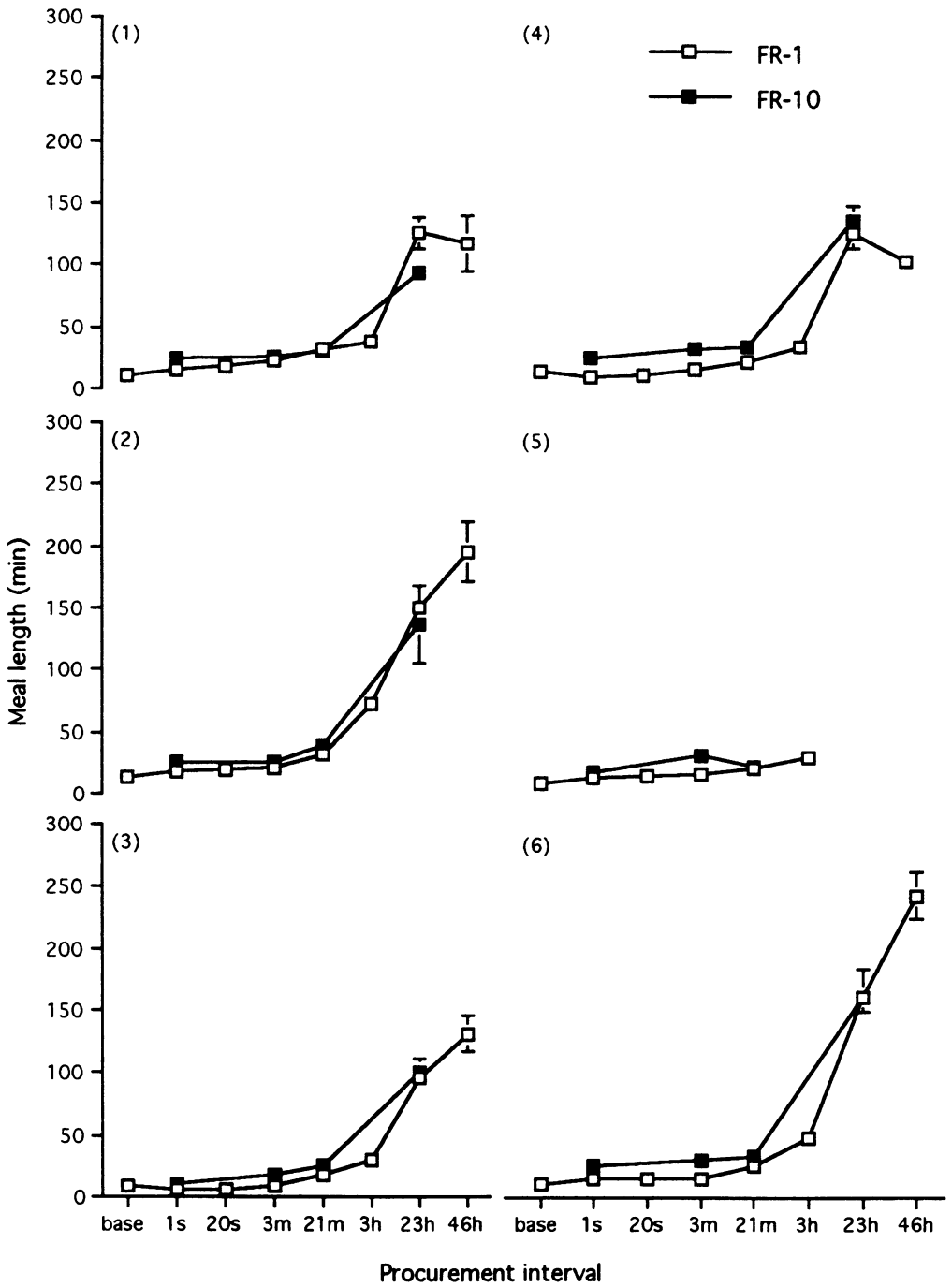


Fig. 2. Meal length as a function of the procurement interval (shown on an approximate log scale) for each rat when the bar-press requirement was 1 (Phase 1) and 10 (Phase 2). Features of the x axis are as in Figure 1.

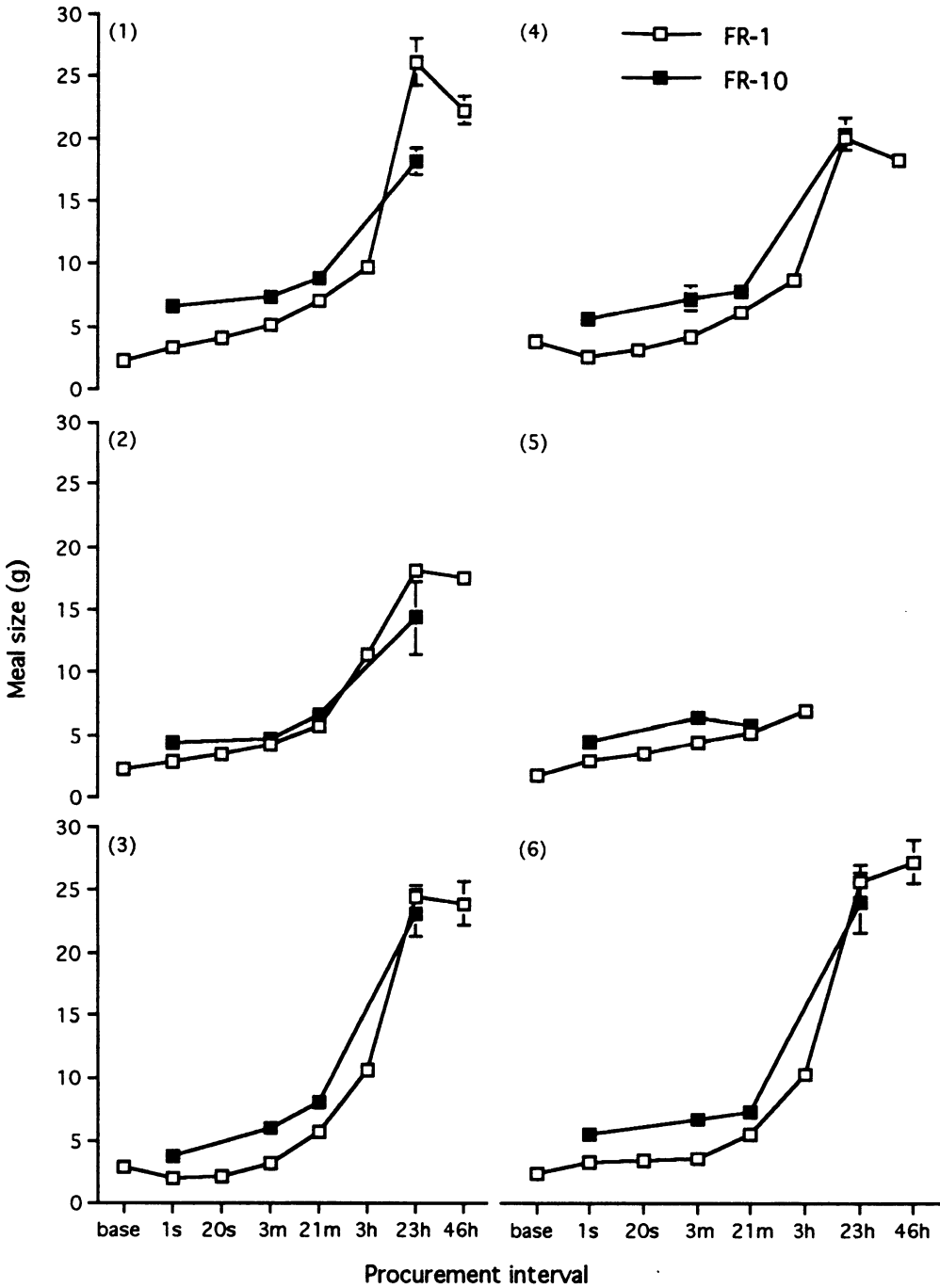


Fig. 3. The amount of food consumed per meal as a function of the procurement interval (shown on an approximate log scale) for each rat. Features of the x axis are as in Figure 1.

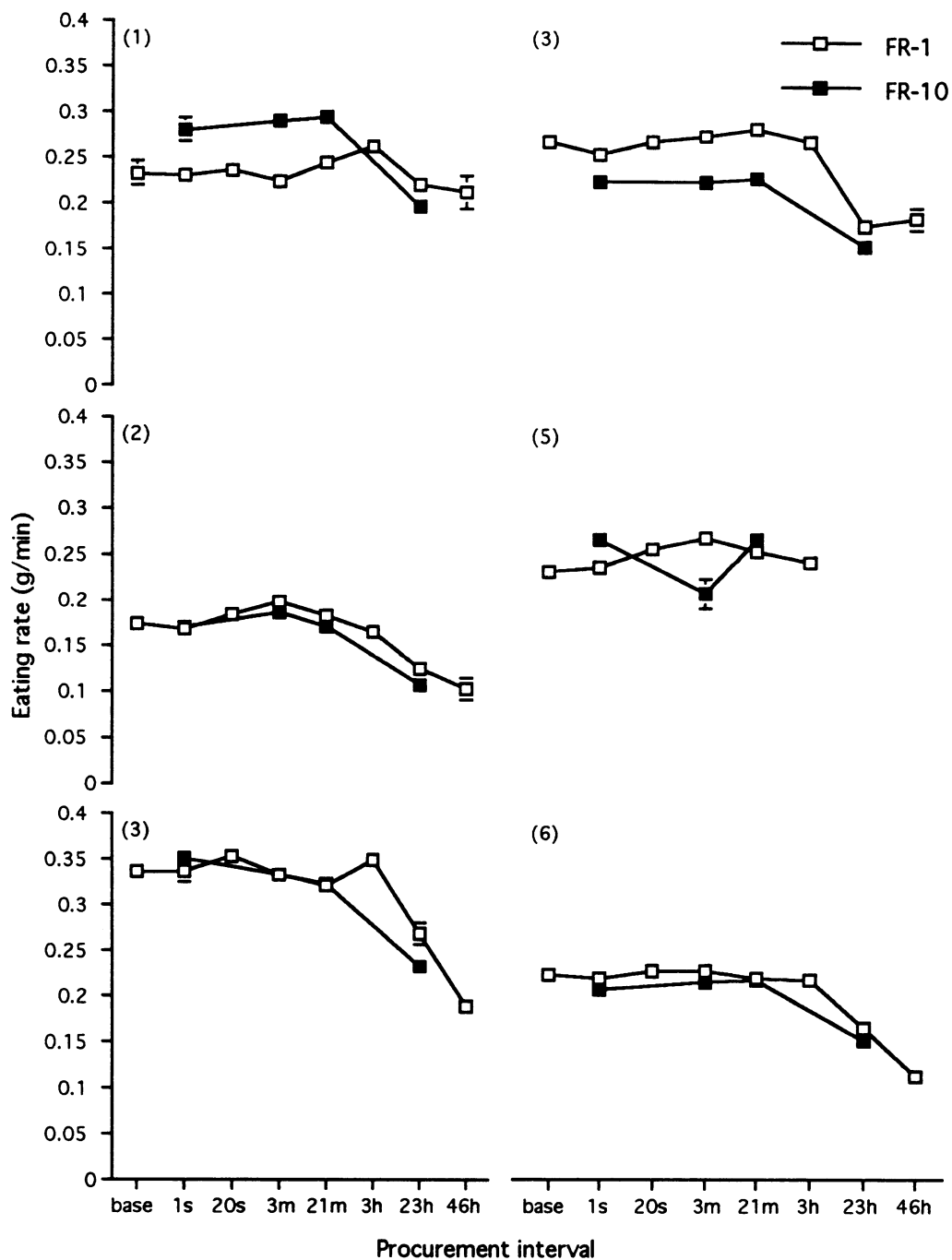


Fig. 4. The rate of eating as a function of the procurement interval (shown on an approximate log scale) for each rat. Features of the x axis are as in Figure 1.

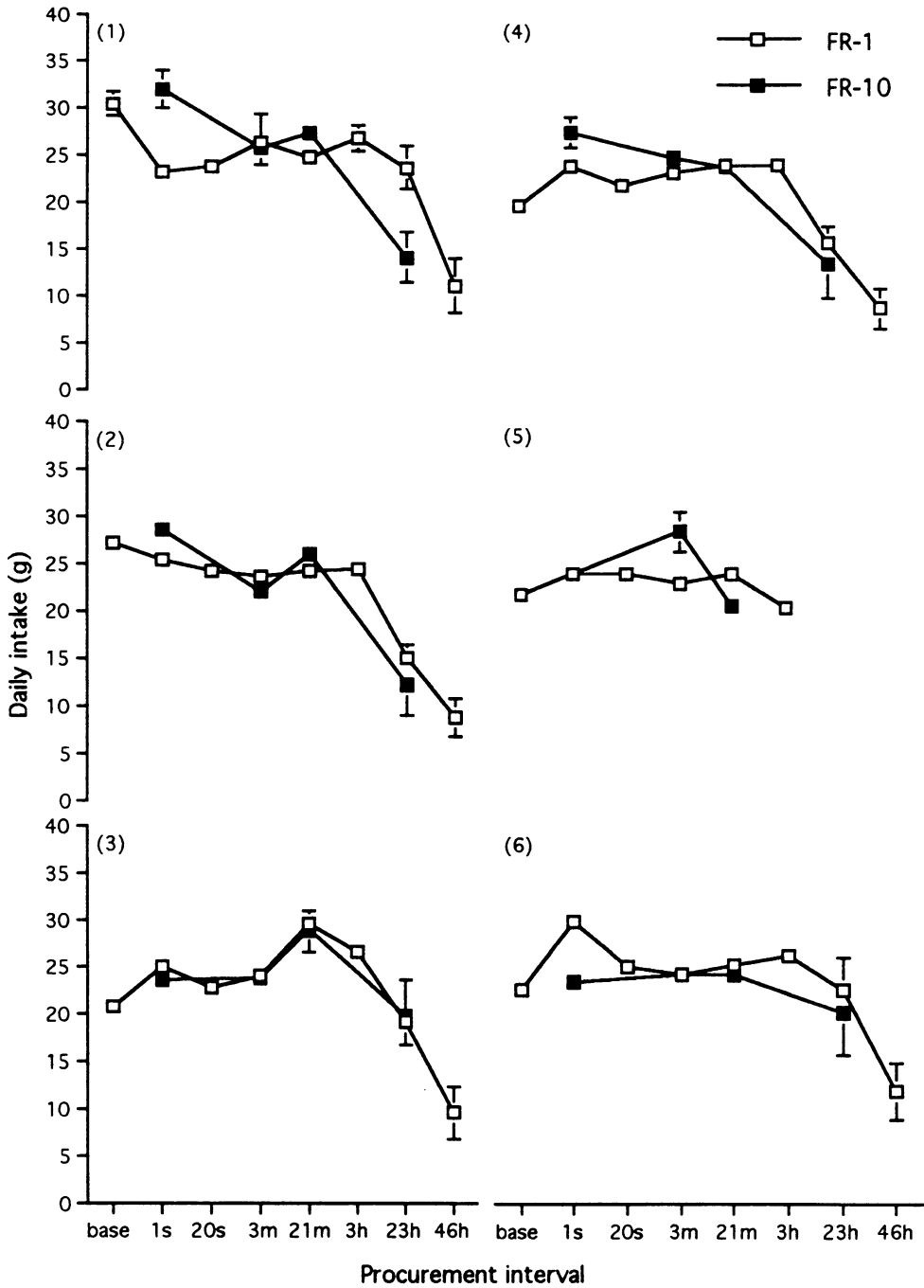


Fig. 5. Daily intake as a function of the procurement interval (shown on an approximate log scale) for each rat when the bar-press requirement was 1 (Phase 1) and 10 (Phase 2). Features of the x axis are as in Figure 1.

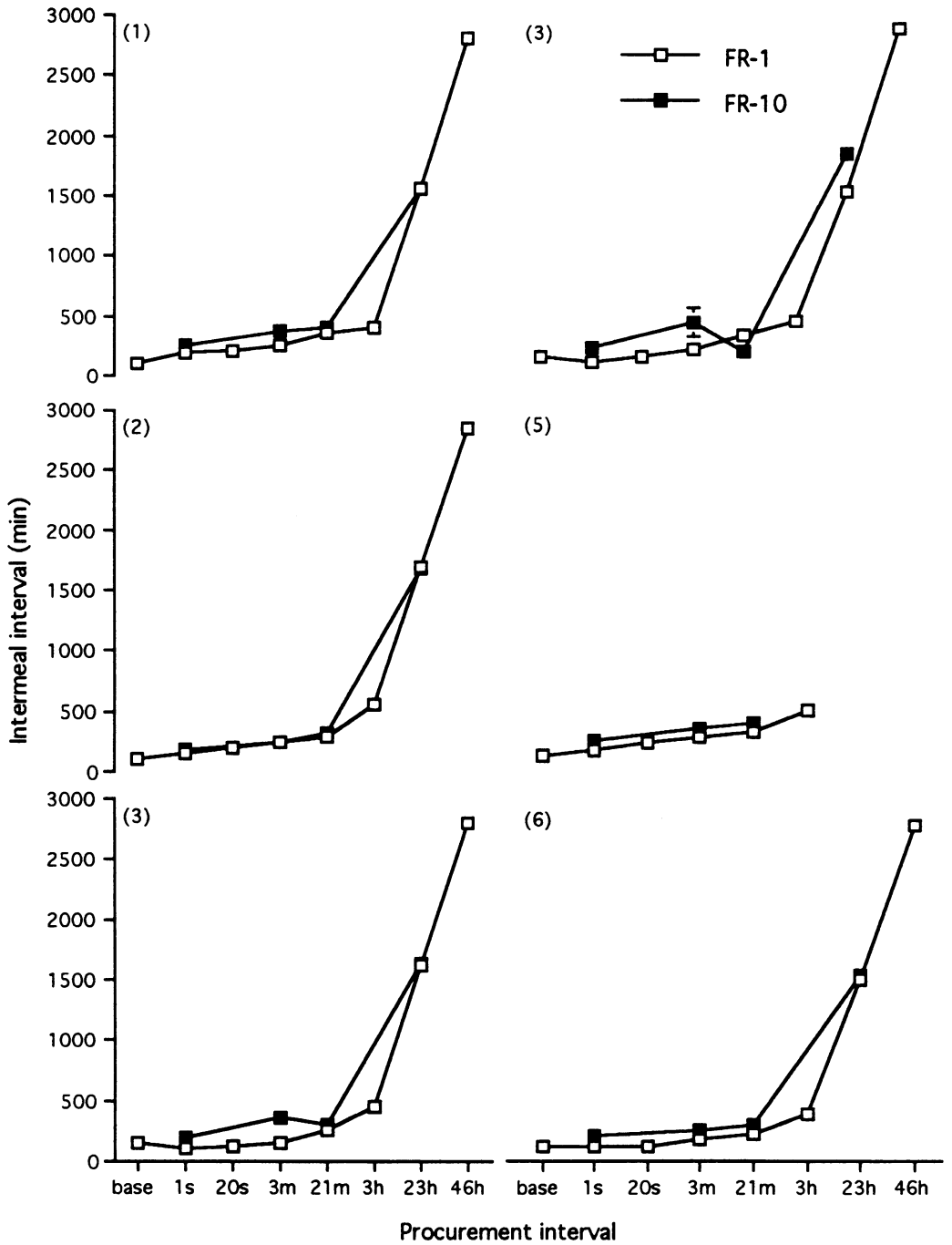


Fig. 6. The intermeal interval plotted as a function of the procurement interval (shown on an approximate log scale) for each rat. Features of the x axis are as in Figure 1.

$F(2, 10) = 6.11, p < .05$. If the rats had maintained a constant bar-press latency, the inter-meal interval would have increased anyway as the procurement interval increased. However, the rats did not maintain a constant latency (Figure 7). In Phase 1, the group-mean latency increased regularly from approximately 2 hr to 6 hr as the procurement interval increased to 85 min, but then the latency decreased as the procurement interval continued to increase, Phase 1: $F(6, 28) = 16.92, p < .05$. At the 46-hr procurement interval, the bar-press latency averaged about 1.5 hr. In Phase 2, 4 of 6 rats showed latency functions similar to those in Phase 1. However, variability of Rats 3 and 4 across and within intervals resulted in a lack of statistical significance in Phase 2, $F(3, 14) = 1.859, ns$.

Through a procurement interval of 3 hr in Phase 1, approximately 5% of procurement bar presses resulted in a feeder presentation when the rat did not enter the tunnel. The variability among rats in this behavior ranged from 0% to 50% of all feeder presentations at the shortest intervals. Beginning with the 6-hr procurement interval in Phase 1 and over all intervals in Phase 2, 100% of feeder presentations resulted in meals.

There was no statistically significant change in total daily wheel running or tunnel activity at any procurement interval. There were significant increases in wheel running, $F(4, 20) = 71.59, p < .05$, and tunnel activity, $F(4, 20) = 228.38, p < .05$, immediately preceding the bar press from the 0-s through the 3-hr procurement intervals. In Phase 2, a significantly higher percentage of wheel running, $F(1, 5) = 38.96, p < .05$, and tunnel activity, $F(1, 5) = 13.03, p < .05$, occurred prior to the 10th bar press than prior to the first bar press at all intervals.

DISCUSSION

The present study evaluated time as a possible currency of the cost of gaining access to food. The rats responded in the same way to explicit manipulations of time as they do to manipulations of number of bar presses (Collier & Johnson, 1990) or wheel-running requirements (Kanarek & Collier, 1979): As the procurement interval increased, meal frequency decreased and meal duration and size increased in a compensatory fashion, such

that daily food intake was constant. The change in meal frequency occurred before it was forced by the length of the procurement interval. The form of the meal-frequency function was the same as when cost is a bar-press ratio requirement: log linear. The reduction in meal frequency resulted in time savings. Compared to maintaining a constant meal frequency across all procurement intervals, our rats spent less daily time procuring access to food. These data indicate that time is a currency of foraging cost.

Foraging costs are paid during the location and procurement of food resources. There are also costs associated with the actual consumption of food, and support for time as a possible currency of cost can also be found in studies of food consumption. Skinner (1938) suggested that discriminative control of fixed-ratio (FR) performance for food could arise from the number of responses (i.e., the numerosity) or the time taken to complete those responses. This dissociation has been examined using simple reinforcement schedules. Using FR and fixed-interval (FI) schedules, Neuringer and Schneider (1968) found that response latencies were linearly correlated with interreinforcement time and were not correlated with interreinforcement responses. They and others (Killeen, 1969; Zeiler, 1977) have proposed that responding may be controlled by interreinforcement time rather than by the number of responses emitted.

The discriminative properties of schedules have also been examined using conditional discrimination tasks. Lydersen and Crossman (1974) found that accuracy of side-key choice was disrupted as the duration of a blackout between responses was increased, suggesting that time rather than number of responses controlled responding. However, in these studies, operanda were not removed during blackouts. Thus, subjects were able to respond during the blackouts, even though response frequency was lower than nonblackout responding. Other research (Wilkie, Webster, & Leader, 1979) has indicated that number of responses is a more important cost dimension for both time-based and number-based discriminations. Rilling (1967) trained pigeons to discriminate between FI and FR schedules. He found that number of responses was a better predictor of choice than

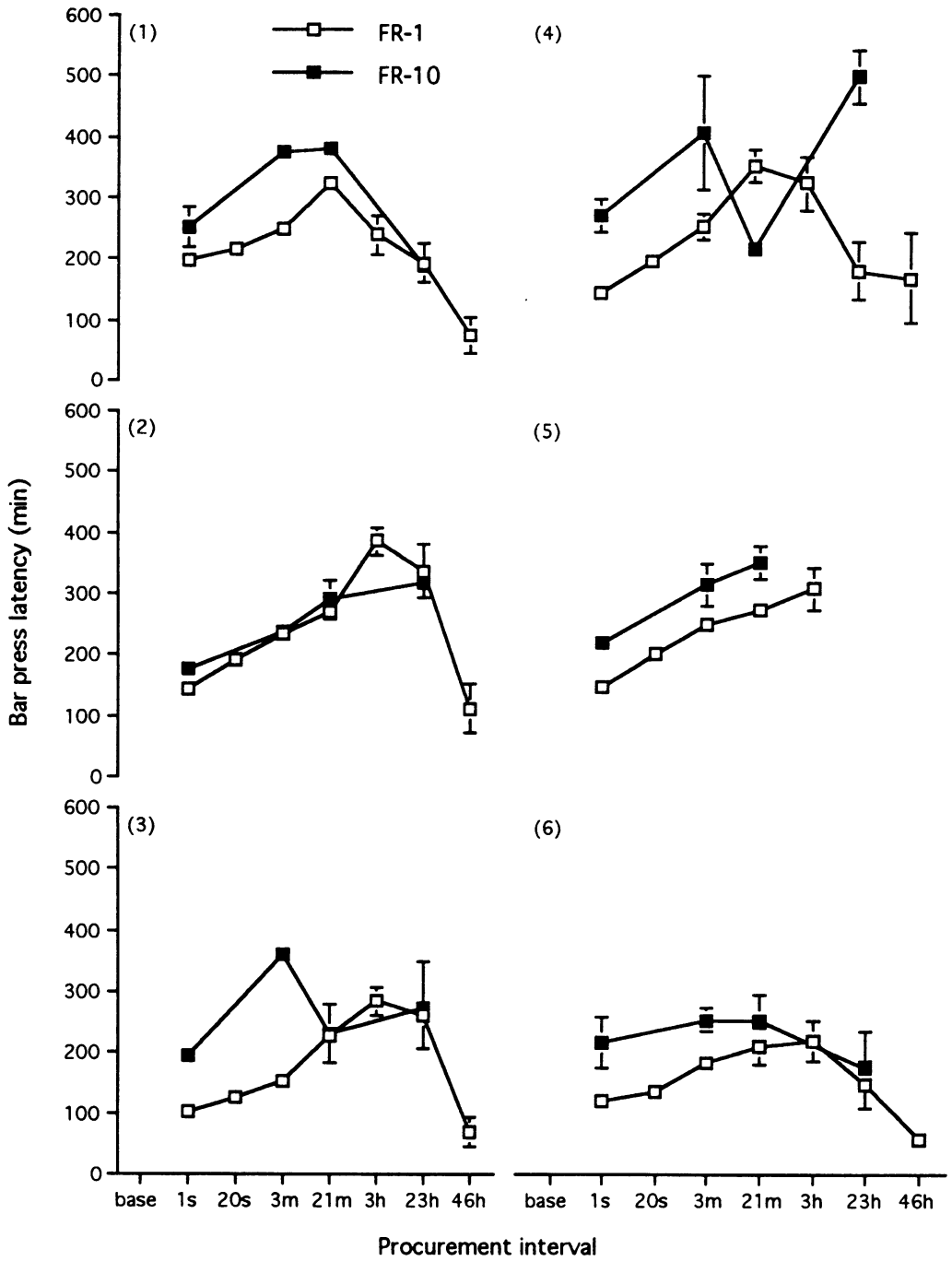


Fig. 7. The bar-press latency plotted as a function of the procurement interval (shown on an approximate log scale) for each rat. Features of the x axis are as in Figure 1.

duration of response runs for both types of schedules. More recently, Fetterman (1993) first trained subjects on a number-based discrimination and then transferred them to an equivalent time-based discrimination. He concluded that choices were based on both duration and number of responses emitted.

Bauman (1991) measured food intake in rats that pressed a bar for pellets on either FR or FI schedules. The interpellet interval in each FI schedule was equivalent to the average time between the first bar press and the delivery of a food pellet in each FR schedule. He found that as the bar-press requirement or the equivalent interpellet interval increased, daily intake decreased by the same amount. Because the rats made more bar presses per pellet during FR schedules than during FI schedules but experienced the same interpellet interval, these data suggest that the reduction in intake that accompanies larger FR requirements is due to increased time taken to complete the responses (Bauman, 1991). Zeiler (1993) has proposed that sensitivity to time or effort may depend upon ecological and motivational factors such as limited resource availability and deprivation level.

Finally, the importance of time as a currency of consumption cost is suggested by rats' choices among available sources of food. We have found the relative rate of eating (grams per minute) or drinking (milliliters per minute) within a patch to be an excellent predictor of relative patch exploitation when more than one patch is available. The relative time-based cost was a better predictor than the response-based cost of relative choice, bout size, and daily intake at each patch (Collier, Johnson, Borin, & Mathis, 1994; Johnson & Collier, 1987, 1989, 1991).

Although these data provide support for time as a currency, they are based on consummatory behavior, which has a different function than foraging behavior. Studies of consumption and foraging differ in part due to the time frame of analysis (Collier & Johnson, 1990). In the classic consumption paradigm, costs are imposed between the ingestion of individual portions (e.g., 45-mg pellets) of food, delaying each "bite" by seconds or minutes. Animals respond to increasing delays between bites by responding faster, counteracting the decrease in the rate of calorie flow

within the short time frame of a meal (Collier, Johnson, Hill, & Kaufman, 1986; Hursh, 1980; Johnson & Collier, 1987, 1989, 1991). In a foraging paradigm, costs are imposed between initiating procurement and initiating ingestion, causing delays of minutes, hours, or days. In this case, animals do not respond to increasing delays by responding faster; instead, response rate is constant under a wide variety of conditions (Collier & Johnson, 1990). They reduce meal frequency, counteracting the increase in foraging time over the long time frame of an entire day. The time spent procuring access to a meal and the time spent consuming each piece of food within a meal are different variables, and each has unique behavioral effects.

Even though our experiment was not specifically designed to investigate delay of reinforcement, one of the most interesting aspects of the present data is that the bar-press response was maintained at long procurement intervals, that is, long intervals between response and reinforcement. Traditional theories of reinforcement (Hull, 1943; Skinner, 1938) predict that the performance of a reinforced instrumental response should decay as the interval between response and reinforcement increases. To provide an additional measure of performance, we increased the bar-press requirement to 10 in Phase 2. The fact that the bar-press rate did not decrease as procurement interval increased indicates that even at the longest intervals there was no decrement in instrumental performance. Our data thus raise a number of questions: Is there a contingent relationship? If so, is there some bridging mechanism or mechanisms between response and reinforcement? If not, does this represent a different class of contingency that is not constrained by the usual time parameters?

First, was responding maintained by a contingent relation between the bar-press response and access to food? An alternative explanation is that operant-level bar pressing was maintained throughout, perhaps as a manifestation of general activity, and resulted in adventitious meals. Several arguments can be advanced against this hypothesis. Nonreinforced spontaneous responding first peaks and then decays over time (Premack & Collier, 1962). This was clearly not the case in the present study. Further, if bar pressing

were a spontaneous operant, one would expect the bar-press latencies and meal sizes to be highly variable and uncorrelated to the length of the procurement interval. This was also not the case: Both latency and meal size were systematically and significantly related to the length of the procurement interval. Moreover, recall that the procurement intervals were sometimes presented in a random order, and the rats' bar pressing increased at shorter intervals and decreased at longer intervals. Operant-level responding typically only decreases over time (Premack & Collier, 1962).

It might be argued that decay of operant-level responding was prevented because the bar was withdrawn following the bar press. However, this explanation seems unlikely given the linear decrease in meal frequency, the consistency of the local bar-press rate in Phase 2 over all procurement intervals, and, most importantly, the pattern of change in the bar-press latency. The rats did not press the bar as soon as it appeared at the end of the meal. If they had done so, they would have earned as many as 75 meals a day at the shortest procurement intervals. The bar-press latency increased up to procurement intervals of 1.5 hr; thus, lengthening of the intermeal interval was due almost entirely to the rat's waiting longer to press the bar after a meal. This trend toward lengthening the bar-press latency did not continue at procurement intervals longer than 1.5 hr, even though meal frequency continued to decrease. Rather, the bar-press latency decreased as the cost increased. If this decrease in latency had not occurred, the intermeal interval would have gotten longer faster than it did, and meal frequency would have decreased faster than it did. For example, at the 46-hr procurement interval, the decrease in the bar-press latency enabled the rat to eat once every 2 days, compared to once every 3 days had the decrease not occurred. Thus, it was the rat's behavior, not the imposed cost, that was responsible for the observed meal frequencies. The bitonic changes in the latency to respond suggest that the rats were actively controlling the length of the intermeal interval and, thus, their meal frequency.

Can the apparent sustained contingency between the bar press and food presentation at long procurement intervals be explained

in terms of an extension of some classical learning phenomena, or do the usual parameters of delay of reinforcement not hold in this paradigm? Although we believe the latter to be the case, we will consider several more traditional potential accounts.

It has been argued that performance is a function of the size of the reinforcement, and that increasing the magnitude of reward maintains performance over increased delays between the instrumental response and the reinforcer (Collier & Myers, 1961; Mackintosh, 1974, 1983; Spence, 1956), although not over intervals as long as those reported here (Wolfe, 1934). If meals can be construed as reinforcers, responding may be maintained at longer intervals because meals are larger at those intervals. However, meal size decreased at the 46-hr interval, and there was no decrement in responding. It should also be noted that in Phase 2, there was no increment in response rate when meals increased in size. These findings suggest that there is no effect of delay on performance when the rat controls meal size (Collier & Rovee-Collier, 1981).

One could also argue that the presence of the bar may have been a Pavlovian negative conditional stimulus indicating that food was not available, and the absence of the bar from the cage was a Pavlovian positive conditional stimulus indicating that food was available (Hearst & Franklin, 1977; Zener, 1937). Thus, the rat may have pressed the bar to enter a context in which food was available or to leave a context in which food was not available. In this case, the delay between the bar press and the food is inconsequential, because there are Pavlovian relationships between the different contexts and food that supersede any instrumental relationship between the bar press and the food. Even animals that have just eaten have been reported to show differential responding to conditioned stimuli that signal either the absence or presence of food (Davey & Cleland, 1984; Rudenko, 1984; Weingarten & Martin, 1989; Wise & Raptis, 1985). If our rats were merely changing contexts, one would expect them to have pressed the bar as soon as the bar was extended into the cage, but they did not. Moreover, if the rats were only changing context, they should have made more tunnel entries during the procurement interval than

during the intermeal interval. This did not occur until procurement intervals of 6 hr and more when the rats spent 50% or more of the day in the procurement interval.

The contiguity between bar withdrawal and food presentation at the short procurement intervals may have turned the bar withdrawal into a conditioned reinforcer, thus conferring associative strength to the bar. Again, the delay between the bar press and food would be inconsequential, because the bar withdrawal itself is reinforcing and predicts food presentation (Cohen, Calisto, & Lentz, 1979). However, if the bar withdrawal were a conditioned reinforcer, one might expect bar presses to result in a feeder presentation when the rat did not enter the tunnel. This behavior was seen in only 5% of procurement bar presses and disappeared in procurement intervals longer than 3 hr. Also, as the interval between the bar withdrawal and food presentation increased, one might expect the acquired reinforcing and predictive properties of bar withdrawal to extinguish because it was no longer contiguously paired with food (Bersh, 1951).

Alternatively, bar withdrawal may not have acquired reinforcing properties of its own but rather may have been a marking stimulus for the bar press. This would have enabled the rats to distinguish the operant response (i.e., the bar press) from the other responses (i.e., wheel running and tunnel entries) made during the interval (Lieberman, McIntosh, & Thomas, 1979). The marking hypothesis has yet to be systematically evaluated over the intervals presented here; thus, the potential effectiveness of marking as a bridge over these longer intervals is not known. However, the continued importance of bar withdrawal is suggested by the fact that in Phase 2 both wheel running and tunnel activity were concentrated in the period prior to the 10th bar press, which was immediately followed by withdrawal of the bar, rather than prior to the first bar press.

Foraging differs from consumption in that foraging involves the discovery of resources that are discontinuously present, whereas consumption involves the ingestion of immediately available food. Consumption is maintained by continuous ingestion (i.e., reinforcement), whereas foraging is maintained by occasional encounters that may be widely

separated in time, location, effort, and probability. These differences in function might lead one to expect that the time parameters for establishing contingencies may be very different for the two categories of behavior (Collier, 1983; Collier & Rovee-Collier, 1983; Zeiler, 1991, 1992). Another example of a learning paradigm that differs in function is conditioned taste aversion. Here contingency is established over long interstimulus intervals (e.g., 3, 6, 12, and 24 hr) (Revusky & Garcia, 1970; Smith & Roll, 1970). We propose that responding in foraging is not a simple case of classical operant learning. The behavior involved in discovering and procuring access to food and the mechanisms responsible for the regulation of daily intake may be fundamentally different from the behavior and mechanisms responsible for consumption that have been examined in more common operant settings.

REFERENCES

- Bauman, R. (1991). An experimental analysis of the cost of food in a closed economy. *Journal of the Experimental Analysis of Behavior*, *56*, 33–50.
- Bersh, P. J. (1951). The influence of two variables upon the establishment of a secondary reinforcement for operant responses. *Journal of Experimental Psychology*, *41*, 62–63.
- Cohen, S. L., Calisto, G., & Lentz, B. E. (1979). Separating reinforcing and discriminative properties of brief-stimulus presentations in second-order schedules. *Journal of the Experimental Analysis of Behavior*, *32*, 149–156.
- Collier, G. H. (1983). Life in a closed economy: The ecology of learning and motivation. In M. D. Zeiler & P. Harzem (Eds.), *Advances in analysis of behavior* (Vol. 3, pp. 223–274). New York: Wiley.
- Collier, G., Hirsch, E., & Kanarek, R. (1977). The operant revisited. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 28–52). New York: Prentice-Hall.
- Collier, G., & Johnson, D. F. (1990). The time window of feeding. *Physiology and Behavior*, *48*, 771–777.
- Collier, G., Johnson, D. F., Borin, G., & Mathis, C. E. (1994). Drinking in a patchy environment: The effect of the price of water. *Journal of the Experimental Analysis of Behavior*, *62*, 169–184.
- Collier, G., Johnson, D. F., Cybulski, K. A., & McHale, C. (1990). Activity patterns in rats as a function of the cost of access to four resources. *Journal of Comparative Psychology*, *104*, 53–65.
- Collier, G. H., Johnson, D. F., Hill, W. L., & Kaufman, L. W. (1986). The economics of the law of effect. *Journal of the Experimental Analysis of Behavior*, *46*, 113–136.
- Collier, G., Kaufman, L. W., Kanarek, R., & Fagen, J. (1978). Optimization of time and energy constraints

- in the feeding behavior of cats: A laboratory simulation. *Carnivore*, 1, 34-41.
- Collier G. H., & Myers, L. (1961). The loci of reinforcement. *Journal of Experimental Psychology*, 61, 57-66.
- Collier, G. H., & Rovee-Collier, C. K. (1981). A comparative analysis of optimal foraging behavior: Laboratory simulations. In A. C. Kamil & T. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches* (pp. 39-76). New York: Garland STPM Press.
- Collier, G. H., & Rovee-Collier, C. K. (1983). An ecological perspective of reinforcement and motivation. In E. Satinoff & P. Tietelbaum (Eds.), *Handbook of behavioral neurobiology: Motivation* (pp. 427-441). New York: Plenum.
- Davey, G. C., & Cleland, G. G. (1984). Food anticipation and lever-directed activities in rats. *Learning and Motivation*, 15, 12-36.
- Emlen, J. T. (1966). The role of time and energy in food preference. *American Naturalist*, 100, 611-617.
- Fetterman, J. G. (1993). Numerosity discrimination: Both time and number matter. *Journal of Experimental Psychology: Animal Behavior Processes*, 19, 149-164.
- Hearst, E., & Franklin, S. R. (1977). Positive and negative relations between a signal and food: Approach-withdrawal behavior to a signal. *Journal of Experimental Psychology: Animal Behavior Processes*, 3, 37-52.
- Hull, C. L. (1943). *Principles of behavior*. New York: Appleton-Century-Crofts.
- Hursh, S. R. (1980). Economic concepts for the analysis of behavior. *Journal of the Experimental Analysis of Behavior*, 34, 219-238.
- Johnson, D. F., & Collier, G. H. (1987). Caloric regulation and patterns of food choice in a patchy environment: The value and cost of alternative foods. *Physiology and Behavior*, 39, 351-359.
- Johnson, D. F., & Collier, G. (1989). Patch choice and meal size of foraging rats as a function of the profitability of food. *Animal Behavior*, 38, 285-297.
- Johnson, D. F., & Collier, G. (1991). The relationship between feeding rate and patch choice. *Journal of the Experimental Analysis of Behavior*, 55, 79-95.
- Kanarek, R. B., & Collier, G. (1979). Patterns of eating as a function of the cost of the meal. *Physiology and Behavior*, 23, 141-145.
- Killeen, P. (1969). Reinforcement frequency and contingency as factors in fixed-ratio behavior. *Journal of the Experimental Analysis of Behavior*, 12, 391-395.
- Lieberman, D. A., McIntosh, D. C., & Thomas, G. V. (1979). Learning when reward is delayed: A marking hypothesis. *Journal of Experimental Psychology: Animal Behavior Processes*, 5, 224-242.
- Lydersen, T., & Crossman, E. K. (1974). Fixed-ratio discrimination: Effects of response-induced blackouts. *Journal of the Experimental Analysis of Behavior*, 22, 547-551.
- MacArthur, R. H., & Pianka, E. R. (1966). On the use of a patchy environment. *American Naturalist*, 100, 603-610.
- Mackintosh, N. J. (1974). *The psychology of animal learning*. London: Academic Press.
- Mackintosh, N. J. (1983). *Conditioning and associative learning*. Oxford: Oxford University Press.
- Neuringer, A. J., & Schneider, B. A. (1968). Separating the effects of interreinforcement time and number of interreinforcement responses. *Journal of the Experimental Analysis of Behavior*, 11, 661-667.
- Premack, D., & Collier, G. H. (1962). Analysis of non-reinforcement variables affecting response probability. *Psychological Monographs*, 76, 1-20.
- Revusky, S. H., & Garcia, J. (1970). Learned associations over long delays. In G. H. Bower & J. T. Spence (Eds.), *The psychology of learning and motivation* (Vol. 4, pp. 1-84). New York: Academic Press.
- Rilling, M. (1967). Number of responses as a stimulus in fixed interval and fixed ratio schedules. *Journal of Comparative and Physiological Psychology*, 63, 60-65.
- Rudenko, L. P. (1984). The correlation of conditional and unconditional reflex components in conditioned reflex switching. *Zhurnal Vysshei Nervnoi Delatel'nosti*, 34, 1167-1169.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2, 369-404.
- Schoener, T. W. (1987). A brief history of optimal foraging ecology. In A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), *Foraging behavior* (pp. 5-76). New York: Plenum.
- Skinner, B. F. (1938). *The behavior of organisms: An experimental analysis*. New York: Appleton-Century-Crofts.
- Smith, J. C., & Roll, D. L. (1970). Trace conditioning with x-rays as an aversive stimulus. *Psychonomic Science*, 9, 11-12.
- Spence, K. W. (1956). *Behavior theory and conditioning*. New Haven, CT: Yale University Press.
- Weingarten, H. P., & Martin, G. M. (1989). Mechanisms of conditioned meal initiation. *Physiology and Behavior*, 45, 735-740.
- Wilkie, D. M., Webster, J. B., & Leader, L. G. (1979). Unconfounding time and number discrimination in a Mechner counting schedule. *Bulletin of the Psychonomic Society*, 13, 390-392.
- Wise, R. A., & Raptis, L. (1985). Effects of pre-feeding on food approach latency and food consumption speed in food deprived rats. *Physiology and Behavior*, 35, 961-963.
- Wolfe, J. B. (1934). The effect of delayed reward upon learning in the white rat. *Journal of Comparative and Physiological Psychology*, 17, 1-21.
- Zeiler, M. D. (1977). Schedules of reinforcement: The controlling variables. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 201-232). Englewood Cliffs, NJ: Prentice-Hall.
- Zeiler, M. D. (1991). Ecological influences on timing. *Journal of Experimental Psychology: Animal Behavior Processes*, 17, 13-25.
- Zeiler, M. D. (1992). On immediate function. *Journal of the Experimental Analysis of Behavior*, 57, 417-427.
- Zeiler, M. D. (1993). To wait or to respond. *Journal of the Experimental Analysis of Behavior*, 59, 433-444.
- Zener, K. (1937). The significance of behavior accompanying conditioned salivary secretion for theories of the conditioned response. *American Journal of Psychology*, 50, 384-403.

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APPENDIX

Feeding measures for individual rats.

Measure	Rat	Procurement interval											
		FR 1						FR 10					
		Baseline	1 s	20 s	3 min	21 min	3 hr	23 hr	46 hr	1 s	3 min	21 min	23 hr
Meals per day	1	13.00	7.33	6.06	5.39	3.71	2.88	0.91	0.50	4.86	3.50	3.17	0.78
	2	12.00	9.00	7.00	5.83	4.40	2.18	0.83	0.50	6.60	4.67	4.00	0.86
	3	7.63	13.05	11.06	7.94	5.35	2.61	0.79	0.40	6.43	4.00	3.67	0.86
	4	5.33	9.32	6.94	5.77	3.91	2.47	0.78	0.48	5.00	3.67	3.00	0.67
	5	12.17	8.23	6.69	5.20	4.50	2.87	0.86	0.44	5.17	4.60	3.50	
	6	9.20	9.45	7.61	6.95	4.77	2.70	0.86	0.44	4.17	3.67		0.83
Meal length	1	10.00	14.60	17.30	22.80	30.80	37.70	125.30	116.90	23.80	25.60	29.80	93.50
	2	13.20	17.30	19.20	21.30	32.20	72.50	149.30	195.00	26.00	25.30	38.80	136.80
	3	8.46	5.94	6.07	9.36	17.78	30.34	96.47	131.22	10.60	18.10	25.40	101.00
	4	14.80	10.60	12.30	15.80	22.60	34.10	126.10	103.20	25.10	33.70	35.00	136.20
	5	7.55	12.51	14.04	16.58	20.86	29.10	162.00	244.00	17.00	31.00	21.80	
	6	11.10	15.70	15.90	16.20	26.20	48.80	162.00	244.00	27.00	31.50	34.50	161.70
Daily intake	1	30.50	23.20	23.90	26.40	24.80	26.80	23.70	11.10	32.00	25.80	27.50	14.10
	2	27.13	25.31	24.25	23.67	24.13	24.32	15.00	8.80	28.60	22.00	26.00	12.30
	3	20.88	25.00	22.75	23.94	29.53	26.61	19.28	9.55	23.60	23.80	29.00	19.90
	4	19.67	23.89	21.83	23.29	23.91	24.05	15.63	8.71	27.40	24.80	23.80	13.50
	5	21.00	23.20	23.20	22.20	23.20	19.60	22.60	11.90	23.20	27.80	19.80	
	6	22.60	29.80	25.10	24.30	25.20	26.20	22.60	11.90	23.50	24.30	24.30	20.20
Meal size	1	2.32	3.30	4.04	5.10	6.99	9.73	26.16	22.25	6.64	7.42	8.79	18.14
	2	2.30	2.87	3.51	4.20	5.69	11.35	18.09	17.60	4.41	4.70	6.60	14.33
	3	2.83	1.98	2.14	3.10	5.65	10.58	24.45	23.88	3.71	5.98	8.13	23.17
	4	3.92	2.65	3.26	4.30	6.35	8.89	20.10	18.30	5.66	7.40	7.94	20.43
	5	1.75	2.93	3.56	4.44	5.26	7.02	20.10	18.30	4.51	6.38	5.85	
	6	2.53	3.43	3.54	3.69	5.68	10.55	25.91	27.40	5.67	6.82	7.45	24.20
Eating rate	1	0.23	0.23	0.24	0.23	0.25	0.26	0.22	0.21	0.28	0.29	0.30	0.20
	2	0.18	0.17	0.19	0.20	0.18	0.16	0.13	0.10	0.17	0.19	0.17	0.11
	3	0.34	0.34	0.35	0.33	0.32	0.35	0.27	0.19	0.35	0.33	0.32	0.23
	4	0.27	0.25	0.27	0.27	0.28	0.27	0.17	0.18	0.22	0.22	0.23	0.15
	5	0.23	0.24	0.26	0.27	0.25	0.24	0.17	0.11	0.27	0.21	0.27	0.15
	6	0.23	0.22	0.23	0.23	0.22	0.22	0.17	0.11	0.21	0.22	0.22	0.15
Intermeal interval	1	97.60	198.30	215.10	251.60	354.60	410.10	1,555.60	2,805.90	252.50	377.90	402.30	1,554.10
	2	109.00	143.30	192.30	237.60	292.20	556.00	1,700.80	2,842.60	178.30	239.60	311.10	1,682.20
	3	144.30	100.80	127.50	156.60	248.50	454.50	1,623.60	2,799.60	196.00	361.70	293.00	1,638.20
	4	195.20	145.80	195.90	255.60	374.70	495.40	1,547.40	2,900.40	271.10	477.00	237.90	1,864.50
	5	105.20	150.50	202.40	253.30	297.80	481.40	1,513.40	2,790.90	222.30	319.30	376.40	
	6	129.00	120.80	135.30	188.90	232.70	392.00	1,513.40	2,790.90	217.40	258.70	316.50	1,540.90

APPENDIX
(Continued)

Measure	Rat	Procurement interval																																	
		FR 1						FR 10																											
		Baseline	1 s	20 s	3 min	21 min	3 hr	23 hr	46 hr	1 s	3 min	21 min	23 hr																						
Bar-press latency	1	198.30	214.70	249.00	322.70	299.40	192.10	75.20	252.50	375.20	380.90	188.80	144.00	191.90	234.90	270.90	385.60	112.00	178.30	237.00	289.70	316.80													
	2	100.80	127.10	153.90	226.80	284.40	260.30	68.90	196.00	359.00	230.90	272.90	145.80	195.50	252.90	353.40	182.10	169.70	271.00	406.70	216.60	499.20	150.50	202.10	250.60	310.70	222.30	316.60	355.00	217.40	256.10	253.60	175.60		
	3	120.70	136.50	186.20	211.30	221.30	148.10	60.20	217.40	256.10	253.60	175.60	120.70	136.50	186.20	211.30	148.10	60.20	217.40	256.10	253.60	175.60	120.70	136.50	186.20	211.30	148.10	60.20	217.40	256.10	253.60	175.60			
	4	145.80	195.50	252.90	353.40	324.70	182.10	169.70	271.00	406.70	216.60	499.20	145.80	195.50	252.90	353.40	182.10	169.70	271.00	406.70	216.60	499.20	150.50	202.10	250.60	310.70	222.30	316.60	355.00	217.40	256.10	253.60	175.60		
	5	150.50	202.10	250.60	310.70	310.70	222.30	316.60	355.00	217.40	256.10	253.60	175.60	150.50	202.10	250.60	310.70	222.30	316.60	355.00	217.40	256.10	253.60	175.60	150.50	202.10	250.60	310.70	222.30	316.60	355.00	217.40	256.10	253.60	175.60
	6	120.70	136.50	186.20	211.30	221.30	148.10	60.20	217.40	256.10	253.60	175.60	120.70	136.50	186.20	211.30	148.10	60.20	217.40	256.10	253.60	175.60	120.70	136.50	186.20	211.30	148.10	60.20	217.40	256.10	253.60	175.60			