

THE RELATIONSHIP BETWEEN FEEDING RATE AND PATCH CHOICE

DEANNE F. JOHNSON AND GEORGE COLLIER

RUTGERS, THE STATE UNIVERSITY OF NEW JERSEY

Rats in a laboratory foraging simulation searched for sequential opportunities to feed in two patches that differed in the rate at which food pellets were delivered (controlled by fixed-interval schedules) and in the size of the pellets. The profitability of feeding in each patch was calculated in terms of time (grams per minute) and in terms of effort (grams per bar press). These values were the result of the imposed fixed interval, the size of the pellets, and the rate at which the rats pressed the bar in each condition. The rats ate more food and larger meals, but not more frequent meals, at the patch offering the higher rate of food consumption, calculated as grams per minute. The relative intake at any patch was a function of the relative rate of intake during meals at that patch compared to the other patch. Rats respond to explicit manipulations of feeding time in the same manner as they respond to manipulations of feeding effort.

Key words: food intake, choice, closed economy, fixed-interval schedules, reinforcer size, consumption rate, lever press, rats

Much recent attention has been given to the choices animals make among food sources. Two major perspectives have been taken, one by operant psychologists who have used choice as a measure of response strength (e.g., Williams, 1988) and another by foraging theorists who have investigated the functional significance of different feeding strategies (e.g., Schoener, 1971). Foraging theorists suggest that profitability, defined as the net energy gain per unit foraging time, should be maximized by animals foraging optimally (MacArthur & Pianka, 1966; Schoener, 1971). One would predict, therefore, that the profitability of different food types would be a critical variable influencing food selection. Two sorts of costs contribute to the profitability of a food source: the *effort* expended and the *time* spent consuming the food.

We have investigated food choice from the functional perspective and have developed a laboratory paradigm in which we can manipulate food costs and monitor subjects' foraging

behavior and food selection. In these experiments, subjects' home cages are fitted with two feeding stations at which food is contingent on bar pressing. The subjects "search," by responding on a separate bar, for sequential, randomly occurring opportunities to eat at each feeding station; when they encounter an opportunity, they may accept it and consume a meal or reject the opportunity and search further. These procedures are carried out in closed economies in which the subjects may regulate their daily food intake by means of multiple behavioral adjustments. We monitor instrumental response rates, consumption rates, opportunities accepted and meal sizes at each patch, and total intakes from the two patches. This contrasts with the typical operant procedure in which subjects are tested in short sessions comparable to one meal, the length or size and the timing of which is controlled by the experimenter. In that case the subjects control only their choice of response options and response rate; they are unlikely to demonstrate the repertoire of solutions to economic problems developed over their phylogeny and ontogeny.

We have explicitly manipulated the effort required at each feeding station, or patch, by imposing bar-press requirements on the consumption of small food pellets (Johnson & Collier, 1987, 1989). Increasing the number of bar presses required to earn each pellet increases the unit price of food in bar presses

This research was supported in part by U.S. Public Health Service (NIDDKD) Grant DK-31016 to George Collier. Portions of these data were reported at the annual meeting of the Eastern Psychological Association, Boston, 1989. We thank George King, John Wixted, and an anonymous reviewer for comments that strengthened the manuscript. Correspondence and requests for reprints should be sent to Deanne F. Johnson, Department of Psychology, Busch Campus, Rutgers University, New Brunswick, New Jersey 08903.

per calorie consumed. We have also made calories cost more bar presses by reducing the number of calories in each pellet, either by making the pellet smaller (Johnson & Collier, 1989) or by diluting the food with cellulose (Johnson & Collier, 1987). Using any of these methods to alter the unit price of calories at two food patches available to rats in our procedure results in a differential intake from the two patches. Further, a large portion of the variance in the relative intake from each patch is explained by the price of calories at that patch relative to the price at the other patch.

These manipulations of the bar-press price of calories also change the cost of calories in terms of time—that is, the rate at which calories are consumed. Because more bar presses take more time, calories are consumed more slowly as their bar-press price increases. The changes in the two costs, bar presses per calorie and minutes per calorie, are not perfectly correlated, and when we have compared time costs with effort costs in their ability to predict differences in intake at two feeders, the relative rate of eating at one food source compared to another has explained a greater proportion of the variance in relative intake than has the relative cost in bar presses (Johnson & Collier, 1987, 1989). These findings address but do not answer the question of what currency the animal uses in making these economic decisions.

The concept of a unit price of food, which may be altered by the manipulation of several cost/benefit variables, has also been discussed in relation to the demand for food. Demand is an economic concept relating the intake of a commodity to its price. Food intake, for example, has been shown to decrease as a (non-linear) function of the unit price of food in a number of laboratory paradigms (Collier, Johnson, Hill, & Kaufman, 1986; Hursh, 1980; Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988). It is intriguing that in our above-mentioned choice paradigm, when two food sources are available, daily caloric intake was constant over the choice conditions tested in both studies.

To test further the generality of our findings and to address the question of whether consumption rates determine meal parameters or whether both are the result of a shared set of variables, in the present study we explicitly manipulated consumption rates by imposing

fixed-interval (FI) schedules instead of fixed-ratio (FR) schedules on the delivery of pellets at two feeders. Any particular FI schedule imposes a lower limit on the interval between pellet deliveries, but all such schedules require only one bar press per pellet. Thus, theoretically there is no difference in the effort required for pellets available at different FIs. In practice animals do not take advantage of this fact, but instead make more bar presses for each pellet as the interval increases (Williams, 1988). By using pellets of different sizes (which result in different costs in effort per gram of food) we could manipulate time and effort costs relatively independently to determine how each contributes to food choices and intake patterns.

METHOD

Subjects and Apparatus

Four male Sprague-Dawley-derived rats (Camm Research Institute) were individually housed 24 hr a day in stainless-steel cages (41 cm by 23 cm by 19 cm) equipped at one end with two feeding stations, one on the right and one on the left. Each consisted of a pellet cup mounted on the floor against the end wall (4 cm from the side wall), a 0.6-cm diameter cue light mounted 8 cm above the cup, and a t-shaped response bar (BCS, Inc.), requiring 0.35 N to depress, located on the side wall 10 cm from the floor and 6 cm from the corner and protruding 3 cm into the cage. Pellet feeders (BCS, Inc.) located outside the cage delivered food pellets (BioServ rodent chow formula) into the food cups. At the other end of the cage, an identical response bar (the "search bar") was centered on the wall, 10 cm above the floor, and a third light (the "search light") was mounted 2 cm above this bar. Water was available ad libitum from a tube attached to the front of the cage. The cages were located in a room maintained at 21 ± 2 °C with room lights on from 8:00 a.m. to 8:00 p.m.

The apparatus operated as follows: During intermeal intervals the search light was on and a foraging bout could begin at any time with the completion of five responses on the search bar. This caused the search light to go out and the cue light to come on at one feeding station, chosen randomly, signaling that food could be earned by responding on the cued bar. The rat had two options: to accept or to reject the feed-

ing opportunity. A rejection occurred if no responses occurred on the cued food bar for 1 min. Then the feeder light went out, the search light came on, and the rat could initiate a new search. Alternatively, if the rat began to respond, the first response delivered a pellet and started a clock. This began a "meal." Further responses had no effect until a fixed interval of time elapsed; then the next response delivered another pellet and reset the clock. The rat could continue to feed for any length of time; when 10 min elapsed with no pellet earned, the feeder light went out, signaling the end of the meal, and the search light came on. The rat could begin a new foraging bout at any time. The apparatus was controlled and data were recorded by microprocessors (Commodore® PET 4032) located in an adjacent room.

Procedure

The rats lived continuously in their cages except for a daily maintenance period of approximately 45 min beginning at 10:00 a.m. During this time the rats were weighed and placed together in a holding cage. Data were recorded, food and water replenished, and the equipment cleaned and tested. Any changes in the programmed feeding contingencies were made at this time.

The rats were adapted to the feeding apparatus over several days. First, all response bars were removed for 2 days of magazine training, during which pellets were delivered automatically at random intervals from both feeders. Then one feeder bar was installed, the associated cue light was continuously illuminated, and one pellet was delivered after every response on that bar. No rat required shaping of the response. The next day that bar was removed and the other bar was installed with identical contingencies. Then both bars were installed and feeding opportunities occurred sequentially at the feeders. That is, after a meal ended, a feeder was chosen randomly to be available for the next meal and the cue light at that feeder remained illuminated until a meal was consumed. During the remainder of the training phase, changes in response requirements were made after 1 to 3 days, when the rat had not lost body weight from the day before. Next, the search bar was installed with one response required to complete the search component. The search requirement was in-

creased to two and then to five bar presses. An FI of 10 s was then imposed at both feeders simultaneously. FIs of 20, 40, 60, and 30 s, equal at both feeders, were then presented, with each in effect for 5 to 7 days.

There were two choice phases. In the first, both feeders contained 45-mg pellets and each of the five FIs (10, 20, 30, 40, and 60 s) was paired with each other FI and with itself, resulting in 15 choice conditions with one FI at each feeder. Each rat received all conditions in a random order. Each FI pair was presented for 10 days (or sometimes longer due to equipment failures); after 5 days the location of the FIs was switched between feeders. Eight-day means were calculated for each pairing using 4 days with each FI at the left feeder and 4 days with each FI at the right feeder. Previous results in our laboratory have shown little change in feeding measures after the 2nd day of a condition.

In the second phase, the pellets in one feeder were larger than the pellets in the other feeder. Three pairs of pellet sizes were used: 20 and 45 mg, 20 and 97 mg, and 45 and 97 mg. The FI at both feeders was initially 10 s; then the FI for the larger pellets was increased gradually until the rats switched from eating more food from the larger pellets to eating more food from the smaller pellets. Each large-pellet-FI condition was in effect for at least 7 days; the data presented are means over the last 5 days.

Data Analysis

Data for individual rats are presented in the Appendices. Mean daily food intake, acceptance of feeding opportunities, number of meals, meal size, and feeding rate at each feeder were calculated for each rat for each condition. Data were analyzed using two-factor analysis of variance with repeated measures and $\alpha = .05$. In the first phase the two factors were feeder FI and alternate feeder FI; in the second phase the factors were pellet size and FI for the larger pellet.

RESULTS

The FI schedules were effective in altering the rate of food consumption within meals, although the response rate did not vary with FI (Figure 1). Consumption rates (pellets per minute) were highest at the shortest FIs and decreased as the FI increased. The differences

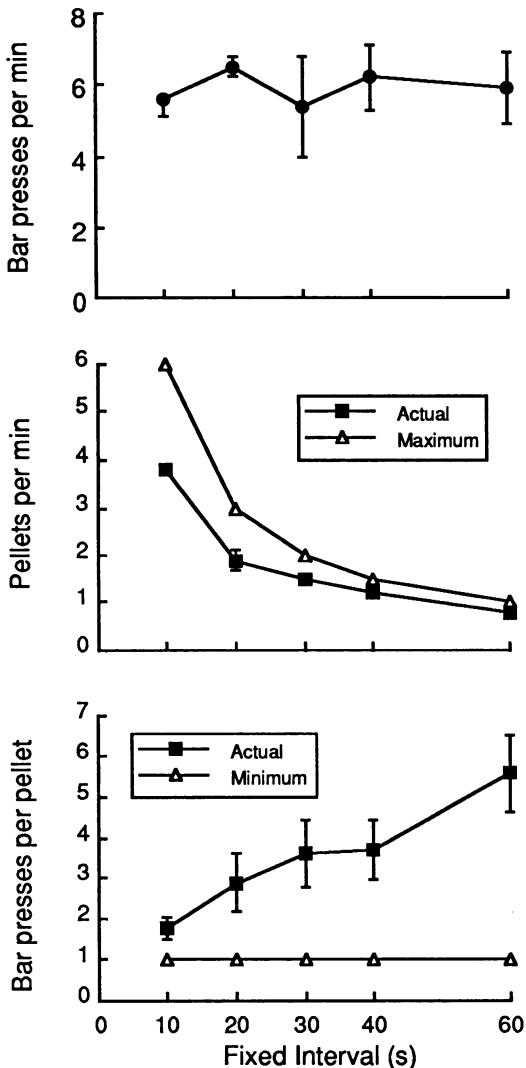


Fig. 1. The response rate (top), the rate at which pellets were earned (middle), and the number of bar presses expended per pellet (bottom) as a function of the fixed interval (FI) between pellets. "Actual" values are means \pm SE of 4 rats. Also shown are the theoretical maximum rate and minimum bar presses per pellet allowed by each FI imposed.

in eating rate were not due solely to the FI, however. The rats earned pellets at nearly the maximum rate at the longest FIs but at less than the maximum rate at shorter FIs.

The cost of food in bar presses also varied across FI schedules (Figure 1). Even though only one bar press per pellet was required by all schedules, the rats made more bar presses per pellet at long than short FIs, the typical result. The FI schedules imposed thus changed

both time and energy costs of food: When eating food at higher FIs, the rats expended more time and more bar presses for each gram of food (Figure 2).

Measures of food intake amount and patterns are shown in Figure 3. The rats ate more food at feeders with shorter FIs, $F(4, 12) = 37.39$, $p < .001$. Additionally, the intake at a feeder with any particular FI increased as the FI at the alternate feeder increased, $F(4, 12) = 24.53$, $p < .001$. The difference in intake between the two feeders thus increased as the FI difference increased.

The intake differences were not the result of differential acceptance of feeding opportunities at the two feeders. The rats accepted nearly 100% (means varied between 95% and 100%) of all opportunities they encountered and therefore ate the same number of meals at each feeder in all conditions. The size of meals, however, did differ between feeders. As with daily intake, the per-meal intake was greatest at feeders with shorter FIs, $F(4, 12) = 23.67$, $p < .001$; but for any FI at one feeder, meal size increased as the FI at the alternate feeder increased, $F(4, 12) = 6.08$, $p < .01$. This meal-size difference would be expected if the rats were eating meals of constant duration, but this was not the case. Meal length increased with FI, $F(4, 12) = 46.68$, $p < .001$, and, to a lesser extent, with alternate FI, $F(4, 12) = 3.76$, $p < .05$. Note that this means that, although the rats ate more food per meal at the feeder with the shorter FI, their meals lasted longer at the feeder with the longer FI.

During the second phase of the study, when different-sized pellets were available in each feeder and the FI for larger pellets was increased, the cost of food in both time and bar presses was influenced by the size of the pellets and the FI imposed (Figure 4). When FIs were equal at 10 s, the rats made one or two bar presses per pellet for both small and large pellets, and, although they pressed at a somewhat higher rate for the small pellets, earned pellets at about the same rate at both feeders. Thus, because each large pellet contained more food than each small pellet, large-pellet food was consumed faster (more grams per minute) and at a lower bar-press cost per gram than small-pellet food. Increasing the FI for the large pellets increased their cost in both time and bar presses but did not affect the cost of small-pellet food, so that at longer FIs the unit cost

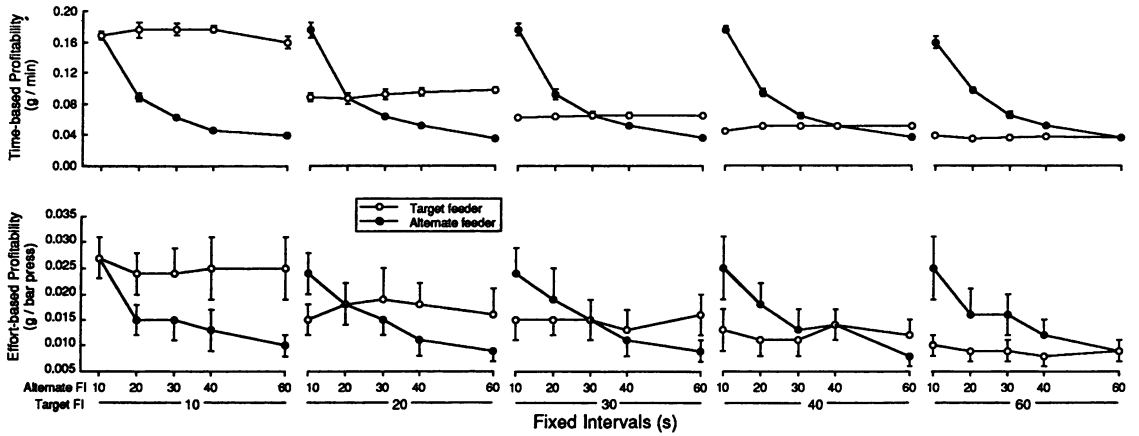


Fig. 2. The time-based (top panels) and effort-based (bottom panels) profitability at two feeders where the fixed-interval (FI) schedule imposed at the feeders differed. Data are plotted for each FI (the “target”) as a function of the FI at the alternate feeder. Values are means \pm SE for 4 rats.

of large-pellet food exceeded that of the small-pellet food.

Intake patterns during this phase are presented in Figure 5. The rats initially ate more

food at the feeder with the large pellets. Then, as the FI increased for the large pellets, the rats ate less at that feeder and more at the feeder offering small pellets. In all cases, the

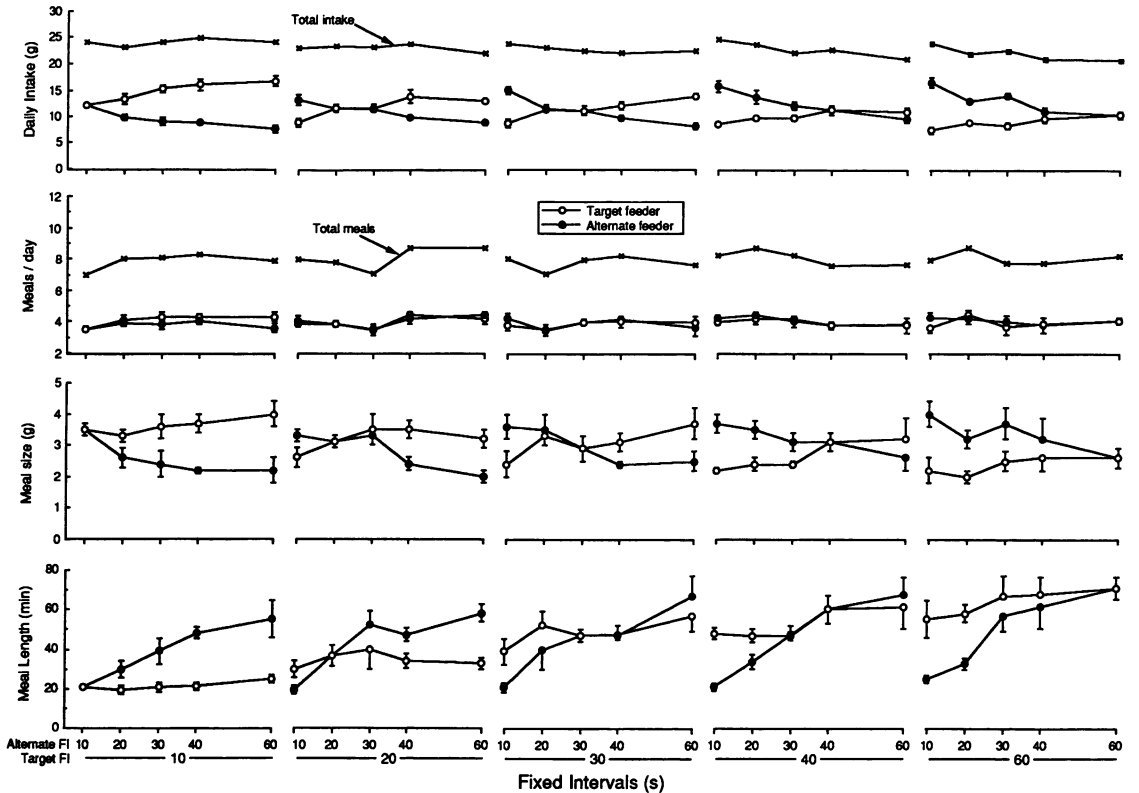


Fig. 3. Measures of feeding behavior at two feeders where the fixed-interval (FI) schedule imposed at the feeders differed. Data are plotted as in Figure 2; values are means \pm SE for 4 rats.

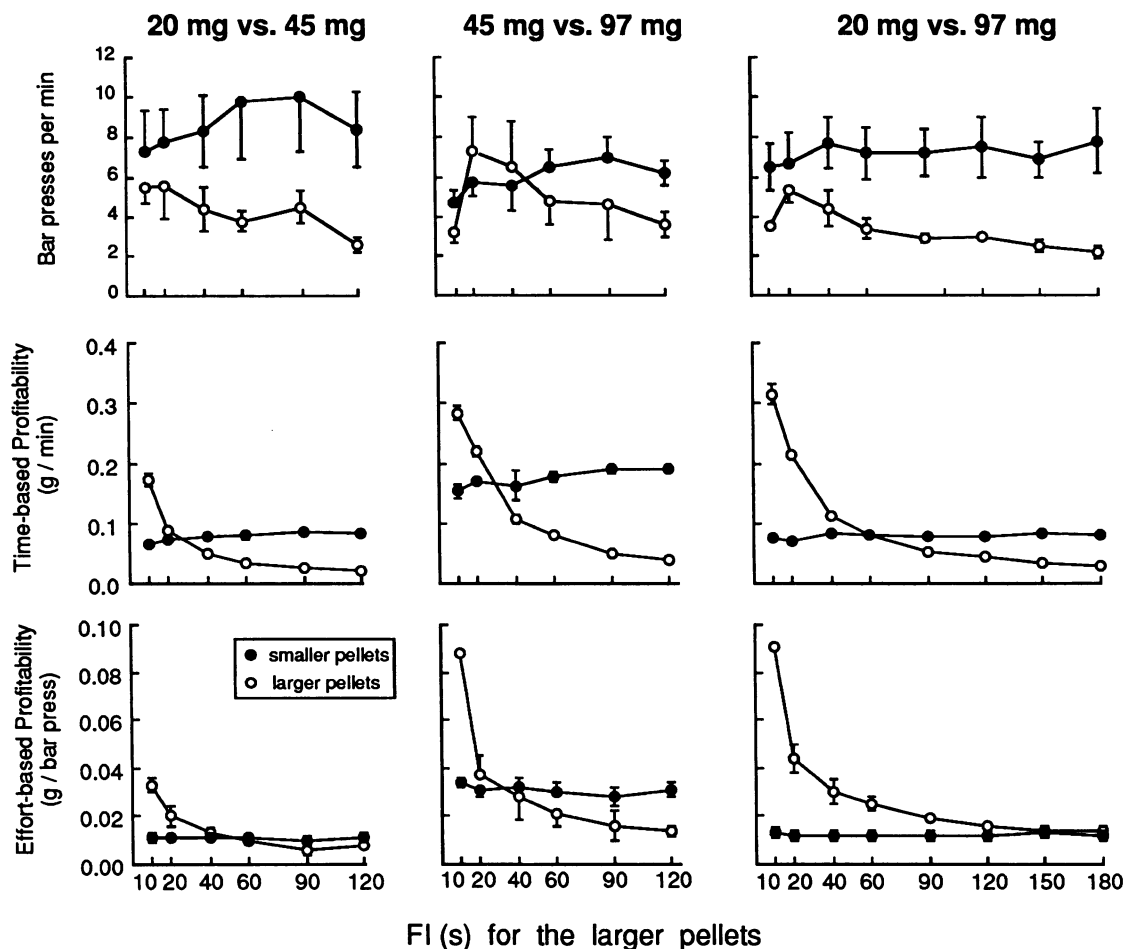


Fig. 4. The response rate (top panels) and the time-based (middle panels) and effort-based (bottom panels) profitability at two feeders offering different-sized pellets as a function of the fixed interval (FI) for the larger pellets. The FI for the smaller pellets was 10 s throughout. Values are means \pm SE for 4 rats.

changes were compensatory, and the total daily intake was constant across these conditions. As in Phase 1, nearly all opportunities (92% to 100%) were accepted in all conditions, and thus meal size rather than meal frequency was responsible for the intake differences.

If these changes in intake and meal size are compared with the changes in the profitability at each patch, it is apparent that intake was equal at the two feeders in conditions in which the time-based profitability (grams per minute), rather than the effort-based profitability (grams per bar press), was equal at the two feeders. Furthermore, over the whole range of relative costs presented in both phases of this study, relative rate of intake was a better predictor of relative meal size and total intake.

We calculated the relative intake (grams per day of small pellets divided by grams per day of large pellets) and each relative profitability measure (e.g., grams per minute for small pellets divided by grams per minute for large pellets) for each rat in each condition and subjected these values to a logarithmic transformation to achieve a linear scale. Correlations of intake with each profitability measure (Figure 6 presents the functions for the means of all 4 rats; Table 1 presents values for each individual) indicate that, although both profitability measures are good predictors of intake patterns, for all of the rats relative eating rate explains a larger proportion of the variance in relative intake. The same is true for the equivalent analyses of relative meal size (in grams)

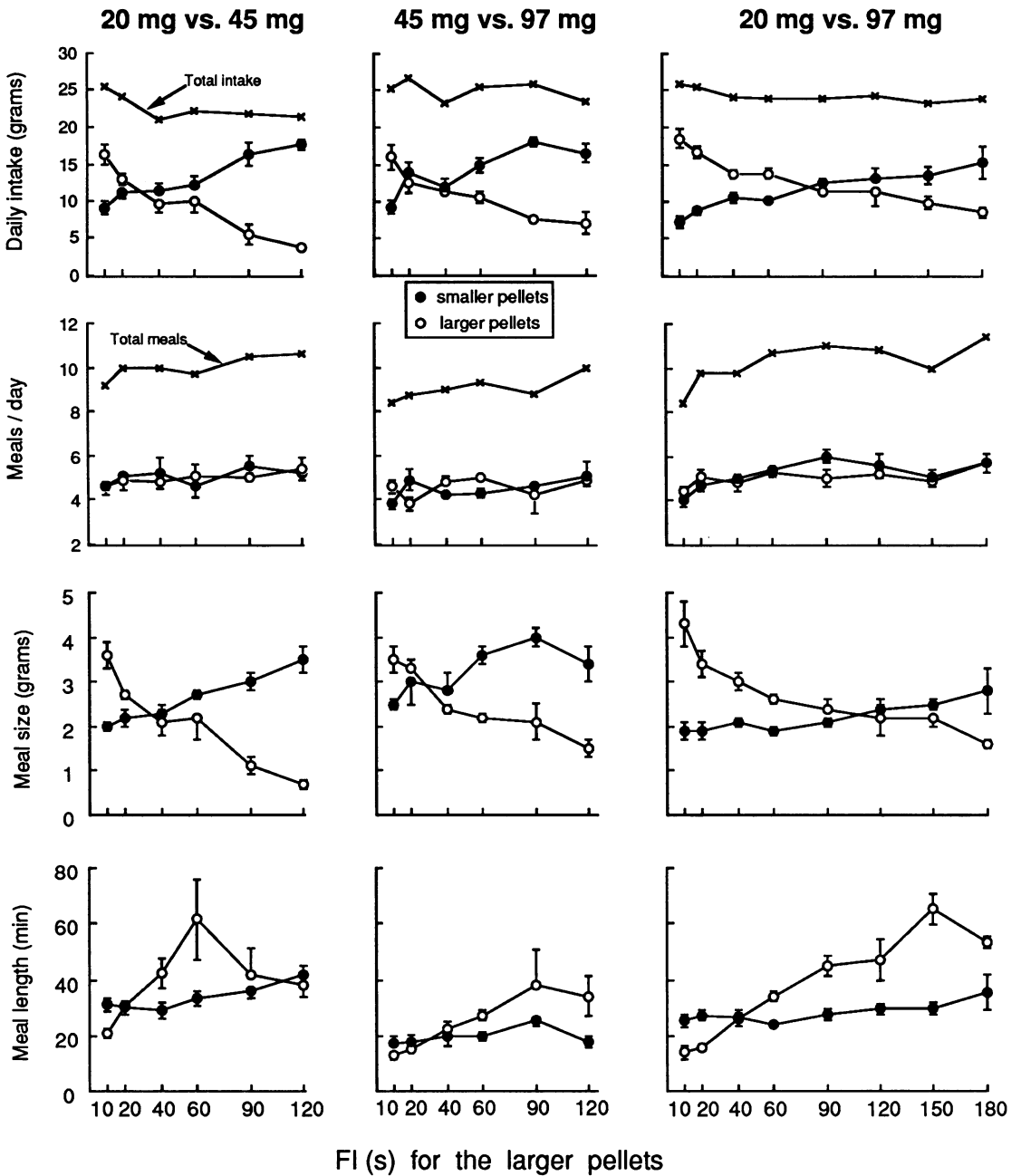


Fig. 5. Measures of feeding behavior at two feeders offering different-sized pellets as a function of the fixed interval (FI) for the larger pellets. The FI for the smaller pellets was 10 s throughout. Values are means \pm SE for 4 rats.

and of relative meal length (Figure 6; Table 1). Note, however, that for meal length the relationships with profitability are inverse—the rats ate longer meals in the less profitable patch.

The regression lines relating these feeding measures to each profitability measure show that, as was seen in the means, 2 of the rats treated the feeders equally when the time-based profitabilities were equal rather than when the

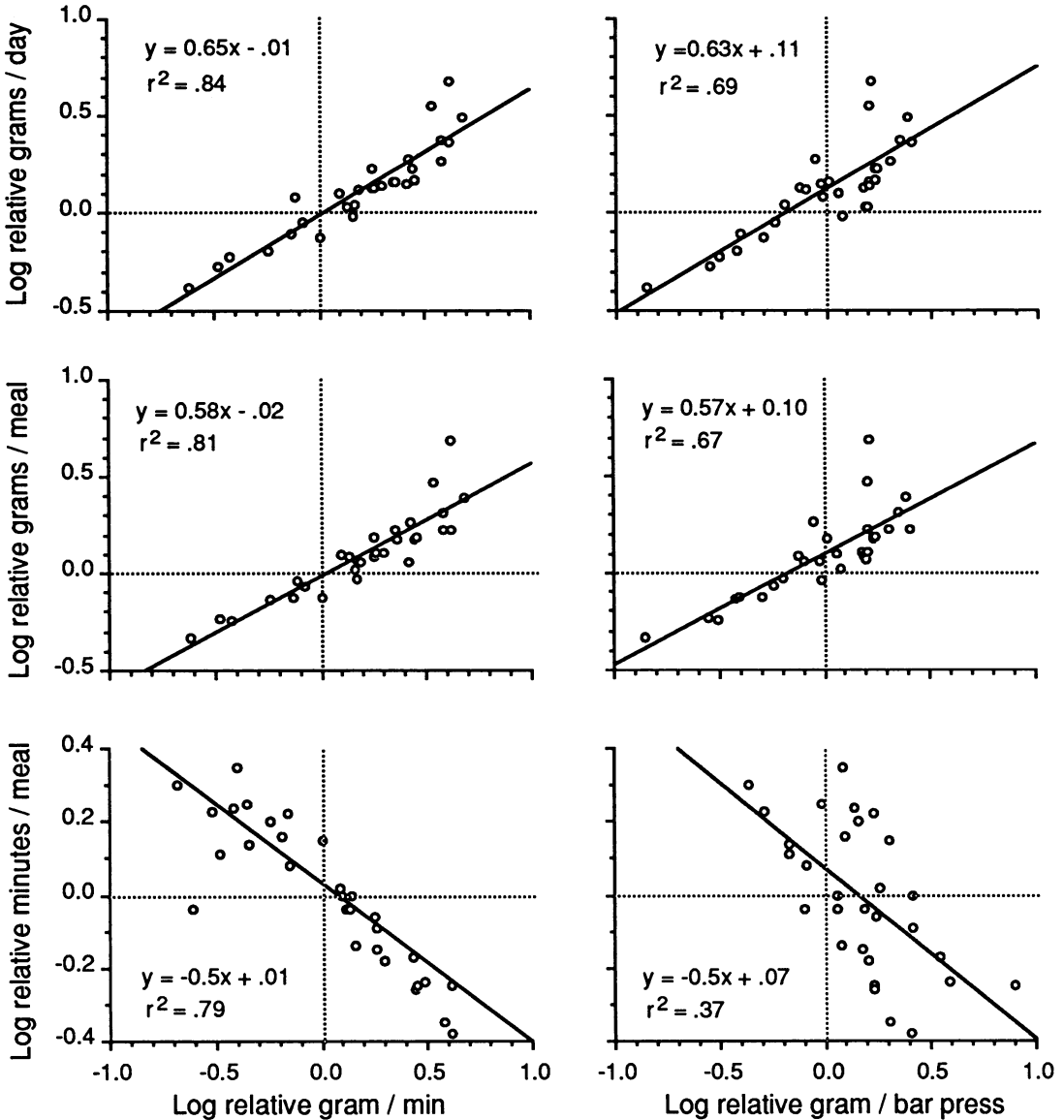


Fig. 6. Daily intake (top panels), average meal size (middle panels), and average meal length at the feeder with the longer FI (Phase 1 conditions) or smaller pellets (Phase 2 conditions) relative to the feeder with the shorter FI or larger pellets, respectively, as functions of relative eating time (g/min; left panels) and relative eating effort (g/bar press; right panels) at the feeder with the smaller pellets. Relative values (means \pm SE for 4 rats) have been log-transformed to create a linear scale; a log value of 0 indicates equal measures at the feeders. The linear regression line and the value of r^2 for each relationship are shown.

effort-based profitabilities were equal. That is, for Rats 1 and 2, the y intercept for the regression line for log relative intake or meal size as a function of log relative feeding time is closer to zero than the intercept for the function of log relative feeding effort. For the other 2 rats, there was no difference between the in-

tercept for the functions of time and effort (Table 1).

DISCUSSION

The feeding patterns seen in this study confirm our previous results using FR require-

Table 1

Values of r^2 and the y intercept from the regressions of relative daily intake, meal size, and meal length on measures of relative food profitability based on time (g/min) or effort (g/bar press).

Rat	Profitability basis	Feeding measure predicted					
		Intake		Meal size		Meal length	
		r^2	Intercept	r^2	Intercept	r^2	Intercept
1	Time	.55	0.01	.45	0.01	.73	-0.03
	Effort	.31	0.15	.21	0.11	.21	0.02
2	Time	.61	0.01	.62	0.01	.68	-0.04
	Effort	.58	0.14	.57	0.12	.20	0.00
3	Time	.78	-0.09	.82	-0.09	.40	0.03
	Effort	.68	0.07	.74	0.07	.06	0.05
4	Time	.59	-0.03	.65	-0.03	.61	0.02
	Effort	.39	0.05	.45	0.04	.59	0.07

ments to manipulate the within-meal cost of food, with the exception that rejection of opportunities to eat more costly food did not occur. Meal size was thus solely responsible for the differential intake from the two feeders. Considering both these data and the results from our previous simulations, we can draw two major conclusions about a habitat with two food patches. First, the absolute intake (acceptance, meal size, or daily intake) at one patch cannot be predicted from the feeding cost/benefit ratio at that patch; one can predict only the relative intake at one patch compared to the alternative patch. Second, the best predictor of relative patch choice, relative meal size, and relative daily intake in a patch is the relative rate of energy flow in one patch compared to the other. Further, regardless of the particular pattern of intake, the total daily caloric intake is constant. This proves to be the case whether we alter the cost (FR) per item, the benefit (calories or grams) per item, or the rate at which items become available. This suggests that the "currency" rats use to meter the feeding cost/benefit ratio is net energy per unit time, a value that has played a central role both in optimal foraging models as profitability (Schoener, 1971; Stephens & Krebs, 1986) and in operant reinforcement models as rate of reinforcement (Ferster & Skinner, 1957; Herrnstein, 1970; Staddon, 1983; see Williams, 1988, for a recent review).

Our simulation differs from conventional tests of these models, which generally measure rates of responding and choice of feeder (or schedule) during single feeding bouts. It permits an analysis of meal patterns of freely feed-

ing, nondeprived subjects that initiate and terminate all of their feeding bouts and are able to reject or accept meal opportunities. Thus, in addition to the conventional measure of response rate, the subject's options include the frequency, size, and distribution of meals and the amount consumed daily. By using this longer time frame, we can examine how individual meals relate to the overall pattern of foraging and feeding behavior and how the regulation of food intake interacts with the economics of food intake.

The relationship we find between relative intake and relative profitability may be homologous to the generalized matching law (Baum, 1974) that describes the performance of animals in certain operant test sessions. When exposed to two concurrent variable-interval schedules of reinforcement, rats and pigeons tend to match the ratio of time spent, or reinforcements earned, at each feeder to the ratio of reinforcement rate at each feeder (Baum, 1974; Herrnstein, 1970; Williams, 1988). These results differ from ours in at least three ways: The matching occurred during a relatively short test session that would be considered one meal, or a part of a meal, by our criterion; the animals in our study could only make sequential between-meal choices; and our rats matched amount consumed but not time spent. Nonetheless, in both paradigms, relative rate predicts behavior. Matching phenomena thus have been seen at several levels—relative time spent within a session, relative size of whole meals, and relative intake over a number of meals during the entire day. It appears that the animal will exploit whatever options are

available in responding to profitability differences between food sources. In the classic paradigm the only options are choice of patch, time spent at the patch, and rate and pattern of responding within a single meal, a small piece of the economic pie. When between-meal choices are also available, as in the many-optioned closed economy, these are also called into play. In any case, the rate of return seems to be the critical variable associated with the behavioral decisions. These data do not demonstrate that animals are in fact measuring the rate of calorie flow, nor has a mechanism by which such measurement might occur been identified.

It is important to emphasize that, in contrast to traditional matching, our rats did *not* match time spent at each feeder to the relative feeding rate. In fact the relationship for meal length was inverse: Although the rats ate less food, meals were longer in less profitable patches. We do not know what information rats use to decide when to end a meal. However, these results, combined with those of previous choice studies, indicate that it is more likely amount consumed than time spent eating that gives rise to the meal-ending cue(s). Relative meal size in calories always is related directly to relative profitability; meal length, however, is sometimes greater and sometimes smaller in the more profitable patch (Johnson & Collier, 1989). The problem for the rat is integrating economic information suggesting an appropriate meal size with information about the amount actually consumed.

The question of how much to eat in a particular food patch has been addressed by foraging theorists with the marginal value theorem (Charnov, 1976), which suggests another sort of meal-ending cue. The theorem predicts when animals will leave one food patch and move on to another in an environment in which the patches are depleted as they are exploited. In depleting patches, the rate of intake is assumed to be a decreasing function of length of time in the patch, and the optimal pattern is to remain in the current patch until the rate of intake falls below the environmental average. This decision is based on the rate of intake in the current patch compared to the average rate in the environment, an assessment comparable to that apparently made by the rats in our study. The marginal value theorem is not directly applicable to our data because the

patches in our simulation were not depleting and the rats' intake rate remained constant during a meal; in the less profitable patch, the intake rate was always lower than the environmental average. However, the behavior of our rats was qualitatively in accord with the theorem in that the rats took larger meals in patches with higher intake rates and the meal size at any particular patch depended on the relative, not the absolute, rate of consumption at that patch.

The effects of the FI schedules of pellet delivery in our study were consistent with previous data from closed economies (Hursh, 1980) in that, as the FI increased, the animals increased their responses per pellet and came closer to earning pellets as fast as possible. This more efficient use of feeding time was interpreted as an economic response to schedules that increased the time required to feed each day. A similar increase in feeding efficiency has been shown for a number of manipulations that affect the time required to earn the daily requirement. For example, previous studies in closed economies have shown that response rate is an increasing function of the unit price (i.e., the bar presses per gram) of food (Collier et al., 1986; Hursh et al., 1988). This means that animals press faster for small pellets than for large pellets. On the other hand, when given a choice, rats eat more food where the unit price is lower (e.g., where pellets are larger). Response rate and preference are inversely related in this situation: Rats press faster at the nonpreferred feeder.

It is intriguing to note an exception to the relation between unit price and response rate: If the caloric density of food pellets is reduced, thereby increasing the unit price of food (bar presses per calorie), rats respond slower, not faster, for the more expensive, lower calorie food (Johnson, Ackroff, Peters, & Collier, 1986). When foods of different caloric densities are offered in a two-patch environment, response rate and preference do coincide: More high-density food is consumed, and intake from each patch is still predicted by the relative rate of caloric intake (Johnson & Collier, 1987). Thus, the rate of bar pressing does not necessarily predict the profitability of a food patch and therefore does not necessarily predict the preferred food source.

The present results differ from those of previous studies of patch choice in which the rats

rejected opportunities to feed in less profitable patches (Johnson & Collier, 1987, 1989) and from the predictions of traditional optimal diet models (MacArthur & Pianka, 1966), which in this case would be to accept no high-cost opportunities. The rats in the current study accepted nearly all feeding opportunities regardless of the food cost. This was a surprising outcome that we cannot explain. The behavior required to reject an opportunity was the same here as required in our other studies: the withholding of all responses on the feeder bar for 1 min. One difference between this study and previous ones was that here the first feeder bar press in a meal delivered a pellet, whereas in other studies a larger number of responses (at least 10) had to be made before the first pellet was earned. It may be that this initially equal rate of pellet delivery at both feeders decreased any tendency to reject food that would be less profitable later in the meal. However, this hypothesis does not account for the lack of rejection of smaller pellets in this study, because the profitability for the first small pellet would be lower than that for the first large pellet. An alternative explanation might be offered by the delay-reduction hypothesis (Fantino, 1981), which suggests that all opportunities were accepted because the first pellet was always immediately available (i.e., with no imposed delay).

It should be emphasized that the changing patterns of feeding we observed occurred within the framework of a constant daily food intake. This result is contrary to the decline in intake as a function of food cost (in bar presses per gram) obtained when only one feeding station is available to an animal (Collier et al., 1986; Hursh, 1980, 1984; Hursh et al., 1988). We can calculate the unit price of food that results from the rats' performance during each condition, that is, the total bar presses emitted (or time spent) divided by the total grams consumed. Although the rats' behavior did reduce unit price compared to that resulting from a random pattern of intake from the two patches, the overall unit price was not constant across conditions but varied from approximately 20 to 150 bar presses (and 5 to 25 min) per gram. Demand functions tend to be relatively flat at low unit prices, and it may be that the variation in unit price in this study was not great enough to produce a noticeable change in demand.

Overall, then, our results extend the gen-

erality of certain optimality concepts and of the matching law from single feeding bouts to a longer time frame. Our results also question the usefulness of response-rate measures in predicting results over a longer time frame and suggest that food profitability, measured in net energy gain per unit time, either is the primary currency in animals' food economies or is a surrogate of that currency. Major questions remaining include how organisms determine food profitability, how and over what time window the profitabilities of several food sources are integrated, how profitability considerations are related to other constraints on food intake (e.g., requirements for specific nutrients: Belovsky, 1978; Pulliam, 1975; and avoidance of toxins: Freeland & Janzen, 1974), and how the economy for food relates to the economies for other resources and behavior in the animal's repertoire.

REFERENCES

- Baum, W. M. (1974). On two types of deviation from the matching law: Bias and undermatching. *Journal of the Experimental Analysis of Behavior*, **22**, 231-242.
- Belovsky, G. E. (1978). Diet optimization in a generalist herbivore: The moose. *Theoretical Population Biology*, **14**, 105-134.
- Charnov, E. L. (1976). Optimal foraging: The marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.
- 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.
- Fantino, E. (1981). Contiguity, response strength, and the delay-reduction hypothesis. In P. Harzem & M. D. Zeiler (Eds.), *Advances in analysis of behaviour: Vol. 2. Predictability, correlation, and contiguity* (pp. 169-201). Chichester, England: Wiley.
- Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement*. New York: Appleton-Century-Crofts.
- Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals: The role of plant secondary compounds. *American Naturalist*, **108**, 269-289.
- Herrnstein, R. J. (1970). On the law of effect. *Journal of the Experimental Analysis of Behavior*, **13**, 243-266.
- Hursh, S. R. (1980). Economic concepts for the analysis of behavior. *Journal of the Experimental Analysis of Behavior*, **34**, 219-238.
- Hursh, S. R. (1984). Behavioral economics. *Journal of the Experimental Analysis of Behavior*, **42**, 435-452.
- Hursh, S. R., Raslear, T. G., Shurtleff, D., Bauman, R., & Simmons, L. (1988). A cost-benefit analysis of demand for food. *Journal of the Experimental Analysis of Behavior*, **50**, 419-440.
- Johnson, D. F., Ackroff, K., Peters, J., & Collier, G. H. (1986). Changes in rats' meal patterns as a function of the caloric density of the diet. *Physiology & Behavior*, **36**, 929-936.

- 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 & Behavior*, **39**, 351-359.
- Johnson, D. F., & Collier, G. H. (1989). Patch choice and meal size of foraging rats as a function of the profitability of food. *Animal Behaviour*, **38**, 285-297.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimum use of a patchy environment. *American Naturalist*, **100**, 603-609.
- Pulliam, H. R. (1975). Diet optimization with nutrient constraints. *American Naturalist*, **109**, 765-768.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **2**, 369-404.
- Staddon, J. E. R. (1983). *Adaptive behavior and learning*. Cambridge: Cambridge University Press.
- Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.
- Williams, B. A. (1988). Reinforcement, choice, and response strength. In R. C. Atkinson, R. J. Herrnstein, G. Lindzey, & R. D. Luce (Eds.), *Stevens' handbook of experimental psychology: Vol. 2. Learning and cognition* (2nd ed., pp. 167-244). New York: Wiley.

Received May 24, 1990

Final acceptance August 2, 1990

APPENDIX 1
Feeding measures for individual rats in Phase 1.

Measure	Rat	FI (s) during equal FI conditions						FI (s) at each feeder during paired-FI conditions					
		10	20	30	40	60	10	20	30	40	60		
Grams per minute	1	0.176	0.077	0.068	0.054	0.036	0.185	0.090	0.066	0.185	0.045	0.171	0.036
	2	0.176	0.104	0.072	0.054	0.036	0.194	0.099	0.180	0.185	0.050	0.135	0.050
	3	0.153	0.072	0.054	0.054	0.036	0.149	0.077	0.153	0.162	0.041	0.158	0.036
	4	0.171	0.095	0.072	0.054	0.041	0.176	0.090	0.180	0.176	0.050	0.171	0.036
Grams per bar press	1	0.018	0.009	0.008	0.009	0.006	0.014	0.008	0.012	0.013	0.007	0.016	0.007
	2	0.023	0.014	0.010	0.010	0.008	0.021	0.012	0.020	0.016	0.011	0.012	0.008
	3	0.034	0.028	0.024	0.021	0.014	0.031	0.023	0.035	0.035	0.023	0.036	0.014
	4	0.034	0.022	0.016	0.016	0.008	0.029	0.018	0.032	0.035	0.018	0.035	0.009
Grams per day	1	12.1	12.3	12.1	12.1	11.0	13.9	10.7	15.6	16.7	10.8	16.4	9.2
	2	11.1	9.7	9.1	9.3	9.2	10.5	8.8	13.1	12.7	6.8	14.1	8.0
	3	12.7	13.7	10.9	10.8	9.7	13.9	10.7	15.6	17.4	9.3	19.1	5.7
	4	12.6	11.6	13.3	12.7	12.0	15.4	9.1	16.3	17.1	9.0	16.7	7.5
Grams per meal	1	4.0	3.4	3.7	3.4	2.8	3.7	3.2	4.3	4.5	3.6	1.9	3.0
	2	3.2	2.8	2.1	2.1	2.0	2.8	2.3	2.6	3.0	1.8	3.1	2.6
	3	3.5	3.4	2.5	3.2	2.5	3.7	3.0	3.9	3.8	2.3	4.4	1.5
	4	3.4	2.7	3.4	3.7	3.3	3.1	2.0	3.6	3.7	2.1	3.5	1.7
Minutes per meal	1	22.7	44.2	54.4	63.0	77.8	20.0	35.6	22.8	24.3	54.5	11.1	83.3
	2	18.2	26.9	29.2	38.9	55.6	14.4	23.2	14.4	16.2	26.5	23.0	52.0
	3	22.9	47.2	46.3	59.3	69.4	24.8	39.0	25.5	23.5	39.0	27.8	41.7
	4	19.9	28.4	47.2	68.5	80.5	17.6	22.2	20.0	21.0	33.3	20.5	47.2

APPENDIX 1 (Continued)
Feeding measures for individual rats in Phase 1.

Measure	Rat	FI (s) at each feeder during paired-FI conditions											
		20	30	20	40	20	60	30	40	30	60	40	60
Grams per minute	1	0.099	0.068	0.099	0.054	0.104	0.036	0.068	0.054	0.068	0.036	0.068	0.041
	2	0.104	0.068	0.104	0.054	0.104	0.036	0.072	0.054	0.072	0.041	0.054	0.041
	3	0.072	0.054	0.081	0.045	0.086	0.032	0.054	0.045	0.063	0.036	0.045	0.036
	4	0.099	0.068	0.095	0.054	0.099	0.036	0.068	0.054	0.063	0.036	0.054	0.036
Grams per bar press	1	0.010	0.009	0.009	0.007	0.006	0.007	0.005	0.005	0.008	0.006	0.008	0.005
	2	0.010	0.010	0.013	0.008	0.010	0.005	0.008	0.007	0.012	0.006	0.009	0.005
	3	0.033	0.024	0.027	0.018	0.025	0.016	0.023	0.019	0.024	0.013	0.017	0.011
	4	0.022	0.017	0.022	0.013	0.022	0.009	0.018	0.014	0.020	0.011	0.017	0.010
Grams per day	1	12.1	12.1	16.7	9.7	14.0	8.9	13.4	10.3	15.1	8.3	8.3	10.9
	2	10.5	10.1	10.9	9.3	12.4	7.8	10.4	10.2	13.5	7.0	11.0	8.4
	3	13.7	14.0	11.3	10.6	12.8	9.0	14.0	8.6	14.8	9.4	9.0	11.6
	4	10.8	13.0	14.3	10.2	13.7	10.3	11.8	10.9	13.3	9.4	12.7	8.7
Grams per meal	1	3.9	3.7	4.2	2.9	3.7	2.3	3.5	2.7	4.7	3.2	5.1	3.6
	2	2.6	2.6	2.6	2.1	2.5	1.6	2.4	2.3	2.8	1.8	2.4	1.9
	3	4.8	3.8	3.0	2.4	2.9	1.9	2.8	2.3	4.4	2.9	2.3	2.5
	4	2.7	3.1	2.9	2.3	3.6	2.3	3.6	2.4	3.1	1.9	3.2	2.4
Minutes per meal	1	39.4	54.4	42.4	53.7	35.6	63.9	51.5	50.0	69.1	88.9	94.4	87.8
	2	25.0	38.2	25.0	38.9	24.0	44.4	33.3	42.6	38.9	43.9	44.4	46.3
	3	66.7	70.4	37.0	53.3	33.7	59.4	51.9	51.1	69.8	80.6	51.1	69.4
	4	27.3	45.6	30.5	42.6	36.4	63.9	52.9	44.4	49.2	52.8	59.3	66.7

APPENDIX 2
Feeding measures for individual rats during Phase 2.

Measure	Rat	20-mg-pellet feeder, 45-mg-pellet FI (s)						45-mg-pellet feeder, 45-mg-pellet FI (s)					
		FI 10	FI 20	FI 40	FI 60	FI 90	FI 120	FI 10	FI 20	FI 40	FI 60	FI 90	FI 120
Grams per minute	1	0.08	0.08	0.09	0.09	0.09	0.09	0.19	0.09	0.05	0.03	0.02	0.02
	2	0.06	0.08	0.08	0.09	0.09	0.09	0.14	0.09	0.05	0.04	0.03	0.02
	3	0.05	0.06	0.07	0.06	0.07	0.07	0.17	0.08	0.05	0.03	0.03	0.02
	4	0.07	0.07	0.07	0.08	0.08	0.08	0.19	0.09	0.05	0.04	0.03	0.02
Grams per bar press	1	0.005	0.006	0.006	0.006	0.005	0.006	0.024	0.008	0.007	0.007	0.004	0.010
	2	0.011	0.011	0.011	0.011	0.012	0.013	0.039	0.022	0.012	0.009	0.005	0.006
	3	0.014	0.014	0.013	0.014	0.014	0.013	0.032	0.025	0.016	0.012	0.009	0.006
	4	0.012	0.012	0.012	0.012	0.012	0.013	0.038	0.026	0.018	0.013	0.010	0.008
Grams per day	1	8.1	13.4	11.3	9.9	13.3	19.5	16.1	11.2	11.8	12.8	8.7	3.4
	2	8.3	10.4	13.4	12.8	16.0	15.6	16.0	13.9	6.1	6.5	3.8	3.6
	3	7.7	8.8	8.1	10.5	14.0	17.0	20.2	15.0	11.9	13.6	8.7	3.8
	4	12.2	12.1	12.4	15.6	19.5	18.3	12.9	11.7	9.0	7.2	3.9	4.2
Grams per meal	1	1.9	2.7	2.7	2.9	3.2	3.6	4.0	2.9	2.8	2.9	1.6	0.8
	2	1.8	2.0	1.7	2.3	2.6	2.7	2.7	2.4	1.1	1.0	0.8	0.5
	3	1.8	1.7	1.9	2.6	3.0	3.3	4.5	2.6	2.2	3.2	2.0	0.9
	4	2.4	2.5	2.7	2.9	3.3	4.2	3.2	2.9	2.3	1.5	0.9	0.7
Minutes per meal	1	25.2	32.6	30.5	32.3	36.1	41.8	20.9	32.2	51.7	85.6	64.2	45.2
	2	28.5	24.1	28.4	25.6	30.1	31.4	19.2	26.8	23.9	26.6	28.5	26.0
	3	36.5	27.2	28.9	40.6	43.0	45.0	25.7	31.4	46.3	94.2	70.0	45.3
	4	35.1	36.7	36.7	35.8	42.6	49.5	17.4	32.8	47.4	39.8	32.7	36.3

APPENDIX 2 (Continued)
Feeding measures for individual rats during Phase 2.

Measure	Rat	45- vs. 97-mg pellets											
		45-mg-pellet feeder, 97-mg-pellet FI (s)				97-mg-pellet feeder, 97-mg-pellet FI (s)							
		10	20	40	60	90	120	10	20	40	60	90	120
Grams per minute	1	0.11	0.18	0.19	0.18	0.20	0.20	0.16	0.23	0.11	0.07	0.05	0.04
	2	0.17	0.18	0.20	0.20	0.19	0.18	0.38	0.24	0.12	0.09	0.07	0.04
	3	0.16	0.15	0.08	0.16	0.19	0.19	0.25	0.20	0.08	0.08	0.05	0.04
	4	0.17	0.17	0.18	0.17	0.19	0.19	0.34	0.21	0.12	0.08	0.06	0.04
Grams per bar press	1	0.036	0.024	0.021	0.020	0.022	0.021	0.087	0.018	0.008	0.009	0.007	0.009
	2	0.028	0.028	0.029	0.025	0.027	0.031	0.091	0.036	0.023	0.016	0.013	0.010
	3	0.034	0.036	0.040	0.035	0.033	0.034	0.091	0.061	0.060	0.036	0.025	0.021
	4	0.037	0.037	0.037	0.038	0.038	0.038	0.084	0.031	0.022	0.023	0.019	0.014
Grams per day	1	12.2	18.4	16.2	17.9	19.0	15.1	12.0	10.2	10.0	8.8	7.4	10.2
	2	8.7	13.8	9.0	15.0	16.5	18.1	13.8	9.4	11.5	9.8	6.5	3.1
	3	9.3	12.2	10.7	13.9	17.2	19.8	17.3	14.6	12.3	11.5	8.0	5.3
	4	7.0	11.6	11.8	12.9	12.9	12.9	21.0	16.2	11.8	12.4	10.7	9.0
Grams per meal	1	2.9	4.6	4.0	4.1	4.2	3.6	3.0	3.4	2.6	1.8	2.6	2.1
	2	2.5	2.2	2.2	3.2	2.9	2.5	3.3	2.6	2.1	2.0	1.4	0.8
	3	2.3	2.9	2.4	3.7	3.7	4.5	3.2	3.7	2.6	2.4	1.5	1.0
	4	2.1	2.4	2.7	3.2	3.0	2.8	4.4	3.6	2.4	2.4	2.2	1.9
Minutes per meal	1	27.0	25.3	21.7	22.8	22.9	19.3	18.9	14.7	22.8	24.5	56.0	51.4
	2	14.2	11.7	11.5	16.1	14.9	13.6	8.6	11.0	17.0	22.3	20.0	17.2
	3	14.1	19.1	31.4	22.2	28.5	24.0	13.0	18.6	30.6	31.9	20.7	23.2
	4	12.7	14.5	15.1	18.6	16.6	14.5	12.9	16.8	20.3	30.8	38.0	44.5

APPENDIX 2 (Continued)
Feeding measures for individual rats during Phase 2.
20- vs. 97-mg pellets

Measure	Rat	20-mg-pellet feeder, 97-mg-pellet FI (s)										97-mg-pellet feeder, 97-mg-pellet FI (s)									
		10	20	40	60	90	120	150	180	10	20	40	60	90	120	150	180				
Grams per minute	1	0.08	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.30	0.22	0.12	0.08	0.05	0.04	0.03	0.03				
	2	0.08	0.08	0.09	0.09	0.09	0.08	0.09	0.09	0.35	0.21	0.12	0.08	0.05	0.04	0.03	0.03				
	3	0.07	0.06	0.08	0.08	0.08	0.08	0.08	0.08	0.27	0.21	0.10	0.08	0.05	0.06	0.03	0.03				
	4	0.07	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.34	0.22	0.11	0.08	0.06	0.04	0.04	0.03				
Grams per bar press	1	0.007	0.006	0.006	0.007	0.007	0.006	0.008	0.006	0.090	0.033	0.017	0.015	0.016	0.013	0.012	0.012				
	2	0.013	0.012	0.011	0.011	0.011	0.012	0.011	0.012	0.088	0.038	0.028	0.023	0.019	0.017	0.017	0.021				
	3	0.015	0.014	0.014	0.015	0.013	0.014	0.015	0.013	0.094	0.062	0.045	0.033	0.022	0.019	0.018	0.015				
	4	0.015	0.016	0.015	0.016	0.016	0.016	0.016	0.015	0.092	0.041	0.030	0.027	0.017	0.014	0.010	0.009				
Grams per day	1	8.6	9.4	11.5	10.7	13.4	17.7	16.8	22.0	18.2	19.3	13.9	12.6	11.2	10.0	9.7	7.0				
	2	8.9	8.5	9.5	10.5	11.5	13.7	12.7	10.2	14.8	14.9	12.9	12.8	11.5	6.4	7.4	10.5				
	3	5.4	7.4	11.9	8.8	11.5	10.4	10.1	14.4	21.9	17.1	12.4	16.0	11.5	12.1	11.6	7.9				
	4	6.2	9.8	8.9	10.9	13.8	10.7	14.2	14.6	19.0	15.6	15.4	13.7	11.3	16.5	10.7	9.0				
Grams per meal	1	2.5	2.5	2.3	2.1	2.0	2.8	2.9	4.2	4.3	3.7	2.8	2.6	2.1	1.9	1.9	1.4				
	2	1.9	1.9	2.0	1.9	2.1	2.0	2.3	1.5	3.2	2.5	2.3	2.2	1.9	1.1	1.8	1.5				
	3	1.4	1.5	2.3	1.8	2.0	2.4	2.3	2.8	5.8	3.6	3.5	3.0	2.9	2.8	2.6	1.6				
	4	1.6	1.8	1.9	1.9	2.4	2.2	2.3	2.8	3.8	3.7	3.2	2.7	2.5	3.0	2.5	1.7				
Minutes per meal	1	33.2	33.8	30.1	25.4	26.5	34.5	35.8	51.3	14.5	17.2	23.3	33.0	42.5	48.9	58.7	49.8				
	2	23.6	23.8	23.3	20.9	24.4	24.7	25.2	16.9	9.0	11.8	18.7	28.5	35.7	27.2	52.5	49.6				
	3	21.2	24.9	29.6	23.2	24.5	29.0	27.3	34.5	21.0	17.0	33.7	38.8	56.9	44.7	80.3	56.3				
	4	24.1	26.6	23.6	26.6	34.5	30.3	30.8	39.0	11.2	16.7	29.4	36.5	44.5	68.2	69.0	57.8				