

AN EXPERIMENTAL ANALYSIS OF THE COST OF FOOD IN A CLOSED ECONOMY

RICHARD BAUMAN

WALTER REED ARMY INSTITUTE OF RESEARCH

Rats lived in individual chambers in which the only food available was delivered for lever pressing. During Stage I, a fixed number of presses was required for each food pellet. As this fixed ratio of presses per food pellet was increased daily, a rat's daily intake of food was reduced. During Stage II, the cost of a food pellet was increased by replacing each fixed ratio with its interval equivalent. Each interval was a rat's mean time between the first press of a ratio and the delivery of a pellet during Stage I. During Stage II, only two presses were every required for a food pellet: The first press initiated a delay and the second activated the pellet dispenser after that delay elapsed. Food intakes for the series of fixed ratios and a rat's series of delay equivalents were very similar when plotted as a function of delay, but not when plotted as a function of presses per pellet. Consequently, the fixed ratio reduced food intake because larger ratios increased delay to food from the first press of a ratio. Observations and an analysis of interresponse times further revealed that as the fixed ratio increased, and local as well as overall rate of food intake decreased, lever pressing became more stereotyped. Because this increased stereotypy resulted in greatly increased rates of lever pressing, delay to food was minimized, and perhaps more importantly, so too was the reduction of a rat's baseline daily intake.

Key words: behavioral economics, closed economy, demand, cost, delay, lever press, rat

During the last 15 years, several psychologists have proposed that the laboratory tools of experimental psychology could be used to study certain basic economic principles (Allison, 1983; Hursh, 1980, 1984; Hursh & Bauman, 1987; Rachlin, Green, Kagel, & Battalio, 1976). One such principle is demand. Demand is defined as the relation between the consumption of a commodity and the cost of each unit of that commodity. According to economic theory and confirmed by empirical study (Deaton & Muellbauer, 1980), consumption of a

commodity decreases as its unit cost increases. Consequently, demand curves slope downward.

In laboratory studies of demand, an animal is required to live in a closed economy (Hursh, 1980, 1984) in which it must repeatedly execute a simple instrumental act for its entire daily intake of some biologically essential commodity. The unit cost of that commodity is typically increased by increasing the number of instrumental responses required to obtain each unit. In two such studies (Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988; Raslear, Bauman, Hursh, Shurtleff, & Simmons, 1988), rats lived in individual operant conditioning chambers in which the only food available was delivered for lever pressing; a fixed number of presses was required for the delivery of each 45-mg food pellet. The cost of each unit of food was increased by increasing the ratio of presses per pellet.

The resulting demand curves included the following effects: As the fixed ratio (FR) increased, food intake was initially constant as increases in output of presses offset increases in the FR. Further increases in the FR reduced food intake gradually, because increases in output failed to increase in exact proportion to increases in the FR. Ultimately, food intake decreased precipitously as continued increases

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in the FR resulted in an overall reduction in output of presses.

The question that the present study addresses is: Why does food intake decrease as the fixed ratio of presses per pellet increases? One answer to this question focuses on the number of presses required for the delivery of a food pellet. In studies such as that of Raslear et al. (1988), the smallest FR is typically one press per pellet and the largest is almost 300 presses per pellet. As a consequence, an adult rat who perfectly defends its daily food intake must increase its daily output of presses more than two orders of magnitude. For example, an average adult rat who consumes 500 pellets per day at a fixed ratio of one (FR 1) must execute 150,000 presses per day at FR 300 to defend the same daily intake. It is therefore possible that the sheer number of presses might be responsible for the ultimate decline of food intake in the Raslear et al. (1988) and Hursh et al. (1988) studies.

An alternative explanation focuses on time. If rate of lever pressing does not increase with the fixed ratio, then as daily output of lever presses increases, so too must the time between the first press of a ratio and food delivery. Because an increase in this time constitutes an increase in delay to reinforcement, and delay has been shown to be a potent determinant of the strength of operant behavior, food intake might decrease because the strength of initiating fixed ratios is weakened by increases in the delay to food from the first press of a ratio.

In the present experiment, the response-number explanation and the delay explanation were compared by first measuring a rat's food intake at each ratio in an increasing series of fixed ratios. The average amount of time between the first press of a ratio and the delivery of food was calculated for each ratio and, during the final stage of the experiment, each ratio was replaced by its interval equivalent. During this stage, only two presses were required for the delivery of a food pellet. The first press initiated a delay, and the second produced a food pellet after that delay had elapsed. If a rat's daily food intake is reduced by the series of intervals in a manner similar to that produced by the series of fixed ratios, and if the responses per pellet for each series are sufficiently different, then one may conclude that increases in the fixed ratio reduce food intake because they generate increasingly longer delays to food.

METHOD

Subjects

Six adult male Sprague-Dawley rats served as subjects. The weights of these rats ranged from 525 to 925 g.

Apparatus

Each rat was housed in a Coulbourn rat chamber (25 cm by 29 cm by 29 cm), which was enclosed in a ventilated, sound-attenuating fiberglass shell. At the center of the front wall of each chamber, a rectangular opening (3.2 cm wide by 4.1 cm) led to a recessed food trough. A lever was mounted 4.5 cm to each side of the opening into the food trough. A houselight was mounted about 2 cm from the ceiling directly above this opening. At the same level as the houselight, a Sonalert® (Coulbourn Module E12-02) was mounted about 3.5 cm from the left wall. The tube of a water bottle protruded through the center of the right chamber wall.

A PDP 11/73® computer and SKED-11® software were used to implement the experimental contingencies and record all data, including all lever presses executed with a force equal to or greater than 0.20 N and the accumulated time that elapsed between the first press of each ratio and the delivery of a 45-mg Bioserv food pellet.

Procedure

The houselight in each chamber was used to signal a 12-hr light/dark cycle. During each cycle, water was continuously and freely available, but a fixed number of lever presses was always required for the delivery of each food pellet. During the first stage of preliminary training, 30 food pellets were placed in each food trough and the left (food) lever was made available; the right lever was not available. Five pellets were placed on the left lever, and a single press on that lever resulted in the delivery of a food pellet. Aside from the 30 pellets that were placed in each food trough and the pellets that were placed on the left lever, no food was made available except what was delivered for lever pressing. After several (1 to 5) days in their chambers, each rat learned to press the left lever for its entire daily intake of food.

After each rat's food intake had become stable, the right lever was introduced and remained available for the remainder of the study.

During the last stage of preliminary training, a food pellet was delivered for alternating presses. A single press on the food (left) lever resulted in the delivery of a food pellet only if it was preceded by a single press on the right (changeover) lever. This changeover procedure was used because pilot experimentation revealed that if an FR contingency were programmed on a single lever, pressing frequently did not end immediately after the delivery of a food pellet. Because such response overruns compromised the integrity of the pause that followed the delivery of a food pellet (and, in the final stage of the study, prematurely triggered the onset of the delay equivalent of a fixed ratio), a single press on the changeover lever was always required after the delivery of one food pellet before any additional presses on the left lever could result in the delivery of another food pellet. At no time was a stimulus used to signal when a press on the right lever was required.

After each rat's daily food intake became stable, Stage I of the experiment was initiated. During this stage, the FR of left lever presses per pellet was increased. At 9:00 a.m., the onset of the houselight signaled a single step increase in the FR. Between FR 1 and FR 10, the ratio was increased by one or two presses per pellet. Beyond 10, each daily increase was 20% of the preceding day's FR value. The resulting series of FRs was 1, 2, 4, 6, 8, 10, 12, 14, 17, 20, 24, 29, 35, 42, 50, 60, 72, 86, 103, 124, 149, 179, 215, 258, 310, 372, and 446 presses per pellet.

During the day that each ratio was used, the time that elapsed between the first press of a ratio on the left lever and the delivery of a food pellet was accumulated separately for each 12-hr period (light or dark). A press on the changeover lever after the delivery of a pellet did not initiate the accumulation of time within a ratio. Only after the left lever had been pressed, following a press on the right lever, did time within a ratio begin to accumulate. Time spent pressing within a ratio continued to accumulate unless a rat paused more than 4 min between left lever presses. After a pause of more than 4 min, the timer was turned off and another press on the changeover lever was required before time within a ratio could continue to accumulate and additional presses on the left lever could continue to satisfy the fixed-ratio requirement. If a rat paused more than 4 min and did not

press the right lever, further presses on the left lever did not satisfy the ratio requirement and timing was not reinitiated. Although no stimulus was used to signal the necessity of a press on the right lever, feedback was arranged for left lever presses. As long as the changeover time or the time between successive left presses was less than 4 min, each left press activated the Sonalert for 2 ms.

The average delay to food during light and dark periods was calculated for the ratio in effect during that period by dividing the accumulated time spent pressing during a period (light or dark) by the total number of food pellets delivered during that period. During Stage II, these calculated averages served as the delay equivalents of each FR. That is, each delay was initiated by a single press on the food lever that followed the delivery of a pellet *and* a single press on the changeover lever. Because 27 fixed ratios were used and a delay equivalent was calculated for the light and dark period that a ratio was in effect, 27 pairs of delay equivalents were used for each rat. Each pair was imposed in the same order as the ratios were in Stage I.

RESULTS

The enormous quantity of individual data for each stage of the study necessitated the use of summary measures. Because individual differences in lever pressing affected both the delay to food from the first press of a ratio *and* the relation between food intake and the fixed ratio, it was necessary to preserve the data for individual rats. Consequently, summary measures were calculated for the light and dark periods. In so doing, the form of the individual functions was preserved and the overall data presentation was greatly simplified.

Stage I

The effect of the fixed ratio on the time to food from the first press of a ratio was evaluated by first computing the mean time to food for the dark period and light period that a ratio was in effect. Because more than two thirds of a rat's total food intake occurred during the dark period, the mean for each period was weighted by the relative amount of food consumed during that period and the sum of these weighted means was used as the average time to food from the first press of a ratio. These means are shown in Figure 1. The co-

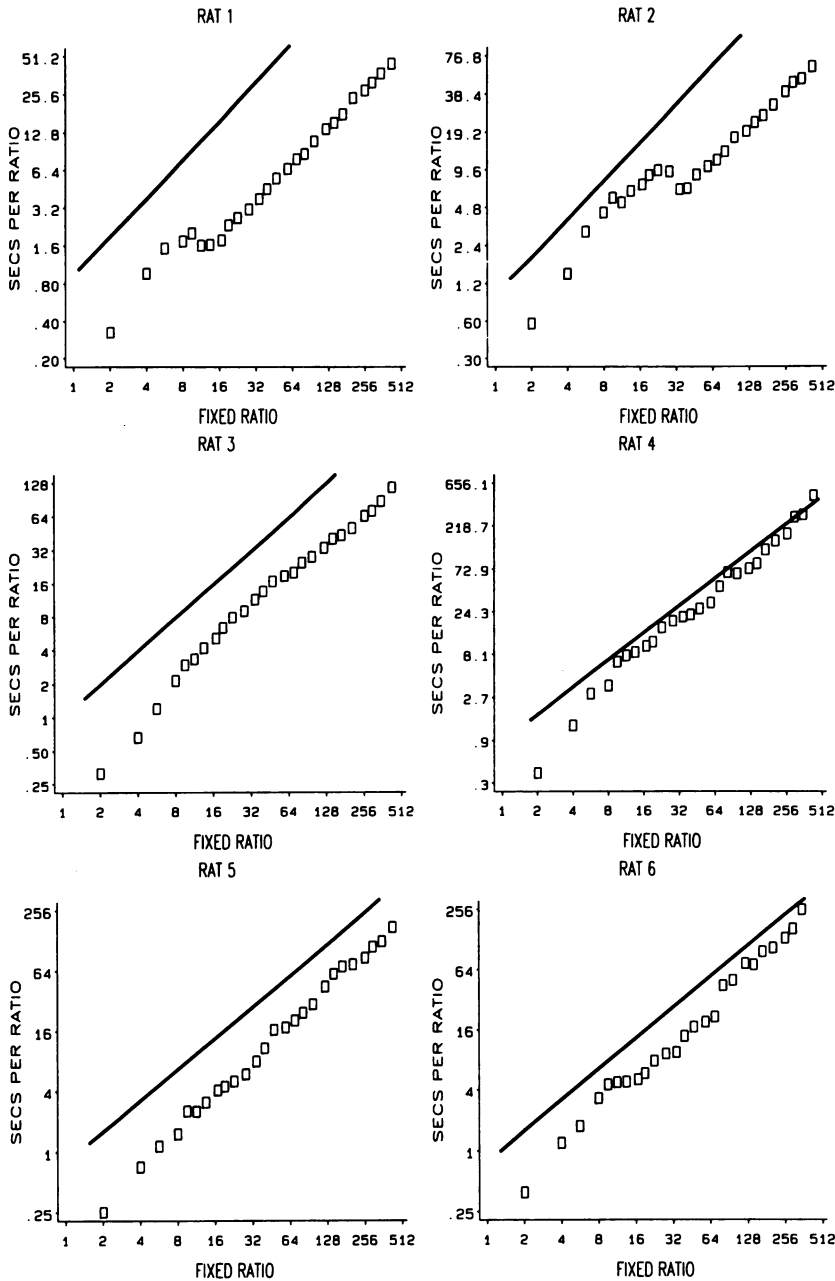


Fig. 1. Mean time between the first press of a ratio and food delivery for each rat at each fixed ratio. If the time between presses invariably equaled 1 s, all points would fall on the diagonal line in each plot.

ordinates are geometric because the FR increased geometrically beyond 10. All plots begin at FR 2 because at FR 1 the delivery of food was coincidental with the first press on the food lever. The diagonal line segment in each plot is included to show the trajectory

that mean time would follow if each additional press required for food added exactly 1 s to the total time to food from the first press of an FR.

In general, the mean time between the first food press and the delivery of a pellet increased

as the fixed ratio increased. Because the average time between presses within a ratio was almost always less than 1 s, the points in each plot remain below the diagonal line segment. However, there were significant individual differences. In particular, mean time to food decreased abruptly at FR 12 for Rat 1 and at FR 35 for Rat 2. As a consequence, increases in mean time to food were more continuous and spanned a wider range for Rats 3 through 6 than for Rats 1 and 2.

Daily output of lever presses and total food intake at each fixed ratio are shown in Figure 2 for all rats. Each point represents the sum of pellets or presses for the light and dark periods on a single day. Because the FR increased geometrically beyond 10, the axes are scaled geometrically. In all plots, daily output increased as the fixed ratio increased. Initially, these increases were sufficiently large to exactly offset increases in the ratio; hence, daily food intake remained constant. But, as the ratio continued to increase, the daily output of Rats 3 through 6 increased more slowly, so their food intake decreased gradually; eventually their output also decreased, at which point intake decreased precipitously. The food intakes of Rats 1 and 2 also decreased, albeit not precipitously, because they were able to sustain larger increases in their daily output over a wider range of fixed ratios.

The time between presses on the food lever is shown in Figure 3, in which the median interresponse time (IRT) for presses on the left lever is plotted at each fixed ratio. Each median IRT is a weighted sum of the median IRT for the 12 hr of light and the median IRT for the 12 hr of darkness that an FR was in effect; the weight for a photoperiod was again the relative frequency of food eaten during that period.

In general, median IRT on the left lever was not monotonically related to the fixed ratio, and for Rats 1 through 5 the similarity between successive median IRTs increased as the fixed ratio increased. This invariance is best illustrated by the median IRTs of Rats 1 and 2. Median IRT, as well as mean time to food (see Figure 1), abruptly decreased at FR 35 for Rat 2 and at FR 12 for Rat 1, rapidly stabilized, and remained approximately unchanged across the remaining ratios. Moreover, these relatively invariant IRTs (0.10 for Rat 1 and about 0.13 for Rat 2) were short

compared to the IRTs of the other rats, which suggests that such extremely high rates of lever pressing were an important determinant of the relatively large daily outputs of these rats (Figure 2).

In this study, the time that preceded the first lever press of a fixed ratio was an IRT. This IRT equaled the time spent switching from a press on the right (changeover) lever to a press on the food lever. Figure 4 shows the median changeover (CO) IRT for individual rats at each FR. In the same way that subsequent IRTs on the food lever were calculated, each median CO IRT for an FR was calculated as the weighted sum of the median CO IRTs for the photoperiods that an FR was in effect. In general, the CO IRT increased as the fixed ratio increased, although these increases were small or not evident for 5 of 6 rats (the exception being Rat 4) at fixed ratios less than 32.

Figure 5 shows the median time that elapsed between the delivery of a food pellet and a press on the right lever at each fixed ratio. These median postfood pauses were calculated in the same way that the IRTs were calculated. Postfood pause increased as the FR increased for all rats, although the pauses of Rats 1, 2, 3, 6, and perhaps 5 were little affected by ratios equal to or less than 32. A similar effect was noted for the CO IRT.

Stage II

The effect of delay to food from the first press of a ratio on food intake is shown in Figure 6. Each point is the sum of the food intakes for the light and dark periods on a single day, and each sum is plotted above the average delay that was in effect on that day. The average delays for each rat were plotted in Figure 1. To allow a comparison of intakes from Stages I and II, the food intakes for the series of fixed ratios are replotted from Figure 2. In general, food intake was reduced similarly by increases in the fixed ratio and by increases in the delay equivalents of those fixed ratios. Moreover, food intake was reduced more for those rats who incurred longer delays to food. The longest delay intervals for Rats 1 and 2 are considerably shorter than the longest delays for the other rats, and food intake was reduced least for Rats 1 and 2. Food intakes for Rats 1 and 2 also overlap more than the intakes for the other rats because, as shown in

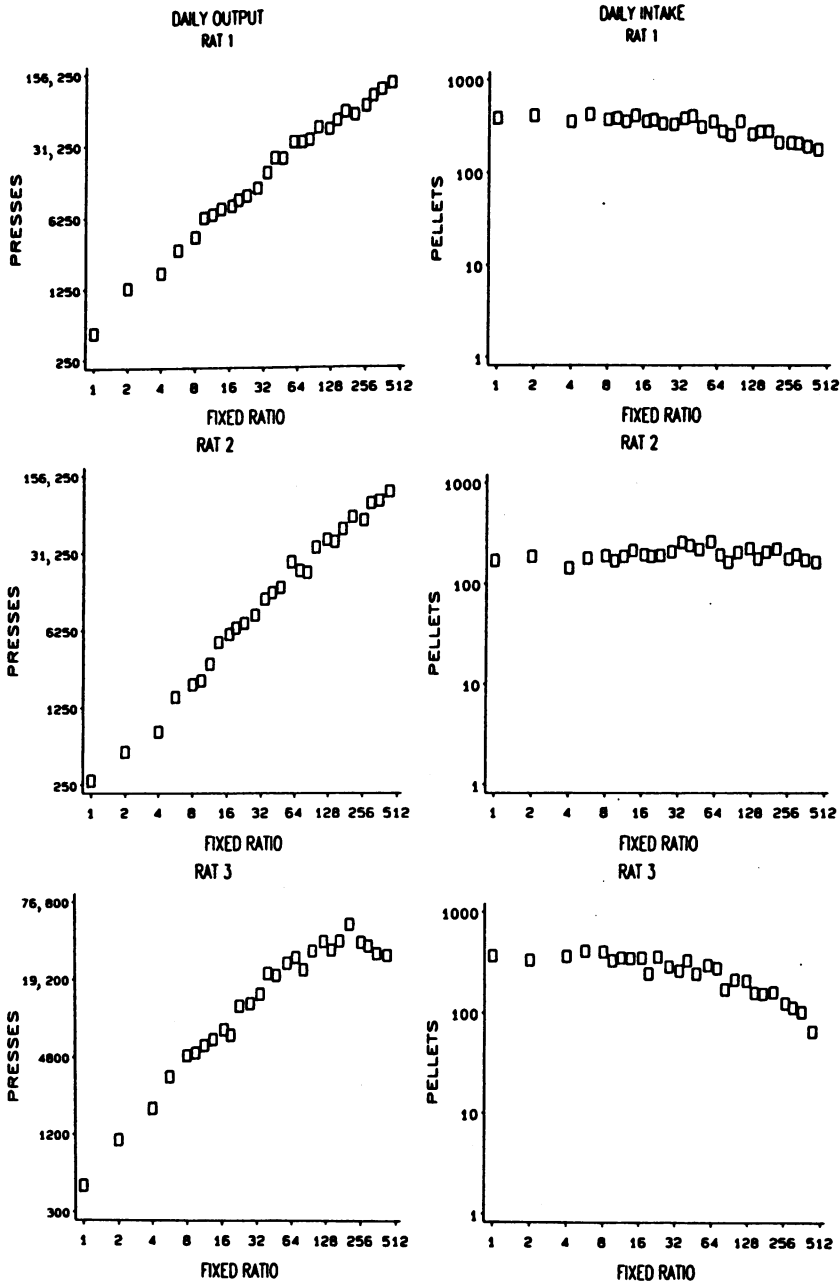


Fig. 2. Lever presses and food intakes for each rat at each fixed ratio.

Figure 1, mean time to food for Rats 1 and 2 was abruptly reduced.

Figure 7 shows the correlation for each rat between the ratio of presses per pellet for the series of delays and the series of fixed ratios. The ratio of presses per pellet for each delay or ratio was calculated by dividing the total

presses for a delay by the total food pellets delivered at that delay. If the presses per pellet for the series of fixed ratios and their delay equivalents were equal, then all points would fall along the positive diagonal in each plot. With the exception of Rat 1, the ratios of presses per pellet for the intervals are displaced from

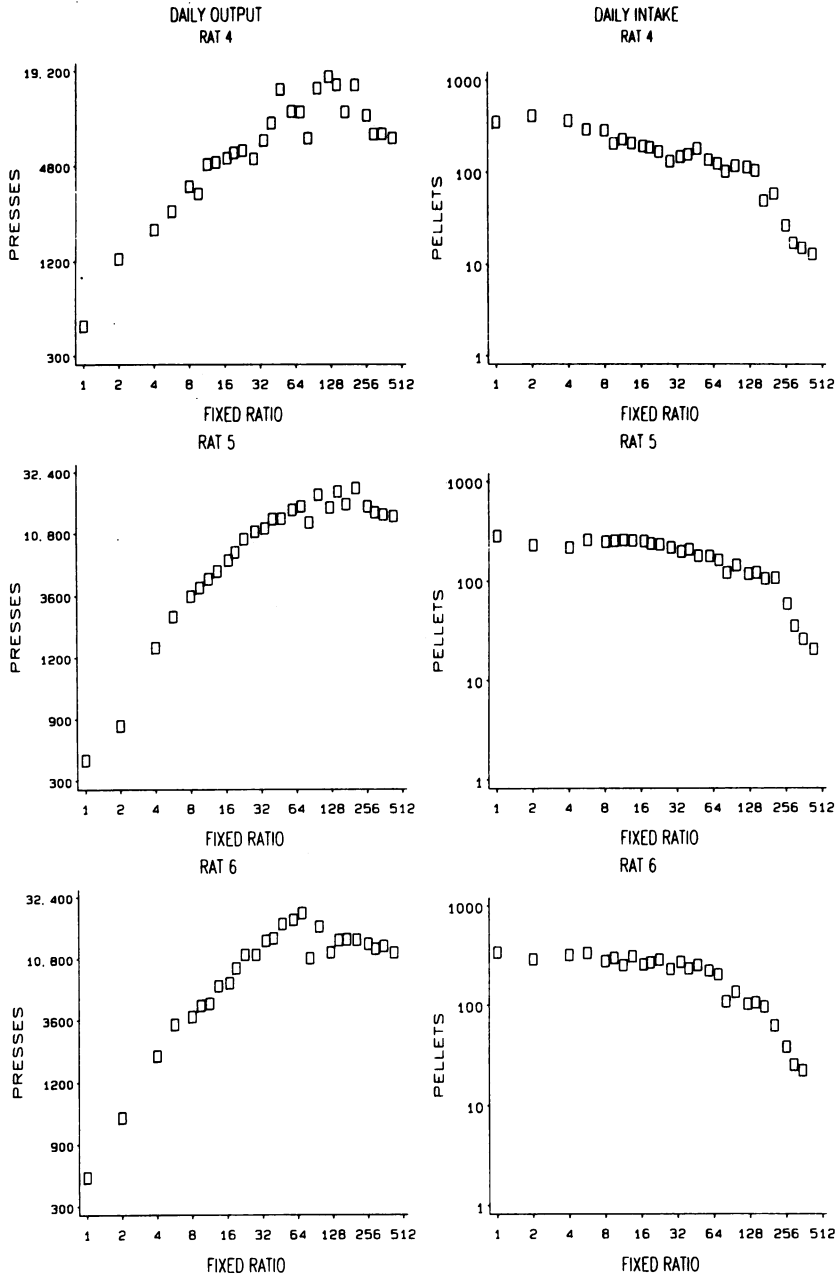


Fig. 2. Continued.

this diagonal. For Rats 3 through 6, presses per pellet for the delays are generally less than the presses per pellet for the fixed ratios, especially at the very largest of the fixed ratios. For Rat 2, presses per pellet for the delays were greater than presses per pellet for fixed ratios less than 32 and significantly less than

the presses per pellet for fixed ratios larger than 179.

In Figure 8, the food intakes for the series of fixed ratios and their delay equivalents are plotted at each of the presses per pellet that were shown in Figure 7. If the ratio of presses per pellet for each series were similar, then

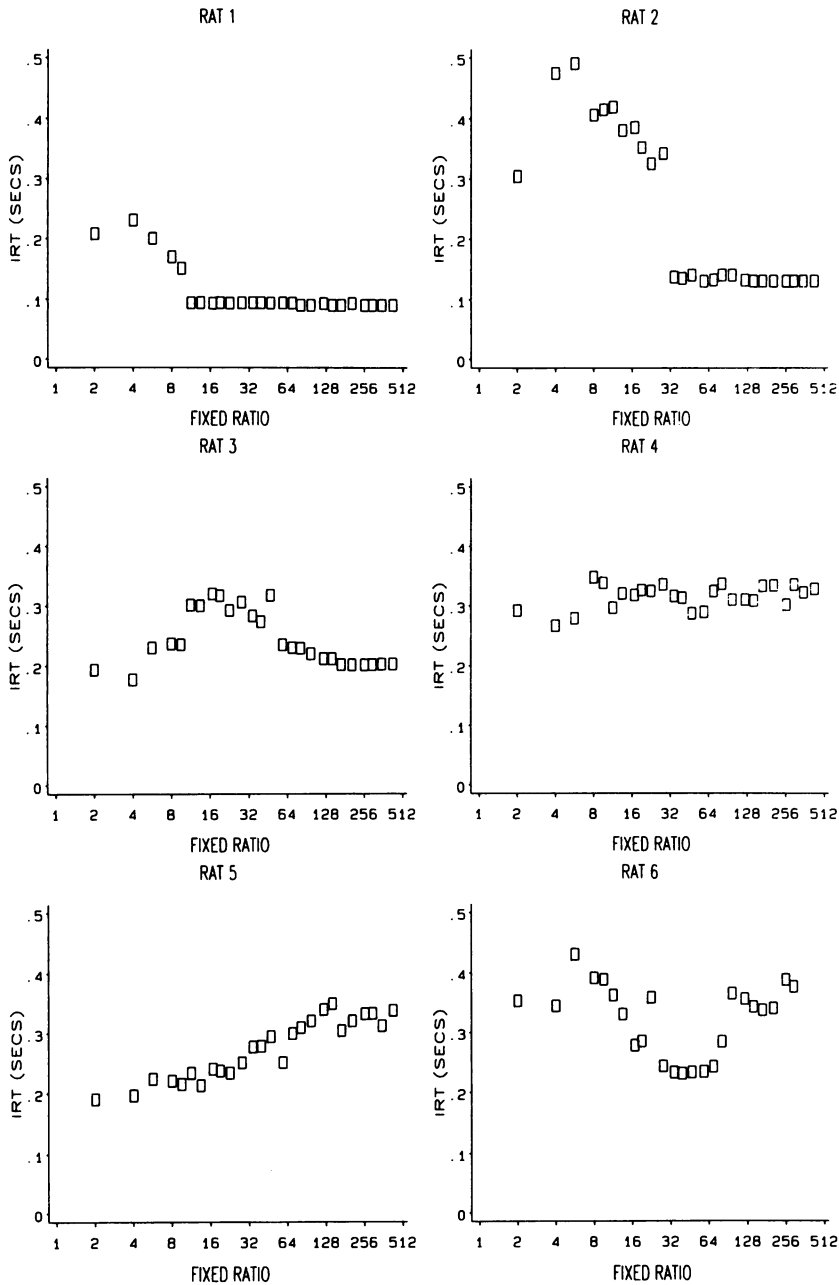


Fig. 3. Median IRT for each rat at each fixed ratio.

the food intakes for each ratio and delay equivalent would be located above the same point along the x axis. In general, this equivalence does not hold. The food intakes for the series of delays overlapped more, and were generally not a monotonic function of presses per pellet, as were the food intakes for the series of fixed

ratios. This absence of monotonicity is most noticeable for Rats 3 and 4, whose food intakes appear to cease being a function of presses per pellet at about FR 32.

The median changeover IRTs and median postfood pauses for the series of fixed ratios and their delay equivalents are shown in Fig-

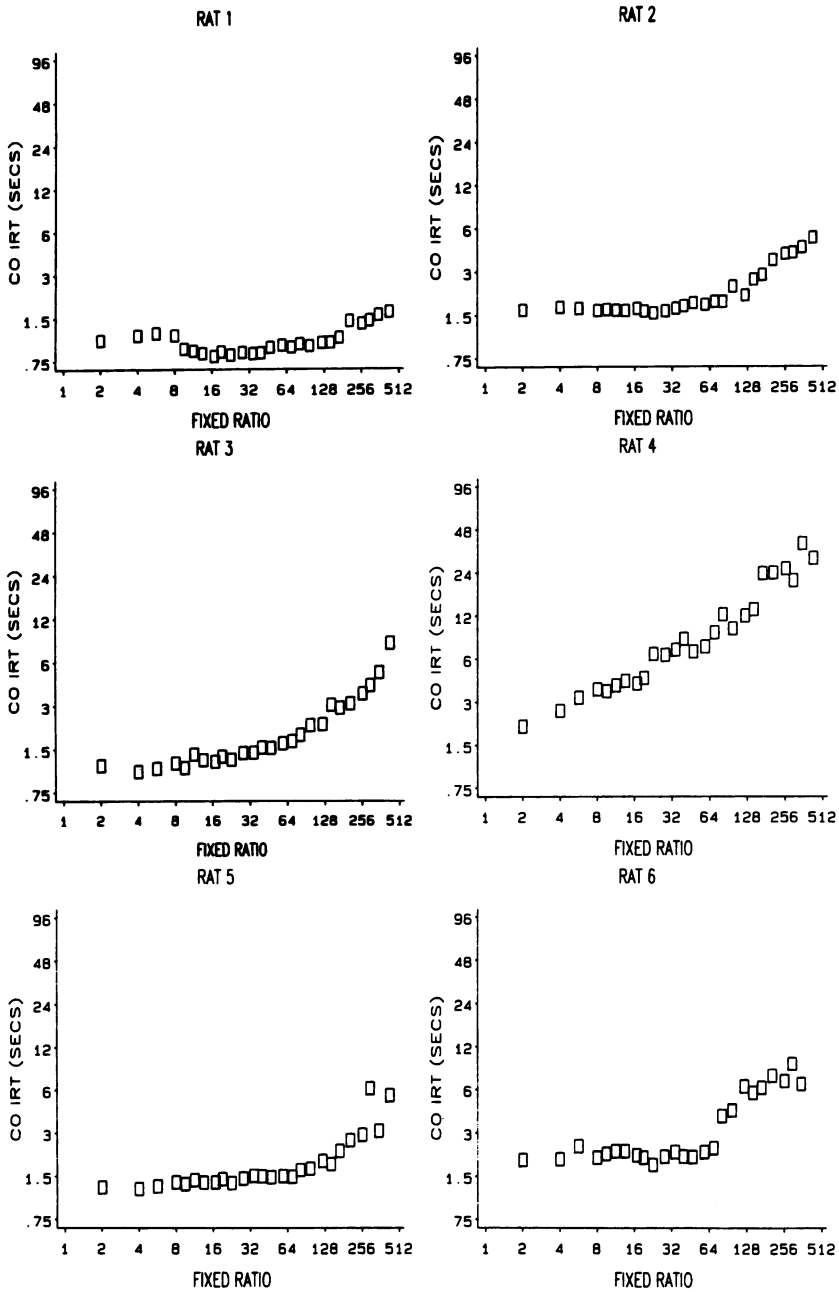


Fig. 4. Median changeover IRT for the first press of a ratio for each rat at each fixed ratio.

ures 9 and 10 for each rat. (An equipment problem rendered uninterpretable the detailed data for Rat 1 at FR 446.) In general, the changeover IRTs and postfood pauses increased as delay increased, and for Rats 2, 3, 4, and perhaps 6 median pause and median CO IRT were somewhat longer after com-

pleting a fixed ratio than after completing the delay equivalent of a ratio.

DISCUSSION

The objective of the present study was to isolate the effect of delay to food on the re-

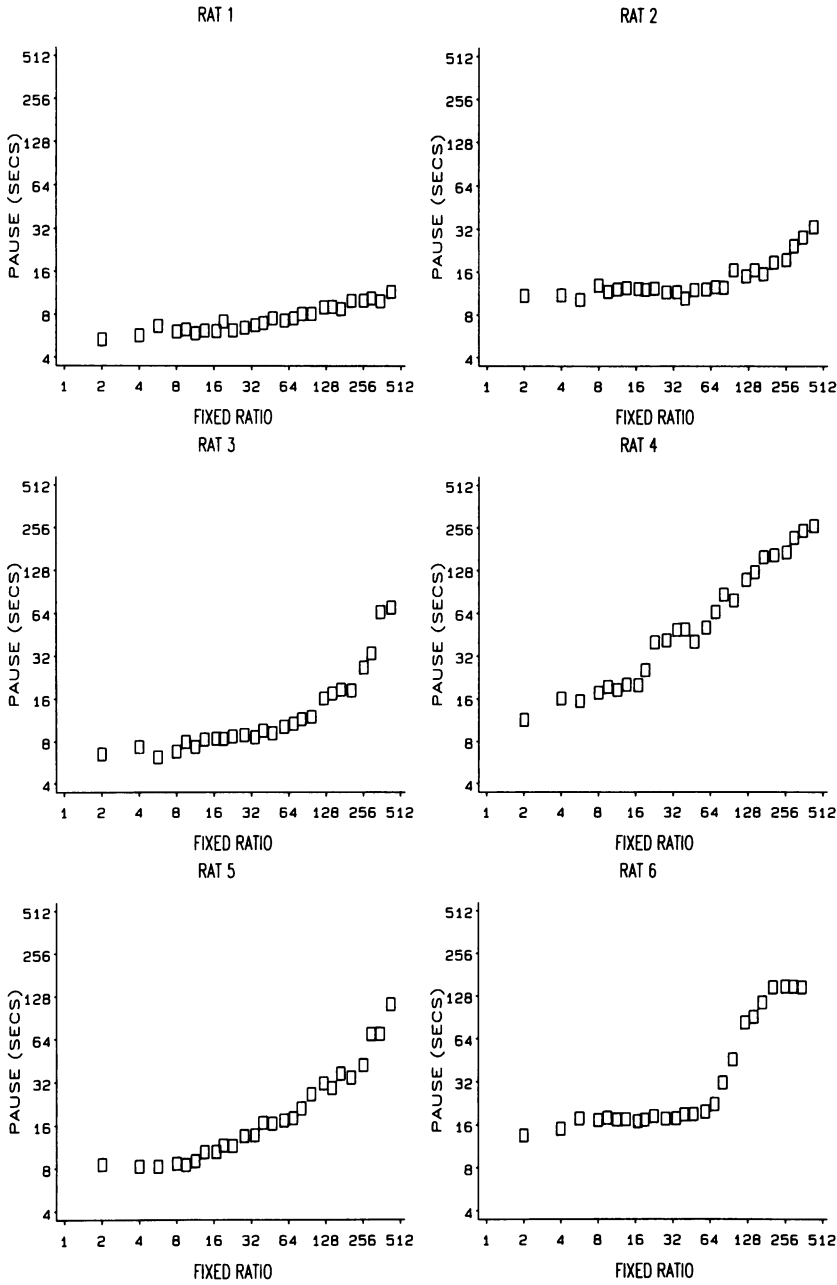


Fig. 5. Median postfood pause for each rat at each fixed ratio.

duction of food intake by the fixed ratio. This objective was accomplished in two stages. In Stage I, food intake was reduced as the fixed ratio and delay to food increased. In Stage II, this imposed correlation between the ratio of presses per pellet and delay was greatly reduced by imposing only the delay equivalent of each ratio. Nevertheless, food intake was

reduced to a similar extent by increases in the fixed ratio in Stage I and by the delay equivalents of these ratios in Stage II. In general, it follows that food intake was reduced by increasingly larger fixed ratios because these ratios increased the delay to food from the first press of a ratio.

In the terminology of behavioral economics,

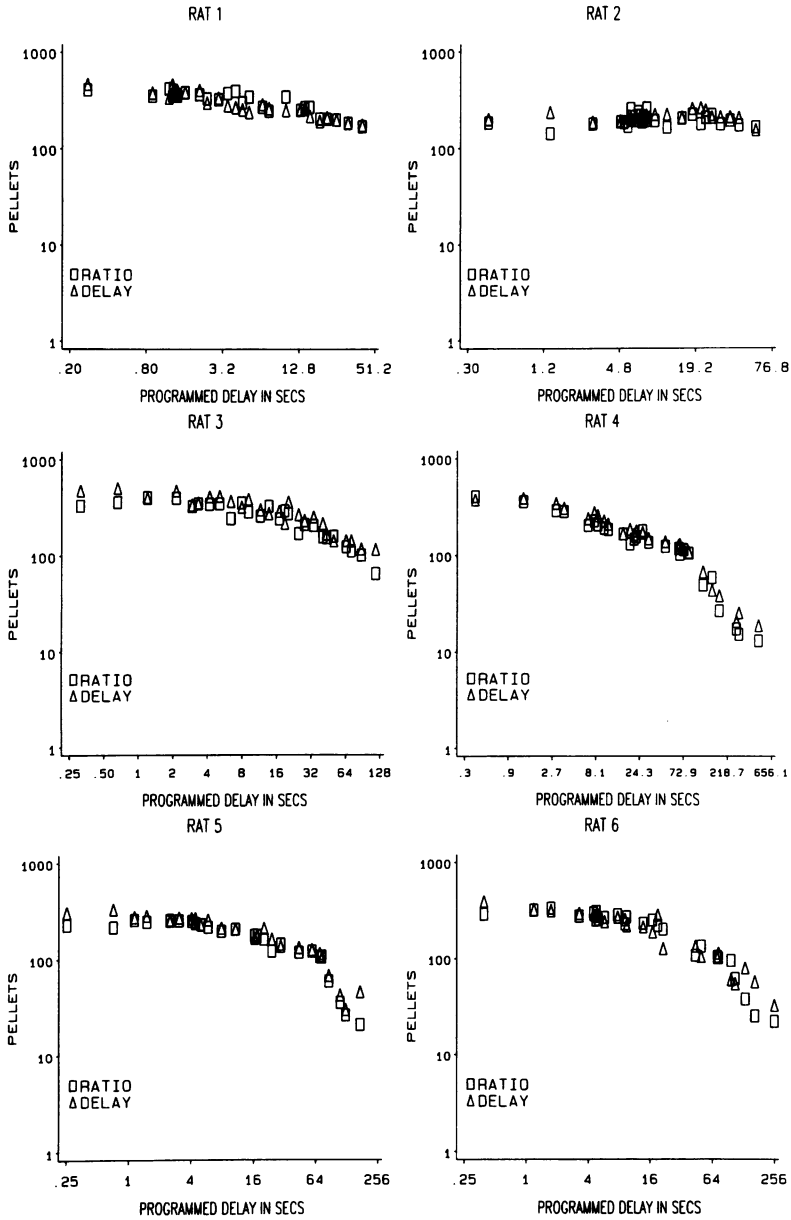


Fig. 6. Daily pellet intake for each rat at each fixed ratio and at the delay equivalent of a ratio.

increases in the fixed ratio function to increase the unit cost of food. Because the demand for food in the present study was reduced by the fixed ratio and by the delay equivalent of a fixed ratio, delay to food from the first press of a ratio is an important determinant of the unit cost of food in a closed economy. A recent finding by Hursh et al. (1988) reveals the general importance of this delay for the study of

demand. Hursh et al. studied the effects of lever weight (20 vs. 40 g), amount of food (one vs. two pellets), and pellet probability (.50 vs. 1.0) on a rat's demand for food. Separate groups of rats were used for each unique combination of weight, amount, and probability. As the FR was increased daily, the large lever weight reduced food intake more than the small lever weight at all ratios. However, this reduction

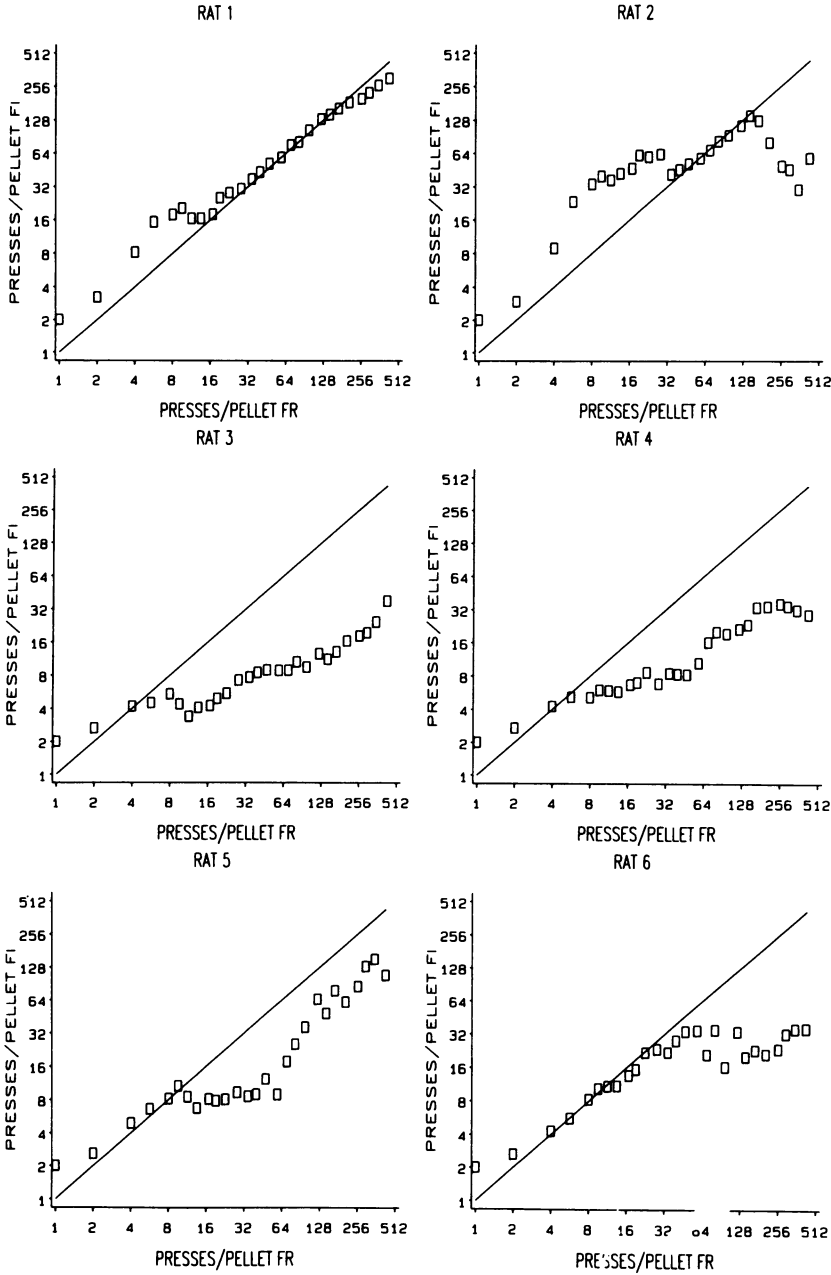


Fig. 7. Correlation between presses per pellet for each fixed ratio and each delay equivalent of a ratio.

could not be attributed exclusively to lever weight because median IRT and lever weight covaried. In particular, the median IRT for the large weight was approximately twice the median IRT for the small weight (see Figure 7 in Hursh et al.).

Delay between the first press of a ratio and food delivery might also be a determinant of

the cost of food in many of the laboratory simulations of foraging and studies of feeding reviewed by Collier (1982, 1983) and Collier, Johnson, Hill, and Kaufman (1986). A typical feature of these studies is that a chain of two fixed ratios (a procurement or search cost followed by a consumption cost) must be satisfied for access to a meal, defined as a bout of food

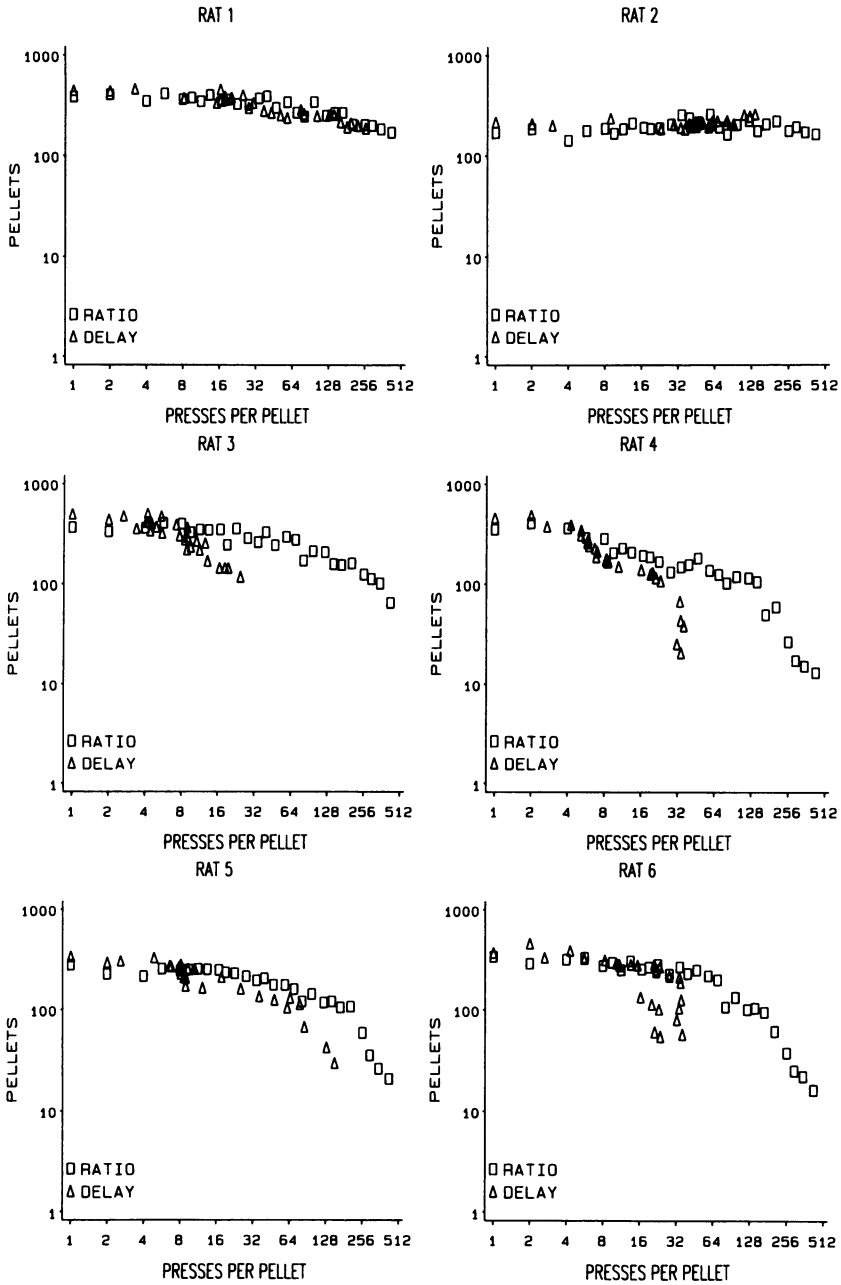


Fig. 8. Daily pellet intake for each rat at each fixed ratio and at the ratio of presses per pellet for each delay equivalent of a fixed ratio.

consumption that is not interrupted by a pause longer than 10 min. Two frequently reported findings of such studies are that, for a fixed consumption cost, meal frequency decreases and meal size increases as the procurement cost increases, whereas for a fixed procurement cost,

meal size (pellets per meal) decreases and meal duration increases as the consumption cost (presses per pellet) increases. Because increases in consumption or procurement costs are typically accompanied by an increase in the delay between the first press of a ratio and

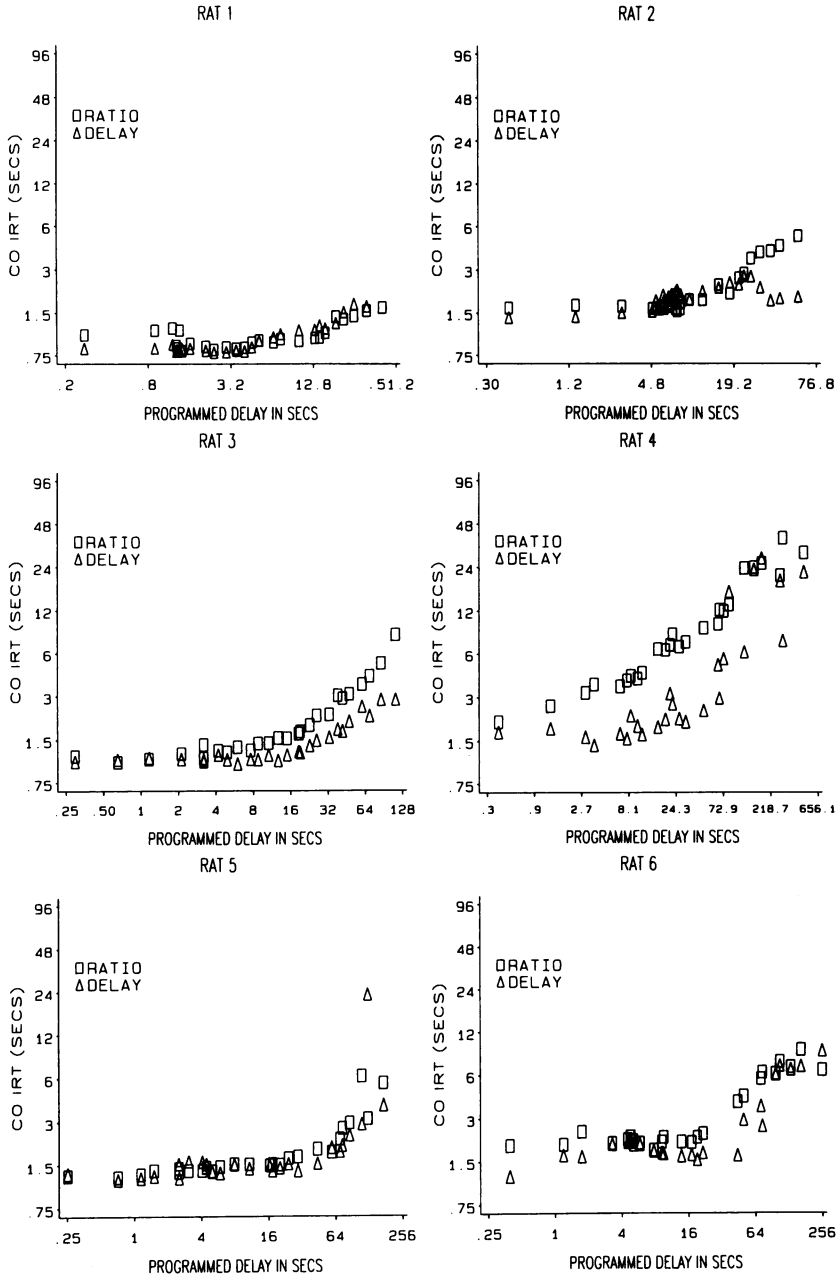


Fig. 9. Median changeover IRT for each rat at each fixed ratio and at each delay equivalent of a ratio.

access either to a meal or to a pellet, it is possible that meal size and frequency are reduced because ever-larger ratios support increasingly longer delays. Two qualifications of this explanation should be noted. First, these proposed reductions by delay do not explain the compensatory changes in meal size or meal

duration that occur as a consequence of increases in the procurement or consumption costs. The second is provided by Gannon, Smith, and Tierney (1986), who separately evaluated the rate, distance, and time of procurement (wheel running) on the intake of a saccharin-and-sucrose solution. Their data

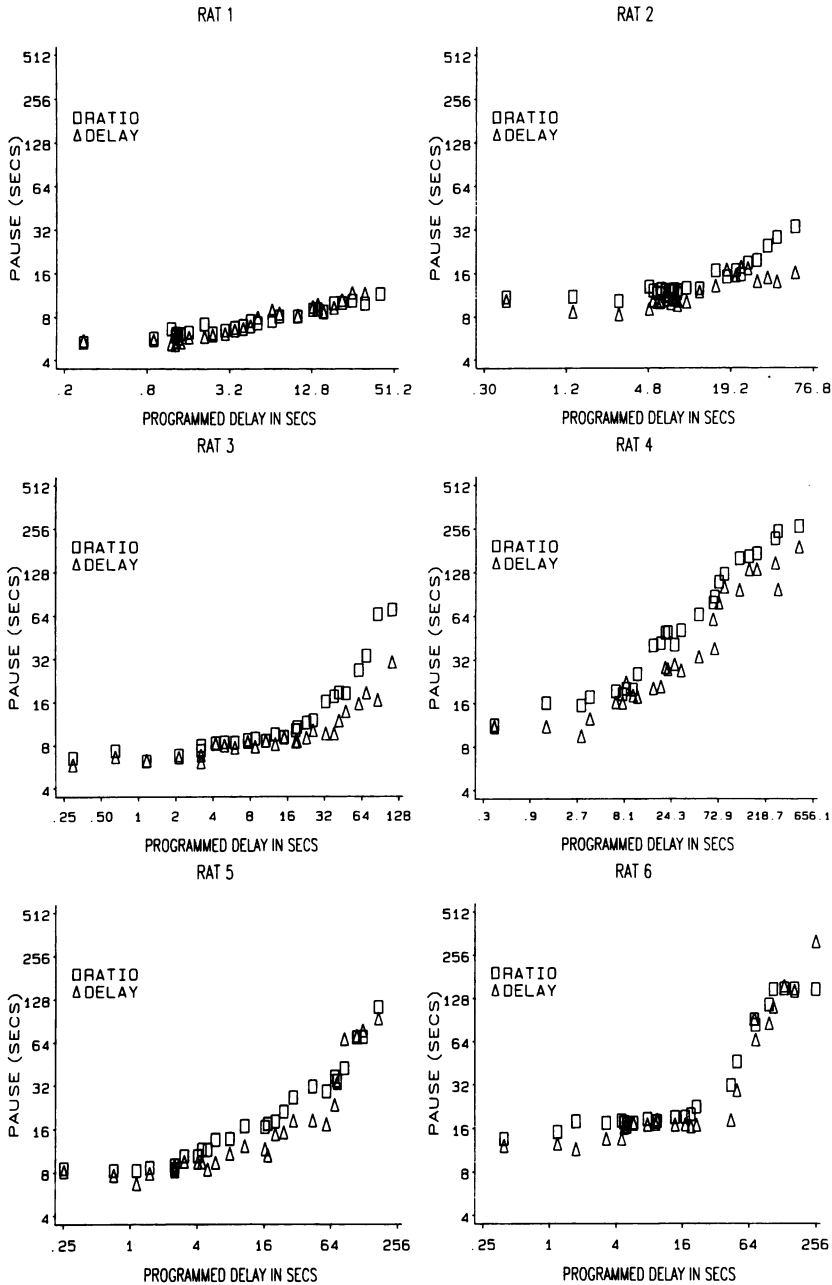


Fig. 10. Median postfood pause for each rat at each fixed ratio and at each delay equivalent of a ratio.

convincingly implicated the physical effort of executing an instrumental response as a determinant of the cost of food in a closed economy.

On the face of it, the reduced frequency or size of meals and the reduced demand for food can be explained by invoking the effect of delay on the strengthening effect of food: Increases

in delay to food weaken the reinforcing effect of food, which in turn reduces the frequency of initiating fixed ratios. In the present study, delay was defined as the time that elapsed between the first press of a ratio and the delivery of food. A more complete definition of delay might have included some fraction of the time that elapsed between a changeover press and

the first press on the food lever or perhaps some fraction of the postfood time. Some support for this suggestion can be found in a comparison of Figures 6, 9, and 10. For some rats, pause and changeover latency increased more for the series of ratios than for the series of delays (Figures 9 and 10). If some fraction of these latencies do contribute to the time cost of food, then food intake for the ratios should be reduced more than food intakes for their delay equivalents. In fact, Rats 3 and 4, which showed some of the clearest evidence for greater pause length and longer changeover times for the series of ratios, also seemed to take in somewhat less food at the very largest ratios than at their delay equivalents (see Figure 6).

Regardless of what the most complete definition of delay is, delay alone cannot explain the individual differences in the shapes of the food intakes curves shown in Figure 2. In other words, delay alone cannot explain why, for example, Rats 1 and 2 were able to sustain much larger outputs of lever pressing and thereby defend their daily food intakes more effectively than the other rats. The justification for this assertion requires a consideration of the finding that the fixed ratio affected both delay and the topography of lever pressing.

Daily observations of each rat's pressing in the present study revealed that, as the fixed ratio increased, all rats modified their topography of pressing. These modifications were most evident for Rats 1 and 2. At small ratios, each of these rats positioned itself in front of the food magazine and used its left paw to press the lever. But, as the fixed ratio increased beyond 10 for Rat 1 and 29 for Rat 2, each rat altered its position and posture. Rat 1 positioned itself directly in front of the lever and vibrated the lever with its head. Rat 2 adopted a position slightly to one side of the lever, from where it also used its head to vibrate the lever.

Independent evidence for these shifts in topography can be seen in the individual plots of median IRT. Notice that the median IRT for Rat 2 decreased from about 0.30 to about 0.13 s as the ratio exceeded 29, and the median IRT for Rat 1 decreased from about 0.20 at FR 2 to about 0.10 s as the ratio exceeded 10. Beyond FR 10 for Rat 1 and FR 29 for Rat 2, median IRTs were extremely invariant for both rats. This implies that lever pressing became more stereotyped.

An important question posed by this finding

concerns why lever pressing should suddenly become more stereotyped. Neither the emergence nor the persistence of this stereotypy is easily or parsimoniously explained by appealing to a decrease in the reinforcing potency of food, because it is well documented (e.g., Antonitis, 1951; Eckerman & Lanson, 1969) that operant behavior becomes less stereotyped as the density of reinforcement decreases and the density of reinforcement necessarily decreased as the fixed ratio increased.

The data in Figure 1 suggest a different explanation. As the pressing of Rats 1 and 2 became more stereotyped and IRTs shortened, the time to food from the first press of a ratio was reduced. Consequently, if the delay between the first press of a ratio and food delivery is in fact a principal determinant of the cost of food in the present study, then these shifts in topography effectively reduced that cost. Moreover, because the cost of food, as defined here, is an integral part of what Johnson and Collier (1987) have termed the *profitability* of food, these topographically mediated delay reductions constitute an increase in the profitability of food. It will be useful to consider the very similar results of Collier (1978) and Allison, Buxton, and Moore (1987) before addressing the functional significance of the minimization of cost in a closed economy.

In an extensive parametric study of the effect of effort on the feeding of cats, Collier (1978) factorially manipulated lever weight and the fixed ratio of lever presses for access to a meal. As the effort (FR \times lever weight \times 1 cm excursion) required for access to a meal was increased (these increases in effort were substantial given that the largest ratio was 10,240 and the largest lever weight was 1.3 kg), only 1 of his 2 cats was able to sustain its lever pressing at the largest ratio. The reason for this was that, in Collier's words, Cat 2

... shifted from a single paw bar press to a two-paw bar press at the heavier weights. It seems likely that this response strategy accounts for the ability of Cat 2 to respond at the higher response efforts. (p. 39)

Because the fixed ratio did not affect the local rate of lever pressing in Collier's study, increases in the fixed ratio necessarily increased the delay between the first press of a ratio and access to a meal. Based on the results of the

present study, it is therefore possible that the pressing of Cat 2 was maintained, at least in part, because its two-paw topography minimized the delay to a meal from the first press of a ratio.

In contrast to the topographical modifications in Collier's (1978) study and those of the present study, Allison et al. (1987) reported topographical shifts in the contingent response. In all of Allison et al.'s experiments, rats were required to execute a ratio of lever presses for access to a water tube. Once this instrumental ratio of presses was satisfied, a contingent ratio of licks had to be emitted before additional pressing could result in another opportunity to drink. In two of their experiments, rats reduced a high nominal cost of water, defined as a large number of presses per lick, by licking more efficiently. As a consequence, more water was consumed per lick, which, in Experiment II, allowed rats to greatly increase their total water intake despite the fact that both total licks and lever presses were reduced significantly by the higher costs of water.

The apparatus used by Allison et al. (1987) also supported a reduction in the cost of water. During the 0.5 s that it took the solenoid-driven shutter to close over the water spout, rats executed extra licks, the number of which increased as the nominal cost of water increased. A similar reduction in cost may have occurred in the present study. That is, it is conceivable that the thin Coulbourn rat lever may have rendered it more manipulable than either the thicker Grason-Stadler rat lever or the T-bar type of lever. As a consequence, increases in the fixed ratio may have induced a wider range of effective lever-press topographies, some of which resulted in a reduced delay to food from the first press of a ratio.

Perhaps a more important procedural support for the topographical modifications reported by Allison et al. (1987), Collier (1978), and those observed in the present study can be traced to the fact that all of these studies were conducted in a closed economy. Unlike an open economy, in which feedback from a subject's operant behavior is minimized or eliminated by using ballistic-like responses (e.g., a key peck), variable-interval schedules, short experimental sessions, and free food to keep a subject's body weight constant, the cost and benefit of a subject's operant behavior in a closed economy is predicated on the opportu-

nity for the different dimensions (e.g., frequency and topography) of that behavior to feed back into that subject's intake of the only food or water available to it. In particular, more efficient licking by rats in the high-cost group in Experiment II of Allison et al. eliminated any difference between their total water intake and the water intake of rats in the low-cost group. Similarly, an increase in the stereotypy of lever pressing by rats in the present experiment minimized the reduction of their daily food intake from what it was at FR 1. It is in this sense that topographical shifts that minimize cost acquire functional significance in a closed economy.

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