JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 1991, 56, 445-454 NUMBER 3 (NOVEMBER)

# AN ECONOMIC ANALYSIS OF "DEMAND" FOR FOOD IN BABOONS

RICHARD W. FOLTIN

THE JOHNS HOPKINS UNIVERSITY SCHOOL OF MEDICINE

Responding of 6 adult male baboons (*Papio c. anubis*) was maintained under a fixed-ratio schedule of food reinforcement during daily 22-hr experimental sessions. Completion of the ratio requirement resulted in the delivery of a single 1-g food pellet; supplemental feeding was limited to a daily fruit ration. Ratio values were increased on Mondays, Wednesdays, and Fridays according to the following schedule: 2, 4, 8, 16, 32, 64, 96, 128. Responding under each ratio value was examined four times. Under the Fixed-Ratio 2 conditions, food intake ranged between 300 and 600 g. Ratios were increased for each baboon until food intake decreased to about 100 g (20% to 30% of Fixed-Ratio 2 intake). Increasing the response cost increased total time responding and total daily responding in all baboons, but this increase in responding was not sufficient to maintain stable food intake. Baboons responded between 90 and 180 min per day. The highest running response rates were observed under the Fixed-Ratio 2 and Fixed-Ratio 4 schedules. Running rate was similar across the larger ratio values (greater than Fixed-Ratio 8) but was lower than that observed under the Fixed-Ratio 2 and Fixed-Ratio 4 schedules. Similar results were observed the four times that each fixed-ratio value was tested. Intake as a function of cost was analyzed by fitting data to the nonlinear equation proposed by Hursh, Raslear, Shurtleff, Bauman, and Simmons (1988) for "demand" functions. Demand for food was inelastic over most of the ratio values until food intake decreased to 15% to 55% of baseline. The results indicate that demand functions are appropriate for the study of food intake in baboons, but also caution that intake at the cost when demand shifts from inelastic to elastic and its relationship to maximal intake should also be included in analyses of demand for a commodity.

*Key words:* economic analysis, demand curve, food intake, fixed ratio, lever pull, baboon

The basic tenet of behavioral economics is that reinforcing function is a dynamic process dependent upon environmental circumstances that can be understood only by studying changes in intake as a function of changes in cost (Allison, 1981, 1983; Hursh, 1980, 1984; Hursh & Bauman, 1987; Lea, 1978). In laboratory studies, cost is manipulated by changing the operant response requirement for the delivery of a unit of the reinforcer. Analysis of intake at a single cost provides data on the value (amount taken) of that reinforcer at that cost, but value often changes as cost changes. When intake is measured as a function of increasing cost, it is possible to describe reinforcement in more general "demand" terms. When responding (consumption) stays high in response to increasing cost, demand is said to be inelastic, but when responding decreases in reponse to increasing cost, demand is said to be elastic. The importance of evaluating reinforcement at more than one response cost has been clearly demonstrated in the analysis of intracranial self-stimulation (ICSS) by rats and food intake by rats with ventromedial hypothalamic (VMH) lesions. Although food delivery to VMH obese rats (Miller, Bailey, & Stevenson, 1950) and ICSS (Hursh & Natelson, 1981) maintained large amounts of responding under continuous reinforcement conditions, response rates decreased abruptly with increased cost, indicating that the demand for these reinforcers was elastic.

Demand functions are dynamic in that demand varies nonlinearly as a function of cost. Intake will initially remain stable (or decrease slightly) with small increases in cost, but as cost accelerates, intake will eventually decrease. The cost at which intake begins to decline abruptly varies across commodities and can be used as an index of the overall demand for a commodity. Thus, reinforcers necessary for existence, such as food and water, have inelastic demand across a greater range of costs than nonessential, or luxury, items (e.g., recreational activities). Hursh, Raslear, Shurt-

---

This research was supported by Grant DA-4130 from The National Institute on Drug Abuse and was approved by the Johns Hopkins Animal Care and Use Committee. The assistance of James Thomas, Michelle Woodland, Thomas Kelly, and Marian Fischman is gratefully acknowledged.

leff, Bauman, and Simmons (1988) have developed a nonlinear equation with three constants that can be fitted to demand curves. This equation provides estimates of (a) the initial level of intake (i.e., value at minimal response cost), (b) the initial slope of change in intake as a function of change in cost, and (c) the rate at which the slope changes as a function of cost. From these fitted parameters it is possible to determine the response cost at which intake abruptly declines. The present study evaluated the utility of the Hursh et al. (1988) analysis in describing demand curves generated in baboons for food.

## METHOD

### *Subjects and Apparatus*

Six adult male baboons (*Papio cynocephalus anubis*), ranging in weight from 23.0 to 62.1 kg, were housed in standard primate cages (about 0.94 m by 1.21 m by 1.52 m high for the 4 larger baboons and 0.82 m by 0.94 m by 1.2 m high for the smaller baboons). Five of the baboons (all except X-3639) had 1 to 4 years experience responding under a two-component chain schedule of food delivery. The first component required completion of a fixed number of responses, whereas each lever pull during the second component resulted in the delivery of a food pellet.

The light-dark cycle was controlled by natural light. Chewable vitamins (Goldline) and a piece of fresh fruit (80 to 100 kcal) were given daily. Water was available ad libitum. Because of the necessity of sedating baboons to determine body weight, they were weighed once before and once after the 3-month study. Attached to the front of each cage was a panel holding a food hopper, two stimulus lights, a Lindsley lever (Gerbrands), and a pellet dispenser (BRS-LVE model PDC-005). All schedule contingencies were programmed using an Apple IIe® computer in an adjacent room.

### *Procedure*

Responding was maintained by food delivery (Formula L® banana-flavored 1-g food pellets containing 3.7 kcal/g: 21.0% protein, 4.7% fat, 62.0% carbohydrate, 5.3% ash, 3.1% moisture, and 3.0% fiber; Noyes) under a fixed-ratio (FR) schedule. A 30-s timeout, during which responses, although recorded, had no programmed consequences, followed each pellet delivery. If a baboon had not completed the response requirement within a limited-hold (LH) period that varied with the response requirement (LH = FR value × 5 s), the 30-s timeout was initiated and the ratio was reset. The schedule was in effect 22 hr per day, from 11:00 a.m. to 9:00 a.m. the following morning. The remaining 2 hr of the day were used for cage and subject maintenance. Illumination of a red stimulus light indicated the availability of food. During the timeout and cage maintenance periods, no stimulus was illuminated. Initally, the FR requirement was at two responses for 30 days. After this acclimation period, the response requirement was increased on Mondays, Wednesdays, and Fridays until total daily food intake decreased to about 100 g. Response costs were changed on the same days each week, rather than every other day, to minimize the possibility of inadvertently not changing a ratio value. The response requirement was then systematically decreased until responding was maintained under an FR 2 schedule of food delivery. The response requirement was then systematically increased and decreased again for a total of four determinations of the effects of changing response cost on food intake. The specific ratio requirements varied among the baboons. Responding of A-22, A-33, X-29, and X-3639 was maintained under the following ratios: 2, 4, 8, 16, 32, 64, 96, 128. Responding of V-3 was maintained under the following ratios: 2, 4, 8, 16, 32, 48 (64 was tested once). Responding of R-82 was maintained under the following ratios: 2, 4, 8, 16, 32.

### *Data Analysis*

Data collected on the 2nd day of each FR condition (3rd day if the FR was changed on Friday) were included in the analysis. Total intake, number of responses that led to food delivery, responses emitted during the timeout period, uncompleted ratios, running rate (number of responses divided by time of last response minus time of first response, expressed as responses per second for completed ratios only), and duration of responding (the sum of the durations used to calculate running rate) were recorded daily. Running rate did not include responses emitted during timeout periods or responses contained in uncompleted ratios.

Data were fitted to the nonlinear equation proposed by Hursh et al. (1988) using the Systat® statistical package:

$$\ln Q = \ln L + b(\ln P) - aP,$$

where $Q$ is total daily intake of 1-g food pellets, $P$ is the fixed-ratio value, and $L$, $b$, and $a$ are fitted parameters. $L$ is the predicted consumption under an FR 1 schedule of reinforcement, $b$ is the predicted initial slope, and $a$ is the predicted acceleration in slope with FR value. The predicted FR value at which responding was maximal (the point at which intake started to drop abruptly) was calculated using the formula $(1 + b)/a$. The first and third series of determinations of the effects of changing response costs involved an ascending sequence of FR values with the maximal value included in the calculations. The second and fourth series involved a descending sequence of FR values and did not include the maximal value (otherwise the same maximal values would have appeared in two sets of calculations).

Pellet deliveries separated by less than the limited-hold duration plus 10 min were classified as occurring in a single meal. Similar 10-min minimal intermeal intervals have been widely used in studying the topography of food intake in research animals (e.g., Collier, Hirsch, & Hamlin, 1972; Foltin & Fischman, 1988, 1990). Due to the relatively consistent intake at each FR value across the four determinations, cumulative intake curves were generated under each FR value only for the last series of determinations including the maximal value.

## RESULTS

Figure 1 presents total intake and responses emitted daily for the 4 baboons who were tested under FR values to 128. Data are presented for each of the four determinations of the effects of manipulating the response requirement. Except for responding maintained under the FR 4, FR 8, and FR 128 schedules of food delivery during the first series of determinations, food intake of A-22 was similar across the four determinations. Table 1 presents the fitted parameters of the equation proposed by Hursh et al. (1988) for each baboon and series of determinations. The fitted equation accounted for only 50% to 81% of the variance in intake as a function of increasing cost for this baboon. Of all the baboons, this one's intake remained the most stable as cost increased such that there was little evidence of the predicted decline in intake at large costs; this explained the limited variability accounted for by the equation. About 20,000 responses per day were emitted when the reinforcement schedule varied between FR 64 and FR 128. The predicted cost that would maintain maximal responding varied between 193 and 583, indicating that demand for food was inelastic across the range of response costs tested here.

The upper right panels of Figure 1 also present the data for A-33. Food intake decreased with increasing response cost, with the greatest decrease observed under the FR 128 schedule during the first series of determinations. The increases in responses per day were correspondingly lower than those observed with A-22. As with A-22, similar numbers of responses were emitted as the FR value increased from 64 to 128. With the exception of Series 3, predicted maximal intake ($L$) was consistent across determinations, but the cost with predicted maximal responding varied between 28 and 101 (assuming that the 560 value associated with Series 3 was an anomaly). Both X-29 and X-3639 responded to increases in response cost in a fashion similar to A-33: (a) food intake decreased with increasing FR value, (b) responses increased with increasing FR value, (c) a similar number of responses were emitted as the FR was increased from 64 to 128, (d) predicted maximal intake was consistent across the four determinations, and (e) the predicted cost maintaining the most responding was variable across series. For all 4 baboons, the patterns of changes in daily intake and responding were similar across the four determinations of the effects of manipulating response cost on food intake.

Figure 2 presents total intake and responses emitted daily for the 2 baboons who were tested under FR values to 32 (R-82) or 64 (V-3). Food intake of R-82 decreased with increasing response cost, whereas total daily responding increased to 3,000 responses under the FR 16 schedule and then decreased under the FR 32 schedule. With the exception of Series 4, maximal intake and the predicted cost with maximal responding were consistent across series, and both values were smaller than observed with the baboons whose data are presented in Figure 1. A similar pattern of results was evident for V-3. In this case, with the exception

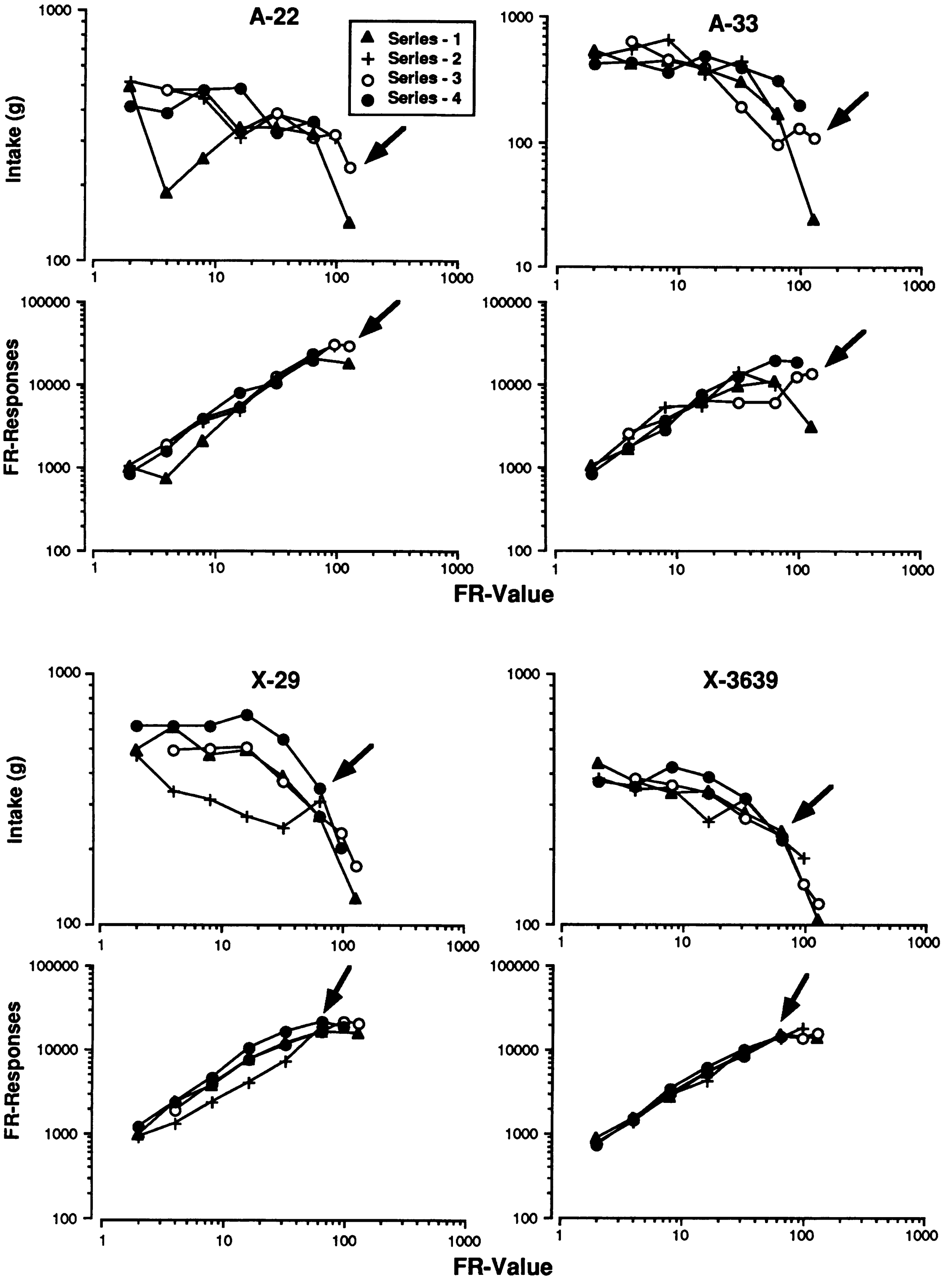

Fig. 1. Food intake and number of FR responses emitted daily as a function of FR response requirement for each baboon tested with FR values to 128, plotted using log scales. The effect of changing the response cost was determined four times with FR values ascending in Series 1 and 3 and descending in Series 2 and 4. Arrows indicate the predicted FR value with maximal responding during the fourth determination.

Table 1

Parameters of nonlinear demand curves.

| | | Parameter | | | | |
|---|---|---|---|---|---|---|
| Baboon | Series | $L$ | $b$ | $a$ | Peak | $r^2$ |
| A-22 | 1 | 405.9 | −0.018 | 0.005 | 203.6 | 0.523 |
| | 2 | 582.3 | −0.167 | −0.002 | 583.5 | 0.755 |
| | 3 | 548.4 | −0.101 | 0.002 | 550.5 | 0.815 |
| | 4 | 411.7 | 0.033 | 0.005 | 193.4 | 0.499 |
| A-33 | 1 | 426.8 | 0.151 | 0.028 | 30.3 | 0.985 |
| | 2 | 460.6 | 0.192 | 0.029 | 27.9 | 0.999 |
| | 3 | 1,823.8[a] | −0.680 | −0.003 | 560.0 | 0.933 |
| | 4 | 387.5 | 0.085 | 0.009 | 101.7 | 0.585 |
| R-82 | 1 | 333.8 | 0.096 | 0.065 | 13.9 | 0.978 |
| | 2 | 333.9 | −0.003 | 0.038 | 26.4 | 0.967 |
| | 3 | 297.7 | 0.332 | 0.083 | 8.0 | 0.999 |
| | 4 | 412.8 | −0.227 | 0.009 | 136.3 | 0.904 |
| V-3 | 1 | 421.1 | −0.278 | 0.016 | 79.9 | 0.986 |
| | 2 | 391.5 | 0.036 | 0.040 | 24.1 | 0.995 |
| | 3 | 324.3 | 0.053 | 0.030 | 31.6 | 0.997 |
| | 4 | 331.2 | 0.163 | 0.049 | 17.1 | 0.983 |
| X-29 | 1 | 534.5 | 0.029 | 0.012 | 80.9 | 0.957 |
| | 2 | 569.3 | −0.361 | −0.014 | 97.2 | 0.950 |
| | 3 | 565.1 | −0.034 | 0.008 | 129.3 | 0.974 |
| | 4 | 554.1 | 0.151 | 0.017 | 49.9 | 0.957 |
| X-3639 | 1 | 409.5 | −0.016 | 0.009 | 112.9 | 0.954 |
| | 2 | 392.6 | −0.062 | 0.005 | 212.4 | 0.882 |
| | 3 | 420.2 | −0.042 | 0.008 | 130.3 | 0.988 |
| | 4 | 340.5 | 0.127 | 0.015 | 58.2 | 0.985 |
| $M$ | 1 | 421.9 | −0.006 | 0.023 | 86.9 | 0.901 |
| $SE_M$ | | 26.4 | 0.061 | 0.009 | 27.6 | 0.076 |
| $M$ | 2 | 455.0 | −0.061 | 0.016 | 161.9 | 0.925 |
| $SE_M$ | | 41.6 | 0.077 | 0.009 | 89.4 | 0.038 |
| $M$ | 3 | 430.4 | 0.060 | 0.027 | 146.7 | 0.960 |
| $SE_M$ | | 45.1 | 0.065 | 0.012 | 83.6 | 0.029 |
| $M$ | 4 | 406.3 | 0.055 | 0.017 | 92.8 | 0.819 |
| $SE_M$ | | 32.8 | 0.060 | 0.007 | 26.4 | 0.089 |

[a] Data for this series were not used in any calculations (data from Series 1 for this baboon were used in calculating the mean for Series 3).

of Series 1, the predicted values were consistent across the four determinations. For these 2 baboons, the lower predicted costs at which maximal responding was observed indicate that demand for food was inelastic across a smaller range of FR values. As was observed with the other 4 baboons, the patterns of changes in daily intake and responding were similar across the four determinations of the effects of manipulating response cost on food intake. Maximal levels of responding, however, were one fifth to one seventh as large as those observed with the other 4 baboons.

Figure 3 presents the predicted demand curve for each series plotted using the group mean values (Table 1) of the parameters of the nonlinear equation proposed by Hursh et al. (1988). The equation accounted for over 88% of the variance in intake as the FR value increased during each series for all baboons except A-22 (and Series 4 for A-33). Predicted maximal intake was consistent across the four determinations, and the predicted FR value maintaining maximal responding varied between 87 and 162. There were small differences between ascending and descending determinations that varied across baboons. Predicted intake under the FR 128 schedule during Series 1 and 3, which included the highest FR value in the calculations, was about 50 g lower than in the other two series.

Figure 4 presents cumulative daily intake curves as a function of time during the session for each response requirement during the fourth series of determinations for the 4 baboons tested with FR values to 128. In contrast to the data in Figure 1, intake is graphed on a linear instead of a logarithmic scale. Baseline

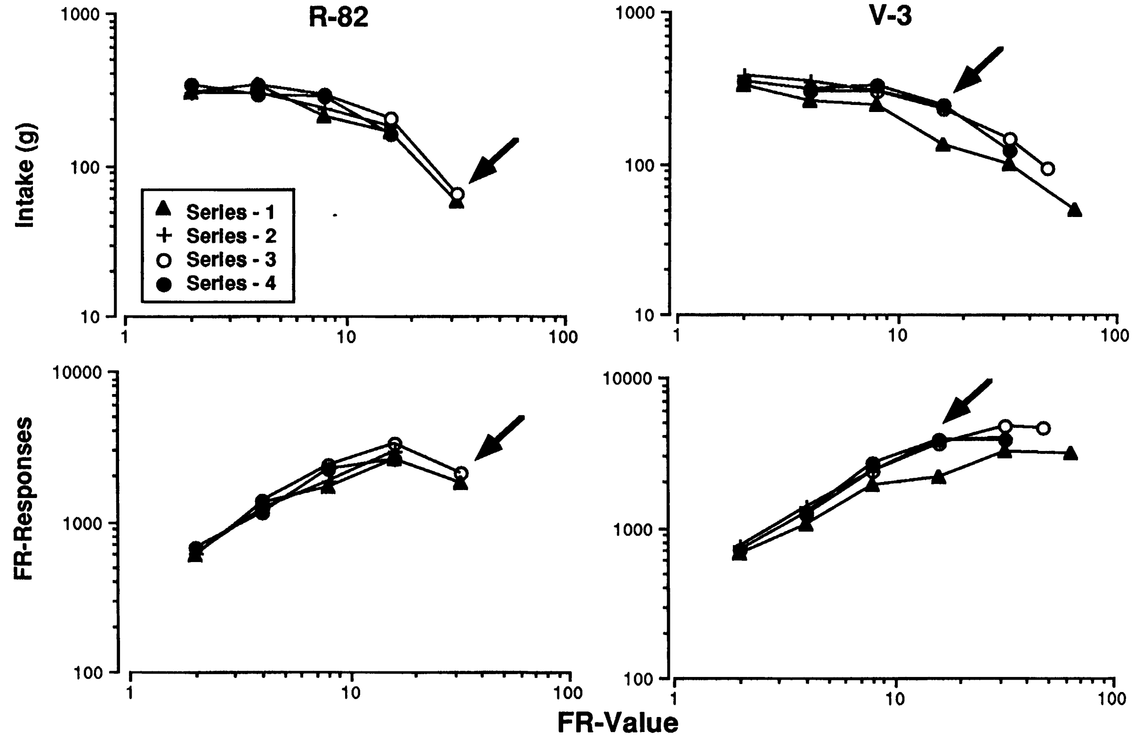

Fig. 2. Food intake and number of FR responses emitted daily as a function of FR response requirement for each baboon tested with FR values to 32 (R-82) or 64 (V-3), plotted using log scales. See Figure 1 for details.

intake under the FR 2 to FR 16 schedules ranged from 400 to 700 g. Most food intake occurred during the first 6 hr of the session, with additional meals occurring towards the end of the session (i.e., between 7:00 a.m. and 9:00 a.m. the following morning). Increasing the response requirement decreased total daily intake to between 100 and 200 g.

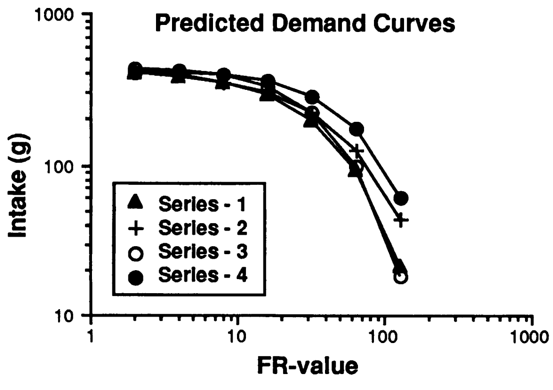

Fig. 3. Predicted demand curves for each series determined using the group mean of the fitted *L*, *b*, and *a* parameters (Table 1), plotted using log scales.

Figure 5 presents cumulative daily intake curves as a function of time during the session for each response requirement during the fourth series of determinations for the 2 baboons tested with FR values to 32 or 64. The baseline intake of about 300 g under the FR 2 to FR 16 schedules was lower than that observed with the other baboons, but the pattern of intake throughout the day was similar for all 6 baboons. Increasing the response requirement decreased total daily intake to between 50 and 100 g.

The top panel of Figure 6 presents running rate of responding (defined above) as a function of response requirement during the fourth series of determinations for all 6 baboons. Although running response rates varied among the baboons, the pattern of changes in response to increasing response cost was similar in all baboons except A-22. Running response rate was largest under the FR 2 schedule of reinforcement and decreased as the response requirement increased to 8 or 16. Further increases in response requirement were then associated with a consistent running response

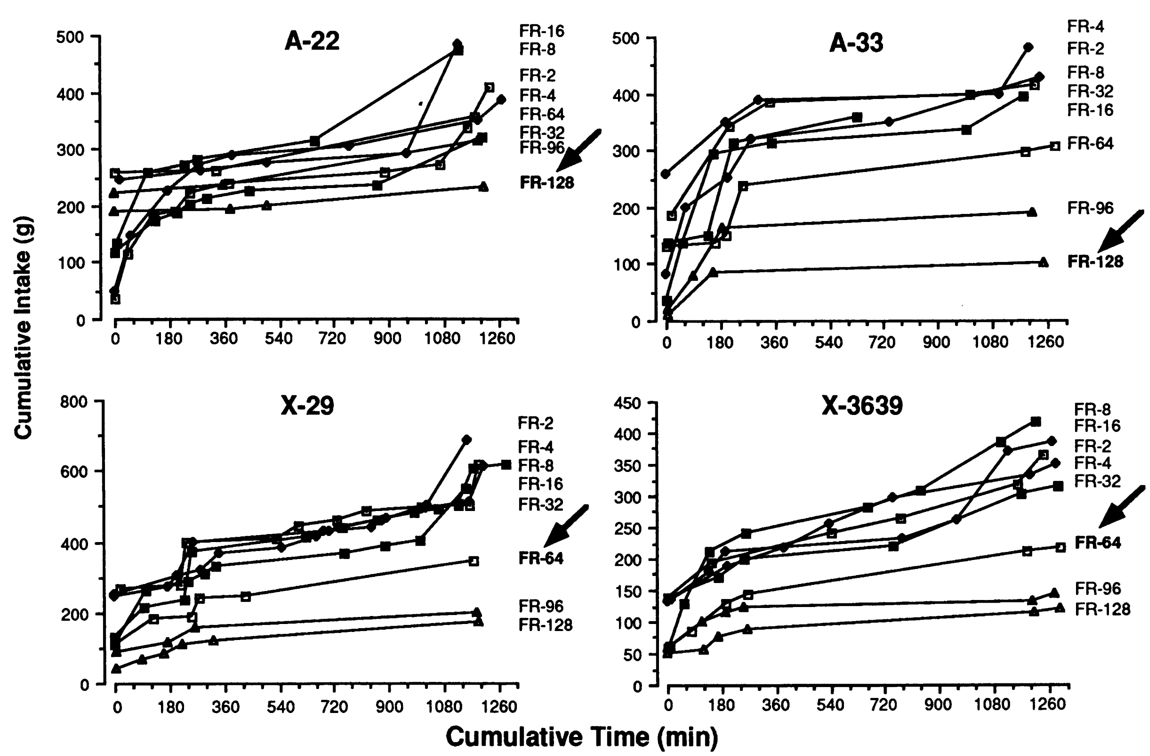

Fig. 4. Cumulative food intake during experimental sessions as a function of time for each FR value during the last series of determinations for each baboon tested with FR values to 128. Arrows indicate the predicted FR value with maximal responding.

rate. The middle panel of Figure 6 presents total duration of responding for each baboon as a function of response requirement. Increases in the response requirement were associated with increases in the duration of responding. For example, A-33 spent 3 min and 133 min responding under the FR 2 and FR 128 schedules, respectively. Thus, across most of the response requirements, increasing the response cost increased duration of responding without affecting running rate of responding, the combined effect being the overall increase in responses per session shown in Figures 1 and 2.

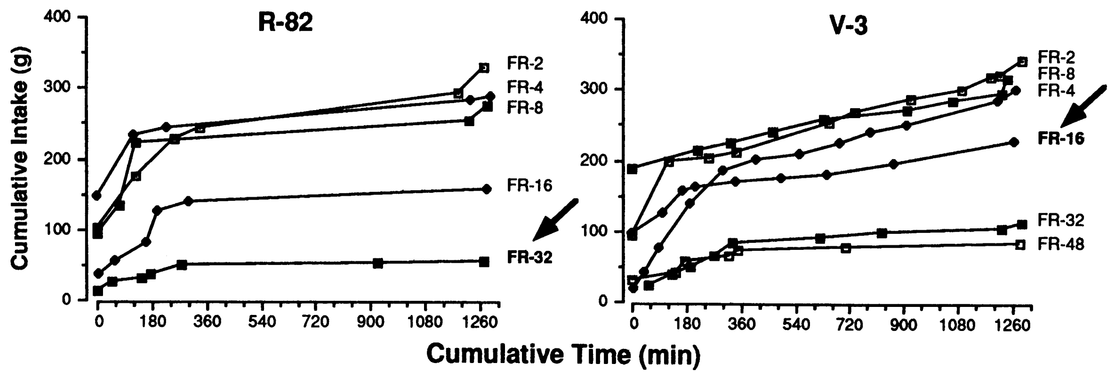

Fig. 5. Cumulative food intake during experimental sessions as a function of time for each FR value during the last series of determinations for each baboon tested with FR values to 32 (R-82) or 64 (V-3). Arrows indicate the predicted FR value with maximal responding.

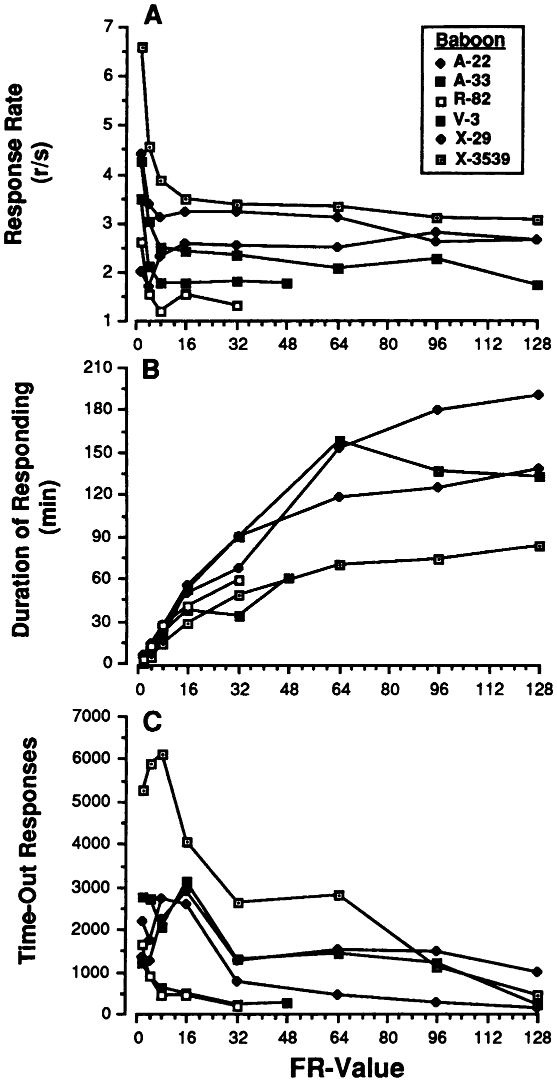

Fig. 6. Running response rate (Panel A), duration of responding (Panel B), and number of responses during timeout periods (Panel C) as a function of FR value during the last series of determinations for each baboon.

The bottom panel of Figure 6 presents responses emitted during the timeout periods as a function of response requirement during the fourth series of determinations for all 6 baboons. When the ratio requirement ranged between 2 and 8, it was common for the baboons to respond as often or more often during timeout periods than under the stimulus conditions for food delivery. Baboons with greater rates of responding tended to have greater numbers of responses during timeout than baboons with lower response rates. Responses during timeout decreased with increasing response requirement. The number of uncompleted ratios (not shown), which varied between 0 and 3, was unrelated to reponse requirement. In general, once a baboon had begun reponding, the ratio requirement was completed.

Small changes in body weight were observed for all baboons over the 3 months of the experiment, with 3 baboons gaining weight and 3 baboons losing weight: A-22 gained 2.9 kg from a baseline weight of 23.0 kg, A-33 gained 2.5 kg from a baseline weight of 29.8 kg, R-82 lost 0.2 kg from a baseline weight of 30.1 kg, V-3 lost 0.6 kg from a baseline weight of 42.1 kg, X-29 lost 2.1 kg from a baseline weight of 62.1 kg, and X-3639 gained 1.5 kg from a baseline weight of 35.2 kg.

## DISCUSSION

Increasing the response requirement for a single food pellet reduced total daily food intake in 6 adult baboons given access to food 22 hr per day. Food intake under the largest FR schedule was about 20% to 30% of intake under FR 2 conditions in 5 of 6 baboons. A similar decrease in intake with an increase in response cost in a range similar to that used here has been reported for a single Mangebey monkey responding for food 24 hr per day (Findley, 1959) and rhesus monkeys responding for 12 hr per day (Hursh, Raslear, Bauman, & Black, 1989). When rhesus monkeys were given access to food for a brief period each day, decreases in food intake with increasing response cost were also evident (Hamilton & Brobeck, 1964). In contrast to the conditions in the present study and those of Findley (1959) and Hursh et al. (1989), the short session length of the Hamilton and Brobeck study may have precluded the monkeys from maintaining food intake. In a related study, Elsmore, Fletcher, Conrad, and Sodetz (1980) maintained 2 baboons under conditions that permitted periodic choices between food delivery and an intravenous heroin injection over each 24-hr session. The time between choice opportunities was varied from 2 to 12 min. When the intertrial interval was 2 min, baboons chose food 90% of the time on 22% of the possible trials. Increasing the intertrial interval to 12 min increased the percentage of completed trials to 63%, with food chosen on 70% of the possible trials. Under these conditions, baboons maintained a more consistent daily food intake than under the conditions used in the present study.

Subjects maintained under limited-access conditions may not be able to increase responding to maintain steady levels of intake given the constraint on available time. In the current protocol, baboons had 22 hr to complete the necessary responding. Even under the FR 128 schedule of food delivery, baboons responded for only 90 to 180 min per day. If the baboons had responded for 9 to 12 hr per day, food intake would have remained stable. Baboons in the Elsmore et al. (1980) study decreased their food intake by 20% with increasing intertrial intervals, although they responded on only 63% of choice opportunities. The baboons could have maintained a steady food intake by responding on more trials. In the present study, food intake might have been more stable if the response costs were increased more slowly, or each response cost was examined for a longer period. Each condition in the Elsmore et al. (1980) study, for example, was tested for a minimum of 14 days. In the present study, baboons were tested under each FR value four times with no differences between the series of determinations, suggesting that multiple brief exposures to the current schedule changes were not sufficient to prevent the decreases in food intake.

Under similar feeding conditions, rats increased responding when response cost per gram of food was increased such that intake remained stable even when the response cost required 20,000 responses per day (Collier, Johnson, Hill, & Kaufman, 1986). Maximal output was 50,000 responses per day, which required about 12 hr. Each condition was tested for at least six sessions. Baboons have a significantly greater fat mass and maintain a more stable body weight than rats do in the face of brief dietary perturbations (Foltin, 1990; Foltin & Fischman, 1990). The apparent greater concordance between economic predictions and biological reality in the rat is probably due to the greater, more rapid, changes in body weight associated with changes in feeding behavior. In the short term, baboons may have alternatives to increasing responding in order to maintain a stable body weight (e.g., changes in activity, metabolic rate, utilization of fat stores). Rashotte and Henderson (1988) reported that in response to increasing cost of food, pigeons reduce nocturnal body temperature, thereby reducing energy needs. These data, in combination with the present results, support the suggestion that species differences and factors other than food intake influence the response to changing feeding costs. The present data also argue that with longer testing of each FR condition, food intake in the baboon may have returned closer to baseline (i.e., FR 2 levels) as fat stores were utilized. In 5 of the baboons, intake was similar across the three highest response costs. Six to 7 days were required to test these three response costs, suggesting that more than 6 days would be necessary for baboons to respond to the combination of increased response cost and decreased body weight.

Baboons and rats also differ with respect to changes in running response rate with increasing response cost. Running rate of baboons remained stable with increasing response cost. Rats, in contrast, have been reliably reported to increase running rate in response to increasing consumption costs (Collier, 1982; Collier et al., 1972). Thus, although baboons and rats both increase total output of responding when exposed to increased feeding costs, there are differences in the structure of these changes.

For all baboons in this study, responding at the two or three highest ratio values was equivalent. This suggests that further increases in response cost would have resulted in either similar or decreased responding. The nonlinear relationships between changes in food intake and FR value (i.e., cost) for each baboon were fitted using an equation derived by Hursh et al. (1988) to describe nonlinear demand functions. In nearly all cases, the resulting equation closely fitted the obtained data and accounted for as much as 98% of the variance. The equation was not accurate in describing demand for food by 1 baboon (A-22) whose demand for food was nearly linear across the FR values. The accuracy of this equation in describing demand for food by baboons confirms an earlier report using rhesus monkeys (Hursh et al., 1989), and suggests that the use of this formulation by researchers will provide a method for rapid comparisons, not only between laboratories but also between commodities.

The equation provides an estimate of the cost at which maximal responding will be observed. Increases in cost above this peak value are predicted to result in decreased responding and food intake. In most cases, this peak value was obtained at the largest ratio (or two) tested with each baboon. Thus, demand for food was inelastic across nearly all of the FR values. The predicted cost associated with maximal responses, or the point at which demand became elastic, was the cost that was also associated with a decrease in food intake to 15% to 55% of intake under the FR 2 response cost. These findings raise some important issues regarding the utility of such analyses. The conclusion that demand was inelastic is both intuitively satisfying and supportive of economic models of behavior. The significant decreases in food intake to 15% to 55% of baseline argue, however, that defining demand under these circumstances as inelastic is biologically inappropiate. Under the conditions of this study, such reductions in food intake, if prolonged, would have deleterious health consequences. Food is necessary for life, and demand must be inelastic within a wide range of response costs.

In its minimal sense, inelastic demand refers only to increases in responding as costs increase, and it may be inappropriate to criticize the concept because it does not take into account the level of intake at the cost associated with maximal responding. The results indicate that demand functions are appropriate for the study of food intake in baboons, but also caution that the value of intake and its relationship to maximal intake are important factors in studying demand for a commodity.

One of the strengths of economic models of operant behavior is that they provide a methodology for comparisons across species, reinforcement schedules, commodities, studies, and other factors. Unfortunately, by emphasizing a single dependent measure, such as demand, the importance of the experimental conditions under which such measures were obtained may be obfuscated. The results suggest that by encouraging comparisons across studies and species, economic models of operant behavior can also be used to highlight the importance of the conditions under which these comparisons are made.

## REFERENCES

Allison, J. (1981). Economics and operant conditioning. In P. Harzem & M. D. Zeiler (Eds.), *Advances in analysis of behaviour: Vol. 2. Predictability, correlation, and contiguity* (pp. 321-353). New York: Wiley.

Allison, J. (1983). *Behavioral economics.* New York: Praeger.

Collier, G. H. (1982). Determinants of choice. In D. J. Bernstein (Ed.), *Nebraska Symposium on Motivation 1981: Vol. 29. Response structure and organization* (pp. 69-127). Lincoln: University of Nebraska Press.

Collier, G. H., Hirsch, E., & Hamlin, P. H. (1972). The ecological determinants of reinforcement in the rat. *Physiology & Behavior,* **9,** 705-716.

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.

Elsmore, T. F., Fletcher, G. V., Conrad, D. G., & Sodetz, F. J. (1980). Reduction of heroin intake in baboons by an economic constraint. *Pharmacology Biochemistry and Behavior,* **13,** 729-731.

Findley, J. D. (1959). Behavior output under chained fixed-ratio requirements in a 24-hour experimental space. *Journal of the Experimental Analysis of Behavior,* **2,** 258.

Foltin, R. W. (1990). Differential development of tolerance to the effects of *d*-amphetamine and fenfluramine on food intake in baboons. *Journal of Pharmacology and Experimental Therapeutics,* **252,** 960-969.

Foltin, R. W., & Fischman, M. W. (1988). The effects of varying procurement costs on food intake in baboons. *Physiology & Behavior,* **43,** 493-499.

Foltin, R. W., & Fischman, M. W. (1990). Effects of caloric manipulations on food intake in baboons. *Appetite,* **15,** 135-149.

Hamilton, C. L., & Brobeck, J. R. (1964). Hypothalamic hyperphagia in the monkey. *Journal of Comparative and Physiological Psychology,* **57,** 271-278.

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., & Bauman, R. A. (1987). The behavioral analysis of demand. In L. Green & J. H. Kagel (Eds.), *Advances in behavioral economics* (Vol. 1, pp. 117-165). Norwood, NJ: Ablex.

Hursh, S. R., & Natelson, B. H. (1981). Electrical brain stimulation and food reinforcement dissociated by demand elasticity. *Physiology & Behavior,* **26,** 509-515.

Hursh, S. R., Raslear, T. G., Bauman, R., & Black, H. (1989). The quantitative analysis of economic behavior with laboratory animals. In K. G. Grunert & F. Ölander (Eds.), *Understanding economic behavior* (pp. 393-407). Dordrecht, Netherlands: Kluwer.

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.

Lea, S. E. G. (1978). The psychology and economics of demand. *Psychological Bulletin,* **85,** 441-466.

Miller, N. E., Bailey, C. J., & Stevenson, J. A. F. (1950). Decreased "hunger" but increased food intake resulting from hypothalamic lesions. *Science,* **112,** 256-259.

Rashotte, M. E., & Henderson, D. (1988). Coping with rising food costs in a closed economy: Feeding behavior and nocturnal hypothermia in pigeons. *Journal of the Experimental Analysis of Behavior,* **50,** 441-456.

*Received July 19, 1990*
*Final acceptance May 1, 1991*