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SUBSTITUTION AND CALORIC REGULATION IN A CLOSED ECONOMY

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Three experiments were conducted to study the effect of an imperfect substitute for food on demand for food in a closed economy. In Experiments 1 and 2, rats pressed a lever for their entire daily food ration, and a fixed ratio of presses was required for each food pellet. In both experiments, the fixed ratio was held constant during a daily session but was increased between sessions. The fixed ratio was increased over a series of daily sessions once in the absence of concurrently available sucrose and again when sucrose pellets were freely available. For both series, increases in the fixed ratio reduced food intake, but body weight was reduced only in the no-sucrose condition. In the sucrose condition, body weight and total caloric intake (sucrose plus food) were relatively unaffected by increases in the fixed ratio. At all fixed ratios, food intake was proportionally reduced by the intake of sucrose. In Experiment 3, monkeys obtained food or saccharin by pressing keys; the fixed ratio of presses per food pellet was increased once when tap water was each monkey's only source of fluid, again when each monkey's water was sweetened with saccharin, and a third time when each monkey had concurrent access to the saccharin solution and plain water. Increases in the fixed ratio, but not the intake of the saccharin solution, reduced each monkey's food intake. Because neither rats' sucrose nor monkeys' saccharin intakes affected the slope of the respective demand curves for food, monkeys and rats increased their daily output of presses and thereby defended their daily intake of those complementary elements of food. However, sucrose reduced rats' food intake. The relative constancy of body weight and total caloric intake in the sucrose condition is consistent with the possibility that rats tended to regulate caloric intake.

Key words: closed economy, demand, substitution, regulation, lever press, rats, monkeys

A critical empirical and conceptual focus within the emerging discipline of behavioral economics is the demand relation between an individual consumer's consumption of a commodity and its unit cost (Hursh, 1980, 1984; Hursh & Bauman, 1987; Kagel, Battalio, & Green, 1995; Lea, 1978; Lea & Roper, 1977). In several laboratory experiments, methods that heretofore were used to study the strengthening of operant behavior by reinforcement were applied to an analysis of the relation between consumption of some biologically essential commodity and its unit cost (Bauman, 1991, 1992; Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988; Raslear, Bauman, Hursh, Shurtleff, & Simmons, 1988). In each of these experiments, a fixed number of lever presses was required for the delivery of a single food pellet, and because the only food available was delivered for lever pressing, individual rats were required to satisfy the fixed ratio (FR) of presses per pellet for access to their entire daily ration of food. In an effort to characterize demand rapidly and comprehensively, a geometric series of FRs was used in these studies, such that each FR in a series was used for a single 24-hr period.

The demand curves that resulted from these studies were remarkably homogenous in shape. When plotted in logarithmic coordinates, it was clear that maximum intake was reduced little by the first few FRs, because daily output of lever presses increased in almost exact proportion to the increases in the FR. Subsequent increases in the FR resulted in more rapid reductions of daily intake as

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increases in daily output were reduced. It was only at the largest FRs that output itself was reduced, at which point food intake decreased precipitously.

In economic theory, the mathematical concept of slope is used to quantify the shape of a demand curve, and, in logarithmic coordinates, the slope of a demand curve is a measure of the economic quantity: price elasticity of demand, or simply demand elasticity (Deaton & Muellbauer, 1982). Demand elasticity (e) equals the percentage change in consumption (q) that occurs for a percentage change in price (p). In the following equation for elasticity,

$$e = (\Delta q/q)/(\Delta p/p), \quad (1)$$

Δq and Δp represent change in consumption and unit price, respectively. For a typical downward sloping demand curve, e is negative, because Δq is negative.

In previous laboratory studies of demand, $\Delta p/p$ was constant, because a geometric series of FRs was used. However, progressively larger FRs reduced q, and Δq grew increasingly more negative. As a consequence, e also grew increasingly more negative. However, e was near zero or at least very small ($0 > e > -0.50$) at small to moderate FRs, because Δq was a very small negative number. It was only with further increases in the FR that the resulting increases in Δq drove e toward -1.0, at which point the relative changes in consumption and price were equal $[-(\Delta q/q) = \Delta p/p]$, and it was only at large FRs that e exceeded -1.0. In economic terms, this means that demand was inelastic ($0 > e > -1.0$), or minimally responsive, with respect to increases in unit cost over a wide range of FRs and only became elastic ($e < -1.0$) at higher unit costs.

This inelasticity of demand over a wide range of FRs in previous studies of demand was not unexpected, because the only food available was delivered for lever pressing. In other words, the economy used in these studies was closed to alternatives, or substitutes, for food (Collier, 1981, 1983; Hursh, 1980, 1984). It is conceivable, therefore, that demand for food might have been more elastic had there been a less costly substitute available. In the extreme, it is conceivable that if the same food (a perfect substitute) were available as the fixed ratio of presses per food pellet increased, few if any food pellets would be demanded, although consumption might not be reduced to zero (Lea & Roper, 1977; Neuringer, 1969). However, if the substitute for food pellets was imperfect, elasticity might be affected in a less than all-or-none fashion. In an effort to evaluate this proposition, a series of three studies was conducted to examine the effect of an imperfect substitute for food on the demand for food in a closed economy. In the first experiment, the ratio of presses per food pellet was increased daily, once when food pellets were a rat's only source of calories and nutrients and again when a rat had free access to an unlimited supply of sucrose pellets, a caloric substitute for food. In the second experiment, the principal objective was to systematically replicate the results of Experiment 1 using a shorter series of FRs in which the daily increment in the FR was about three times that of Experiment 1. In the third experiment, the objective was to study the effects of a sweet but noncaloric substitute for food on the demand for food by rhesus monkeys. A monkey's demand for food was studied once when only tap water was concurrently available and again when saccharin-sweetened water was available.

EXPERIMENT 1

The purpose of the first experiment was twofold. First, the experiment was designed to assess the effects of a freely available caloric substitute for food on demand for food in a closed economy. However, because previous studies of demand for food in a closed economy typically did not provide an animal with access to caloric substitutes for food, body weight as well as food intake were reduced by daily increases in the FR. Consequently, daily increases in response output might have been driven, at least in part, by the loss of body weight. Therefore, another purpose of the present experiment was to use sucrose to minimize or eliminate this reduction of body weight.

METHOD

Subjects and Apparatus

Five adult male Sprague-Dawley rats, weighing between 499 and 537 g, were used.

Rats were individually housed in standard

Table 1

Composition of Bioserv dustless precision food pellets. These numbers summarize data from a representative analysis. The carbohydrate profile was as follows: monosaccharides = 3.6 mg/45-mg pellet, disaccharides = 23.58 mg/45-mg pellet, trisaccharides = 0, and polysaccharides = 0.675 mg/45-mg pellet.

Source	Percentage
Protein	18.5
Fat	5.5
Ash	4.4
Carbohydrates	60.4
Fiber	5.0
Moisture	3.0
Vitamins and minerals	3.0

Coulbourn rodent test cages (25 cm by 29 cm by 29 cm) that were enclosed in ventilated, sound-attenuating fiberglass shells. Within each test cage, a flat, thin, steel lever protruded through the left front wall, and midway along this wall was a rectangular opening that led to a recessed food trough. A standard pellet dispenser was connected to the back of this trough and, when activated, dispensed a 45-mg Bioserv dustless precision food pellet. As shown in Table 1, each pellet consisted of a balanced mixture of the major macronutrients, vitamins, and minerals. Directly above the trough and near the ceiling was a houselight, and near the left wall, at the same level as the houselight, was a Sonalert. In the left corner, a metal cup that was bolted to the floor was used as the reservoir for sucrose pellets. Water was always available from a water bottle accessible through a hole in the right wall.

All test cages were housed in an environmental chamber in which the temperature and relative humidity were maintained at 21 ± 3 °C and 50%, respectively. Outside of this chamber, cables connected the test cages to a computer interface that was linked to a PDP8/E® computer. Supersked® software was used to control all experimental contingencies and record lever presses and pellet deliveries.

Procedure

Within each cage, a 12:12 hr light/dark cycle was imposed by turning the houselight on at 9:00 a.m. and off at 9:00 p.m. Between 9:00 and 9:30 a.m., each rat's cage was cleaned, its water changed, and its body weight recorded to the nearest gram. At all times, water was freely available and, with the exception of the 1st day of preliminary training, a fixed number of lever presses was always required for the delivery of each 45-mg food pellet. On the 1st day of preliminary training, the food trough in each chamber was filled with food pellets and a single food pellet was delivered for each lever press. No special procedures were used to train a rat either to eat from the food trough or press the lever. Within 5 days of being placed in their chambers, all rats came to press the lever and obtained their entire daily intake of food by doing so.

No-sucrose condition. Because the FR was to be increased to a value well in excess of 400, an effort was made to expose each rat to a moderately intermittent rate of food delivery at the smallest ratio. Therefore, each rat's food intake was allowed to stabilize at an initial ratio of 10 presses per pellet. At no time during this condition were sucrose pellets available. The food delivered for lever pressing was a rat's only source of nutrients and calories.

Once intake had stabilized, the FR was increased daily, such that one FR was used for a single day, and the FR on 1 day was 20% larger than that on the preceding day. This pattern of daily increases was continued for 22 days, resulting in the following series of FRs (within rounding error): 10, 12, 14, 17, 20, 24, 29, 35, 42, 50, 60, 72, 83, 103, 124, 149, 179, 215, 258, 310, 372, 446.

Sucrose condition. The day following the imposition of FR 446, the FR value was returned to 10, and each rat's food intake and body weight were allowed to restabilize. At this point, a metal food cup was mounted in the corner directly behind the lever and was filled with 50 g of 45-mg sucrose pellets. This was more sucrose than any rat was capable of consuming in 1 day, even if it ate only sucrose. Food and sucrose intakes were allowed to stabilize before the FR was again increased 20% each day for 22 days.

Daily pellet intakes and lever presses in both conditions were recorded in computer data files. Intake of sucrose was measured each morning by first subtracting any spillage from 50 g before subtracting the weight of what remained in a rat's cup from this difference.

RESULTS

Figures 1 and 2 show the individual intakes of food pellets and the corresponding individual daily output of lever presses at each FR. Fewer than 22 points are plotted for Rats 2 and 5 when sucrose was available because Rat 2 stopped pressing at a ratio of 258, the 18th ratio, and Rat 5 stopped at FR 372, the next-to-last ratio in the series.

In general, food intake decreased and daily output of lever pressing increased as the FR increased in both the no-sucrose and sucrose conditions. During both conditions, intake decreased little for the first 9 or 10 ratios (FR 10 to FR 50) because daily output of lever presses increased sufficiently to offset increases in the FR. However, at larger FRs, food intake gradually decreased as increases in daily output were reduced until, at the largest FRs, food intake decreased precipitously as output also decreased. A notable exception to these effects of the FR on food intake and daily output of lever presses is the data for Rat 1, whose daily output appeared to increase linearly over the entire range of FRs.

Over a wide range of FRs, the individual food intake curves and the lever-press output curves for the sucrose condition appeared to be very similar in shape to, albeit displaced downward from, the corresponding food intake and lever-press output curves for the no-sucrose condition. In logarithmic coordinates, this implies that food intake and lever presses were proportionally reduced by the intake of sucrose.

Figure 3 shows that sucrose intakes were much higher than food-pellet intakes at all fixed ratios. As implied by the pellet intakes in Figures 1 and 2, increases in the FR reduced food intake, but sucrose intake either remained high or increased. Sucrose intakes for Rats 1, 2, and perhaps 4 appeared to increase at FRs greater than 80.

The effects of FR size and the concurrent availability of sucrose on body weight are also shown in Figure 3. In the no-sucrose condition, increases in the FR significantly reduced the body weights of all rats. In the sucrose condition rats were generally heavier (Castonguay & Hirsch, 1981; Sclafani, 1987a, 1987b), but the reduction of food intake by increases in the FR did not result in a significant loss of body weight. Mean body weights were remarkably stable in the sucrose condition.

DISCUSSION

In the no-sucrose and sucrose conditions, increases in the FR reduced demand for food and resulted in sustained increases in daily output of lever presses over a wide range of FRs. Unlike the increases in response output in the no-sucrose condition, the increases in response output in the sucrose condition could not have been motivated by a progressive reduction in body weight, because the intake of sucrose minimized the reductions in body weight that accompanied a reduction of food intake. In fact, even in the no-sucrose condition, it is difficult to reconcile the increases in output that occurred at the small to moderate FRs because body weight remained constant within this range of unit costs.

The constancy of body weight notwithstanding, intake of sucrose reduced the frequency with which rats initiated FRs. This outcome seems to suggest that the intake of sucrose reduced the reinforcing potency of food. However, it is also true that the rate at which daily output of lever presses increased was not affected by the intake of sucrose, because the lever-press functions for the no-sucrose and sucrose conditions were nearly parallel in logarithmic coordinates. Perhaps the clearest and most impressive illustration of this parallelism can be found in the response output functions for Rat 1. Figure 1 shows that these curves were almost perfectly parallel across the entire range of FRs and, at the largest FR, output was in excess of 98,500 presses per day. A most important implication of this parallelism is that lever pressing in the no-sucrose condition was not less resistant to change than lever pressing in the sucrose condition, because the rate at which lever pressing increased in the no-sucrose and sucrose conditions was similar (Nevin, Mandell, & Yarensky, 1983). In other words, resistance to change (which is defined here as an increase in response output to defend food intake) and possibly response strength were not reduced by the intake of sucrose, which clearly reduced drive level, defined in terms of overall body weight (Nevin, Smith, & Roberts, 1987). This apparent invariance focuses attention on what concepts are necessary and

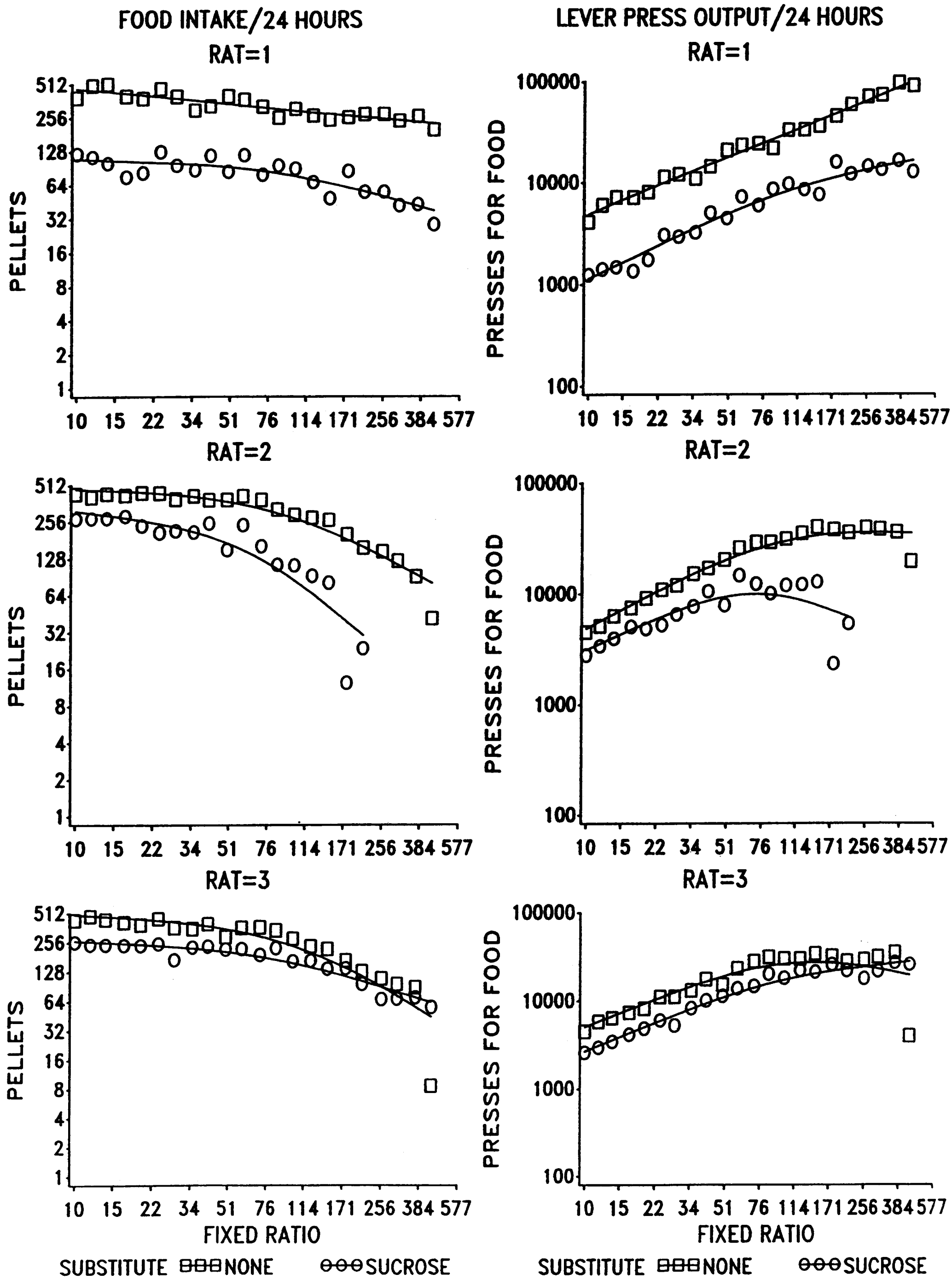

Fig. 1. In the left column, pellet intakes at each FR for Rats 1, 2, and 3 are shown for the no-sucrose (squares) and sucrose (circles) conditions of Experiment 1. In the right column, the corresponding output of lever presses at each FR for these rats is shown. All points represent totals from the light and dark periods, and the smooth lines in this and subsequent figures are simple spline fits that describe the trajectory of points within each coordinate space. The axes are scaled logarithmically.

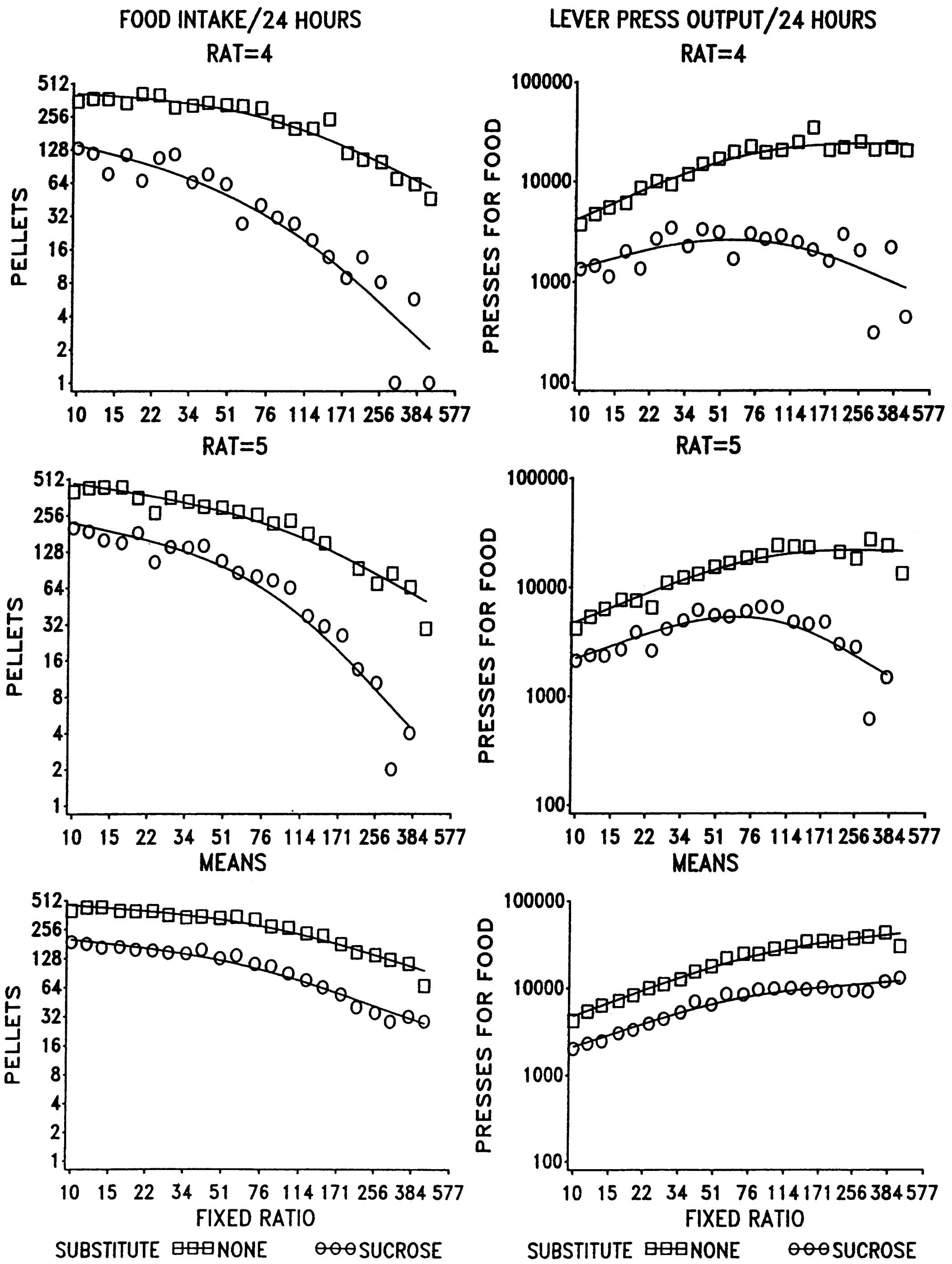

Fig. 2. In the top and middle panels of the left column, pellet intakes at each FR for Rats 4 and 5 are shown for the no-sucrose (squares) and sucrose (circles) conditions of Experiment 1. In the top and middle panels of the right column, the corresponding outputs of lever presses at each FR for Rats 4 and 5 are shown. Mean intake and mean output functions for the 5 rats at each FR are shown for the no-sucrose and sucrose conditions in the lower left and right panels, respectively. The axes are scaled logarithmically.

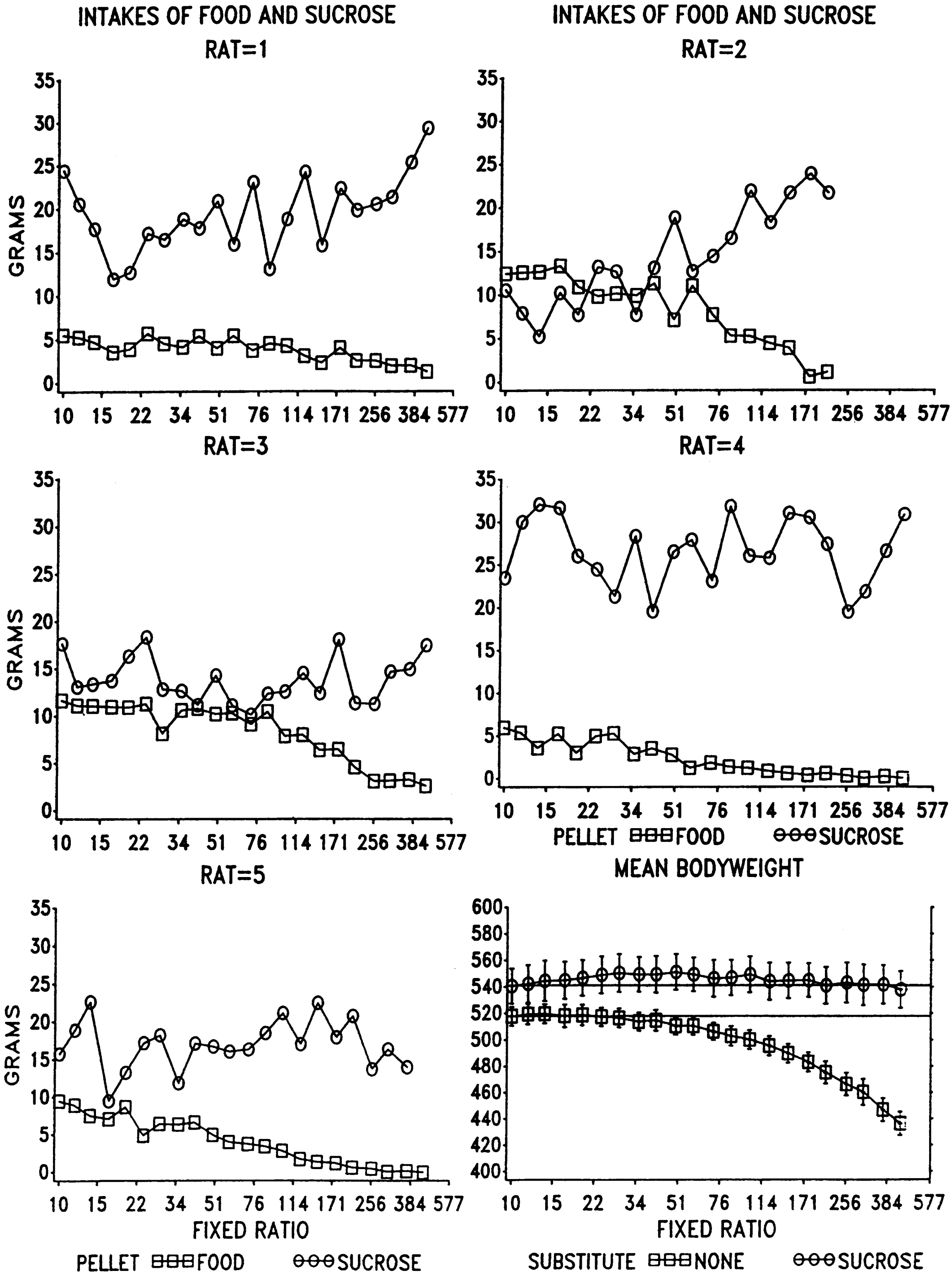

Fig. 3. In the three panels of the left column and the top and middle panels of the right column, food (squares) and sucrose (circles) intakes are shown at each FR for Experiment 1. In the bottom right panel, mean body weights (±*SEM*) are shown for the no-sucrose and sucrose conditions. The horizontal lines in this plot are drawn across from mean body weight at FR 10, the first FR in the series.

sufficient for explaining drive in a closed economy (Collier, 1981; Lea, 1983; Logan, 1964; Richter, 1927, 1942; Young, 1966; Young & Chaplin, 1945). One interpretation is based on the idea that food in a closed economy is a costly economic commodity that can be purchased with an animal's instrumental allocation of responses (Bauman, 1991) or time (Bauman & Kant, 1995) and whose value can be diluted by the presence of substitutes, especially less costly substitutes. In the present study, then, sucrose should have diluted the value of food, which was more costly. As a consequence, food would have supported less lever pressing in the sucrose condition. However, sucrose was an imperfect substitute for food and, thus, the daily increases in lever pressing in the sucrose condition could have been driven by those nutritionally unique or complementary elements of food (essential fatty and amino acids, vitamins, and minerals) that were necessary for maintaining metabolic homeostasis (Nicolaidis & Rowland, 1976; Overmann, 1976; Richter, Holt, & Barelare, 1938; Rozin & Schulkin, 1990; Stricker, 1990).

Sucrose is, however, a perfect substitute for the disaccharide fraction of a food pellet, which was about 50% for each Bioserv pellet (see Table 1).[1] Therefore, if the intake of sucrose completely replaced the disaccharide fraction of food and total caloric intake remained constant, food intake would be reduced by a fixed proportion of what the intake was during the no-sucrose condition. This is exactly what occurred over a wide range of ratios. In fact, the actual reduction was typically less than 50% because a rat could not take in the essential elements of food without also consuming the carbohydrate calories in food, which in turn reduced the need for the calories in sucrose. Consequently, the percentage reduction of food intake was most likely determined by the intake equilibrium that resulted from the settling of a rat's food and sucrose intakes (Wirtshafter & Davis, 1977).

The proportional reduction of food intake by the intake of sucrose implies that over a wide range of FRs, the intake of sucrose did not affect the slope of the demand curve on logarithmic coordinates. According to contemporary and classical economic theory (Deaton & Muellbauer, 1982), the availability of substitutes should affect the slope of the demand curve and, as a consequence, *e*. In particular, one expectation was that the availability of sucrose would accelerate the reduction of food intake by increasingly larger FRs. In fact, the more extreme data points in Figures 1 and 2 are consistent with the possibility that the intake of sucrose may have affected the slope of the food demand curve and *e* (Lea & Roper, 1977). In particular, the intake of sucrose induced an abrupt cessation of lever pressing by Rat 2 at FR 258 and by Rat 5 at FR 372; the rate at which food intake was reduced appeared to accelerate at the largest ratios for Rats 2, 4, and 5.

EXPERIMENT 2

In Experiment 1, the conclusion that sucrose was a substitute for food was not strongly supported by the intake data of Figure 3 because sucrose intake clearly increased as food intake decreased for only 2 or perhaps 3 of the 5 rats. Although it is conceivable that more of the sucrose that was consumed was actually absorbed and metabolized as food intake declined, a more convincing case for substitution, at the level of intake, might be made if it could be shown to be generally true that sucrose and food intakes are reciprocally related to the FR. Thus, a second study was undertaken to examine the strength and generality of the proposed substitution effect.

In the second experiment, a rat again had free access to an unlimited supply of sucrose pellets as the FR of presses per food pellet was increased daily. Because the size of the daily increases in the FR might be expected to affect the rapidity and magnitude of the increase in sucrose intake and reduction of food intake with increases in the FR, the daily step between successive FRs was made larger than it was in Experiment 1 (300% instead of 20% per day). As a consequence, the following shortened series of ratios was used: 1, 3, 9, 27, 81, and 243 presses per pellet. Raslear et al. (1988) reported that rats were capable

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[1] Table 1 shows that the Bioserv pellets used in Experiments 1 and 2 consisted of 60.42% carbohydrate. Table 1 also shows that disaccharides represented (23.58 mg/27.85 mg) × 100 = 84% of the carbohydrates. Because sucrose was the only disaccharide among the ingredients used to manufacture these pellets, each pellet consisted of 60.42% × 84% = 50.65% sucrose.

of sustaining their daily output of presses at each ratio in a similar series.

METHOD

Subjects and Apparatus

Six adult male Sprague-Dawley rats, weighing between 430 and 560 g, were used. They were housed in individual hanging wire cages (24.1 cm long by 20.3 cm wide by 18.4 cm deep). Protruding through the front wall of each cage was a tube that provided continuous access to tap water. A standard Gerbrands lever was connected to a pellet dispenser that when activated delivered a single 45-mg Bioserv food pellet into a small food cup that was mounted next to the lever. An aluminum cup was bolted to the rear floor of each cage and was used as the receptacle for 45-mg sucrose pellets. All cages were maintained in a temperature- and humidity-controlled environmental chamber (see Experiment 1) in which the lights were on between 9:00 a.m. and 9:00 p.m. and off during the remaining 12 hr.

Outside of the environmental chamber a PDP/8e® computer and Supersked® software were used to control the experimental contingencies and to record presses and pellet deliveries. Individual body weights were recorded daily during the sucrose condition. Body weights were not recorded during the no-sucrose condition.

Procedure

The procedural details and conditions of this experiment were identical to those of Experiment 1 except for the series of FRs. During the no-sucrose condition, each rat's daily food intake was allowed to stabilize at FR 1 before the FR was increased daily, such that each ratio in the following series was used for a single day: 3, 9, 27, 81, and 243 presses per pellet.

The day after FR 243 the FR was reset to 1, and each rat's food intake was allowed to recover and stabilize before a daily allotment of 50 g of 45-mg sucrose pellets was made freely available from a cup at the rear of its cage. After food intake and sucrose intake stabilized at FR 1, the FR was again increased daily.

RESULTS

In general, in both the no-sucrose and sucrose conditions, food intake decreased gradually and daily output of lever presses increased between FR 1 and FR 81 (Figures 4 and 5). At FR 243, lever-press output decreased and, as a consequence, intake decreased precipitously. Over a wide range of ratios, many of the individual intake and output curves for the sucrose condition are parallel to, but displaced downward from, the intake and output functions for the no-sucrose condition. In logarithmic coordinates, this implies that food intake and lever-press output were proportionally reduced by the intake of sucrose.

Figure 6 shows the intakes of sucrose and food (in grams) for individual rats and at each FR. Increases in the FR reduced food intake and increased sucrose intake for Rats 1, 2, 3, 4, and 5, although the changes in sucrose intake were less monotonic than the changes in food intake. Although the sucrose and food intakes for Rat 6 decreased between FR 1 and 9, intake of sucrose increased beyond FR 9 as food intake continued to decrease.

DISCUSSION

In both Experiment 1 and Experiment 2, increases in the FR reduced food intake in the no-sucrose and sucrose conditions. It was also true in Experiments 1 and 2 that rats' intake of sucrose reduced food intake but, over a wide range of ratios, food intake was not reduced more rapidly in the sucrose than in the no-sucrose conditions. The logarithmic plots of the food intake curves for the no-sucrose and sucrose conditions in Experiments 1 and 2 showed that over a wide range of FRs, food intake was proportionally reduced by the intake of sucrose, although food intake appeared to be reduced more in Experiment 1 than in Experiment 2. The most likely explanation for this more extreme reduction of food intake in Experiment 1 is that sucrose intake was larger in Experiment 1 than in Experiment 2 (cf. Figure 3 with Figure 6). One likely cause of this discrepancy in sucrose intakes is that the intake of food at the first FR in Experiment 2 was larger than the intake of food at the first FR in Experiment 1, an outcome that most probably resulted from the fact that the first FR in Experiment 2 (FR 1) was smaller by a factor of 10 than the first FR in Experiment 1 (FR 10). Regardless of the reason for the larger intake

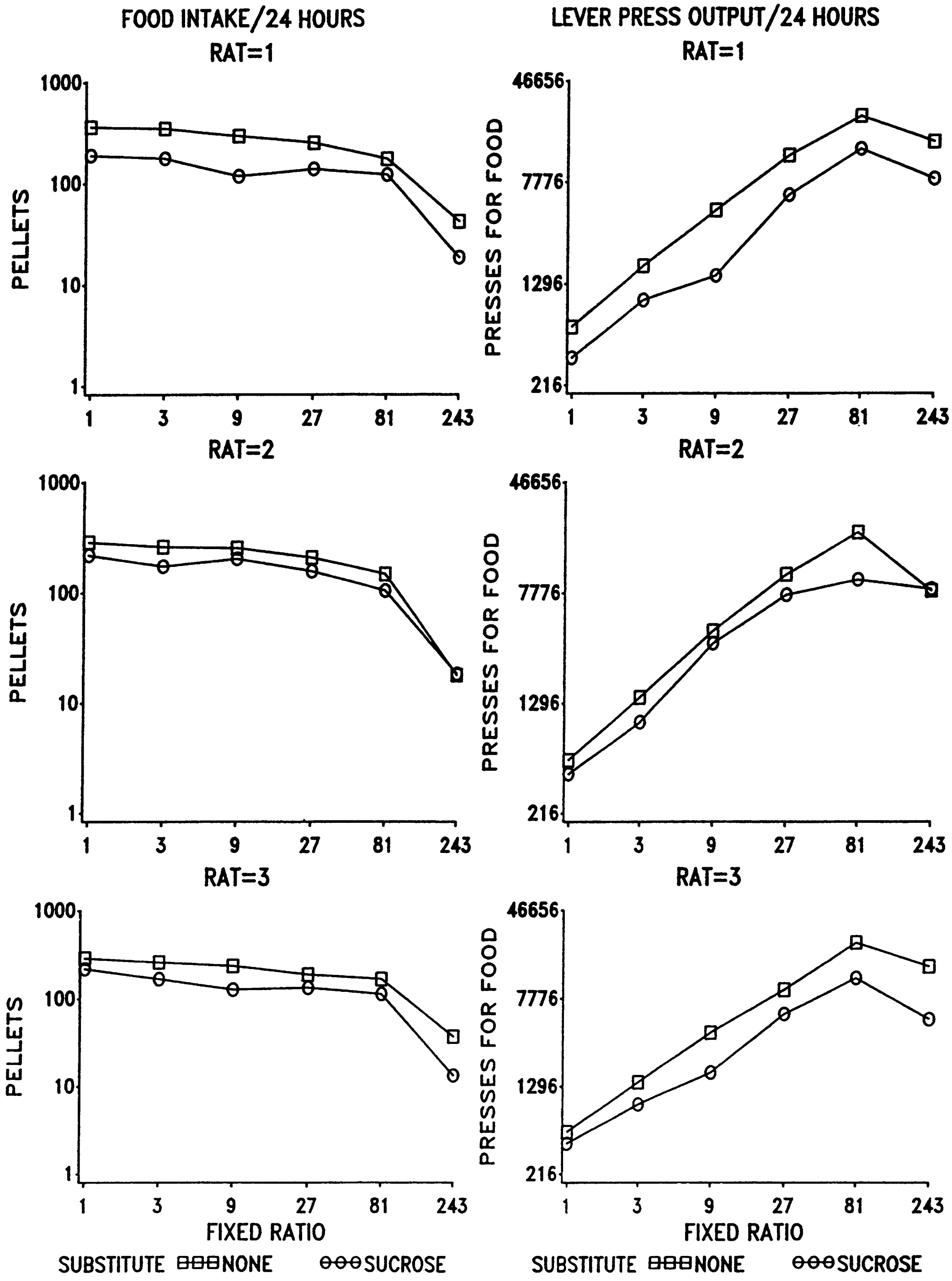


Fig. 4. In the left column, pellet intakes at each FR for Rats 1, 2, and 3 are shown for the no-sucrose (squares) and sucrose (circles) conditions of Experiment 2. In the right column, the corresponding output of lever presses at each FR for these rats is shown. The axes are scaled logarithmically. The data points represent totals for the light and dark periods.

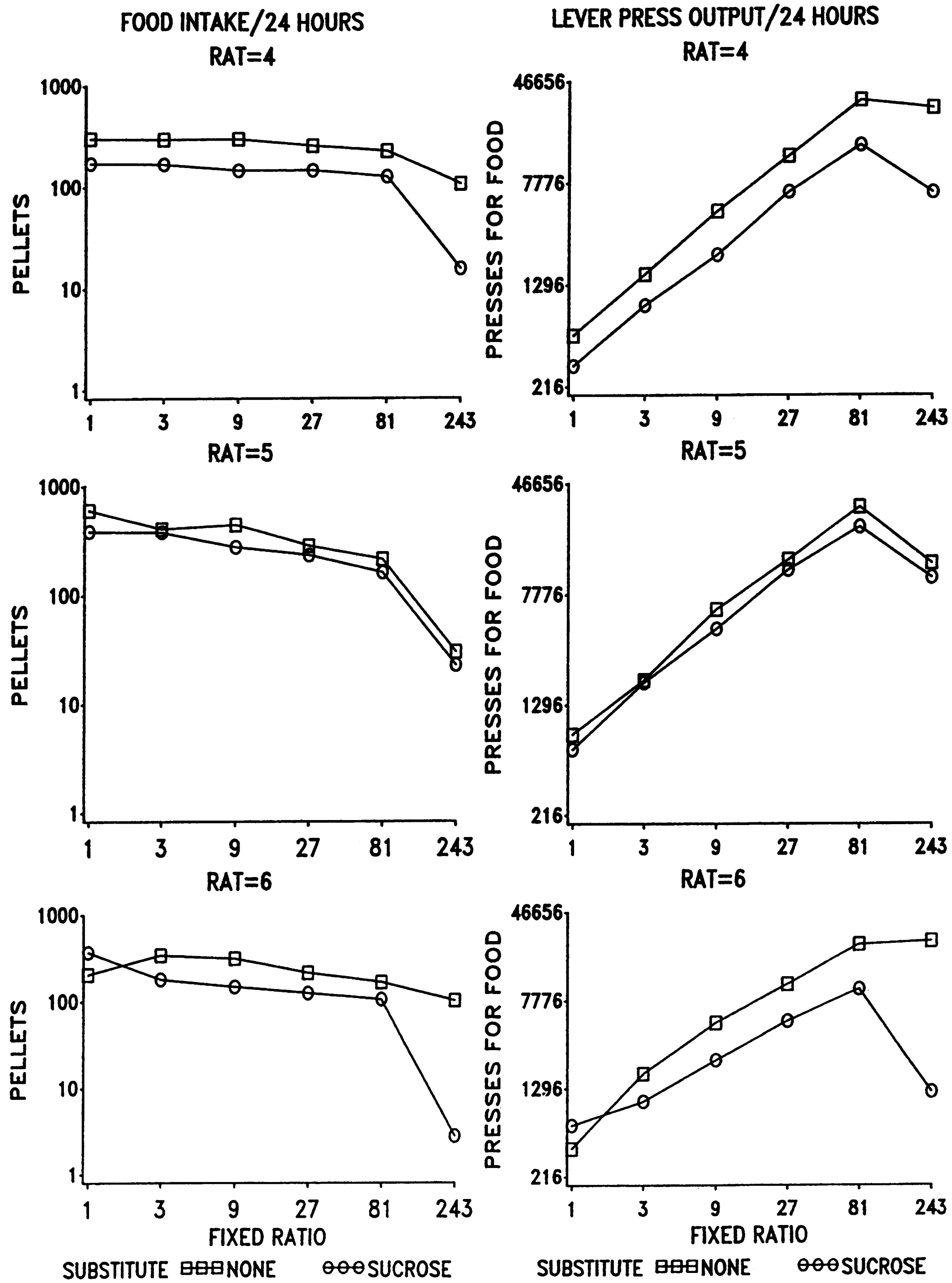


Fig. 5. In the left column, pellet intakes at each FR for Rats 4, 5, and 6 are shown for the no-sucrose (squares) and sucrose (circles) conditions of Experiment 2. In the right column, the corresponding output of lever presses at each FR for these rats is shown. The axes are scaled logarithmically. The data points represent totals for the dark and light periods.

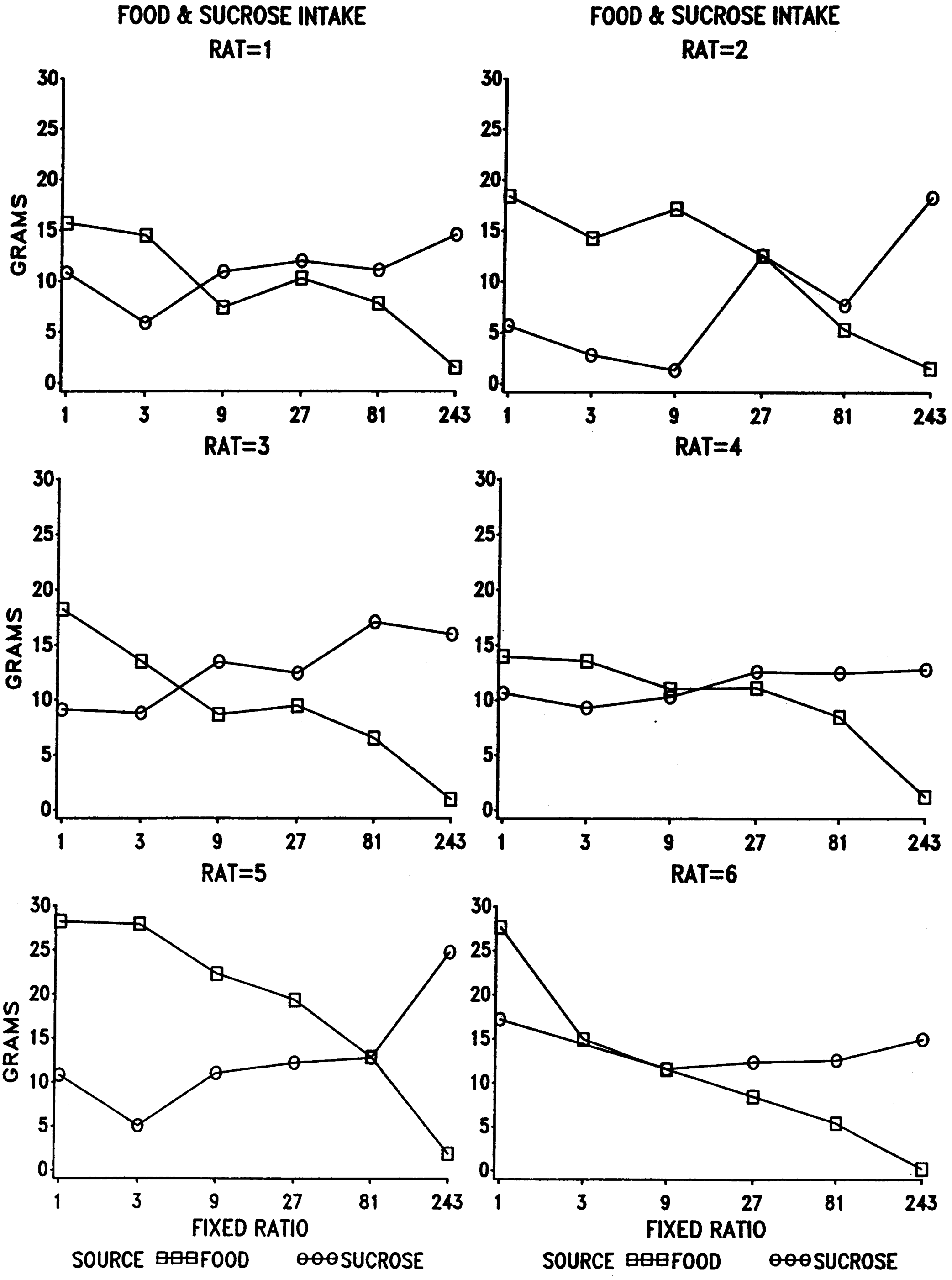


Fig. 6. Food and sucrose intakes are shown for each rat at each FR in the no-sucrose (squares) and sucrose (circles) conditions of Experiment 2.

of food at the first FR in Experiment 2, it is possible that the smaller intake of sucrose at the first FR in Experiment 2 rendered it more susceptible to being increased by the larger daily increases in the unit cost of food in that experiment, as a comparison of Figures 3 and 6 reveals.

EXPERIMENT 3

In Experiments 1 and 2, the reduction of food intake by the intake of sucrose was attributed to the substitution of sucrose for food. An implicit but nevertheless critical assumption underlying this conclusion was that the calories of sucrose were responsible for reducing food intake. In an independently conceived experiment, a monkey's demand for food was used to evaluate this assumption. The original objective of this experiment was to determine whether a relatively inexpensive noncaloric substitute for food would increase the elasticity of demand for food. This was accomplished in three phases. In the first phase, monkeys had free access to water, and daily increases in the FR were used to characterize demand for food. During the second phase, sodium saccharin was added to each monkey's water supply, and daily increases in the FR were again used to determine demand for food. Because saccharin-sweetened water was the only source of fluid in the second phase, a third phase was conducted, in which the intake of saccharin-sweetened water was partially decoupled from a monkey's required daily intake of water by allowing each monkey concurrent access to saccharin-sweetened water and to a large fraction of its normal daily intake of plain tap water.

METHOD

Subjects and Apparatus

Two adult male rhesus macaques (*Macaca mulatta*) were used as subjects. Monkey 4 weighed 14 kg, and Monkey 5 weighed 10 kg.

Each monkey lived in a separate cage (0.64 m long, 0.62 m wide, and 0.78 m high). Along one side of each cage hung a rectangular box (0.58 m long, 0.19 m wide, and 0.46 m high) that housed a pellet dispenser, a water solenoid, and six hinged translucent press plates or keys. At the upper left of this surface, a water spout protruded into the cage, and above the spout was a cuelight. The end of the water spout behind the front panel was connected via a solenoid valve to a gravity-feed watering system that provided continuous access to tap water from a self-replenishing common reservoir. A recessed food cup was located below the spout, and to the right of this food cup was the array of six keys. Only four keys were used in the present experiment.

Both cages were continuously maintained in an environmental chamber in which the temperature was 21 ± 3 °C and the relative humidity was 50%. The overhead lights were on between 6:00 a.m. and 6:00 p.m. and off during the remaining 12 hr. Outside of this chamber, a customized interface was tethered to the box on each cage and to an adjacent PDP8/E® computer. Supersked® software was used to control the delivery of water and food and to record daily food and water totals as well as any press on one of the four keys that equaled or exceeded 0.50 N.

Procedure

During all stages of this study, the upper left key was used as the choice key for water, and the upper right key was used as the choice key for food. Immediately after the delivery of a food pellet or a squirt of water, both choice keys were illuminated, and the lower left and right keys were dark. If a food pellet had been delivered and a monkey chose to continue eating, it could press the upper right key; this darkened it and illuminated the key directly below it. While the lower right key (the food key) was illuminated, a fixed number of presses on it was required for the delivery of each 750-mg Bioserv banana-flavored monkey pellet. If, however, a monkey chose to drink, it could press the upper left key; this darkened it and illuminated the key directly below it. While the lower left key (the water key) was illuminated, 10 presses on it were always required for each squirt of water. After 10 presses on the water key, the water cuelight was immediately illuminated for 2 s before the solenoid was opened. This signaled delay allowed the monkey to position its mouth near the spout before the water was released. The amount of water released was 2 cc per squirt, except in the third stage of this study. As explained below, the specific procedure used in the third stage required an adjustment of the volume per squirt.

The choice key for water was always illuminated during the completion of a ratio on the food key, and the choice key for food was always illuminated during the completion of the FR 10 on the water key. This signaled the opportunity to switch from pressing the food key to the water key during the completion of an FR on the food key or to switch from pressing the water key to the food key at any time during the completion of the FR 10 on the water key, although no such switches were recorded. If, during the completion of a ratio on either the food or the water key, the monkey paused longer than 15 s, the associated choice key was reilluminated.

During the food+H_2O condition, the food intake of each monkey was allowed to stabilize at FR 10. After intake stabilized, the FR for food was increased 20% each day. The series of ratios was identical to the series used in Experiment 1, with the exception that in the present study, the largest ratio was 372. At all times during this stage, plain tap water was the only fluid available.

The day after FR 372, the FR for food was reset to 10 and the first saccharin condition (Food+sac 1) was imposed. Each monkey's water was sweetened by adding enough sodium saccharin to the common reservoir to produce a 0.007-M saccharin solution. Ogawa, Yamashita, Noma, and Sato (1972) reported that the activity of the chorda tympani in rhesus macaques was significantly elevated above threshold by a 0.007-M saccharin solution, and Weiskrantz (1960) reported behavioral data that revealed that rhesus macaques exhibit a moderately strong preference for this molarity of saccharin solution over water.

After each monkey's food and saccharin-sweetened water intakes stabilized, the FR for food was increased daily. The only fluid available was saccharin-sweetened water. The day following FR 372, the food FR was reset to 10, the individual food and saccharin-sweetened water intakes were allowed to restabilize and, the FR for food was again increased. This replication of the Food+sac 1 condition was the Food+sac 2 condition.

In the final condition (food+sac+free H_2O), 300 ml of plain tap water and saccharin-sweetened water were concurrently available as the FR for food was increased daily. This amount of water represented 67% of the 24-hr intake of unadulterated water by these monkeys at the smallest FR for food. Thus, if a monkey did not reduce its fluid intake at the smallest FR, some fluid would have to be obtained by drinking the saccharin-sweetened water. At the beginning of each day's session, the source of plain tap water was made available from a standard water bottle that was hung from the side of each cage. Before the FR for food was increased, the amount of water per squirt was increased by increasing the duration of a squirt. A duration was chosen that resulted in an approximate equality between the daily number of squirts of saccharin-sweetened water and the number of food pellets at the first ratio (FR 10).

RESULTS

Under the food+H_2O condition, food intake decreased gradually between FR 10 and FR 86. Beyond FR 86, the decline of food intake accelerated (Figure 7, top row). As food intake decreased for Monkey 4, water intake also decreased, albeit not as rapidly. This correlated decrease of food and water intake was much less evident for Monkey 5, whose water intake decreased little, if at all, as food intake was reduced from 234 to 34 pellets per day.

When saccharin-sweetened water (Figure 7, middle row) was concurrently available, increases in the FR again reduced food intake; however, over a wide range of FR values, each monkey's food intake curve from the Food+sac 1 condition overlapped the corresponding food intake curve for the food+H_2O condition. The intake of saccharin-sweetened water increased for Monkey 4 beyond FR 179, but the intake of saccharin-sweetened water by Monkey 5 changed little as the FR increased.

In agreement with the results of the Food+sac 1 condition, each monkey's food intake curve for the food+H_2O condition overlapped the corresponding food intake curve for the Food+sac 2 condition (Figure 7, bottom row). Monkey 4 increased its intake of saccharin-sweetened water as the FR value increased, and food intake decreased. This increase emerged at a smaller ratio during the redetermination. During the Food+sac 1 condition, intake increased beyond an FR of 149 but, during the redetermination, intake

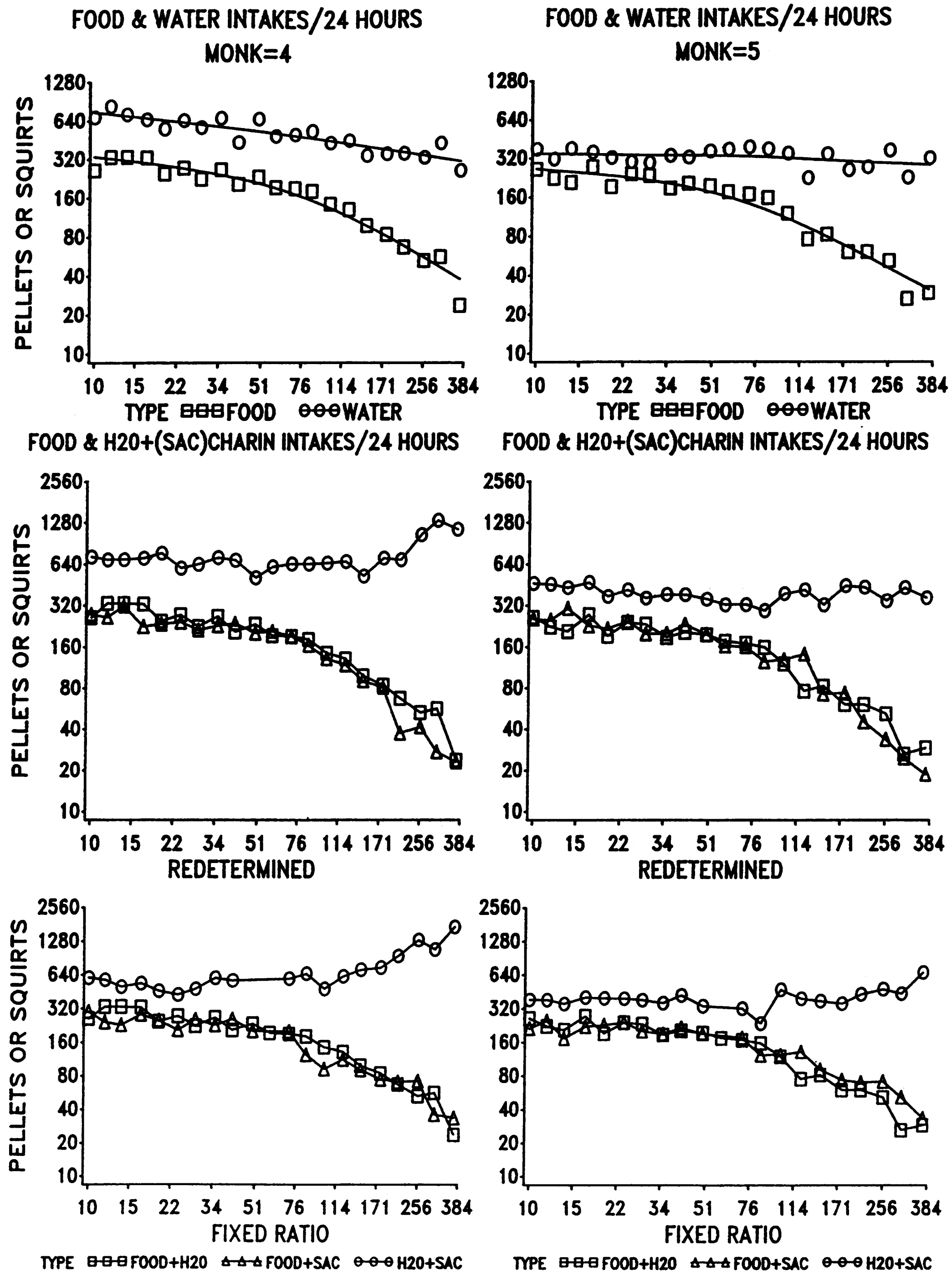


Fig. 7. Pellets of food (squares) and squirts of fluid (circles) are plotted as a function of FR size in the food+H_2O condition (top row), in the Food+sac 1 condition (middle row), and in the Food+sac 2 condition (bottom row), which was a redetermination of the Food+sac 1 condition. The left column shows data from Monkey 4, and the right column shows data from Monkey 5. The axes are logarithmically scaled. The smooth lines are simple spline fits that describe the trajectory of points within the coordinates of the figure. The squares in the middle and lower rows of graphs represent food intakes from the food+H_2O condition (top row) replotted for comparison.

increased beyond FR 103. Once again, the intake of saccharin-sweetened water by Monkey 5 changed little as the FR was increased, although intake did increase slightly at the four largest FRs.

Figure 8 shows each monkey's food intakes with and without saccharin-sweetened water available and the intake of saccharin-sweetened water at each FR in logarithmic coordinates. The individual adjustments of amount per squirt resulted in approximate equality of pellet deliveries and deliveries of saccharin-sweetened water at FR 10 (the first circle and triangle in each plot overlap). In agreement with the results of the Food+sac 1 and 2 conditions, the food intakes for the food+H_2O and the food+sac+free H_2O conditions did not deviate systematically from each other over a wide range of ratios. As the FR increased and food intake declined, intake of saccharin-sweetened water increased for both monkeys. This increase occurred beyond FR 86 for Monkey 4 and beyond FR 72 for Monkey 5.

DISCUSSION

Unlike the intake of sucrose, the intake of saccharin did not reduce demand for food. Taken together, the results of Experiments 1, 2, and 3 are consistent with the conclusion that the calories of sucrose were responsible for the reduction of food intake in Experiments 1 and 2. However, this conclusion neglects the fact that saccharin was in solution and sucrose was solid; therefore, food intake may have been reduced in Experiments 1 and 2 because sucrose was more filling. This possibility is unlikely for several reasons. The first is that sucrose is easily digested. Soon after or even before entering the small intestine, sucrose may have been hydrolyzed to glucose, which rapidly diffuses across the intestinal wall and into the portal blood supply (Krause & Mahan, 1979). This means that sucrose probably did not accumulate in any significant amounts in the stomach or gut and thereby distend the stomach or compete with food for space in the gastrointestinal tract. A less speculative reason is that the food intake of rats, monkeys, and humans is significantly suppressed by oral consumption and intragastric preloads of glucose, fructose, and sucrose solutions (Booth, 1972a, 1972b; Castonguay & Hirsch, 1981; Castonguay, Phillips, & Collier, 1985; Collier & Hirsch, 1977; Moran & McHugh, 1981; Rogers, Carlyle, Hill, & Blundell, 1988; Sclafani, 1987b), but not by equal volumes of air, water, sodium chloride, urea, or 3-methylglucose (Booth, 1972b).

In all three experiments, the reduction of food intake by increases in the FR for food was accompanied by increases in the intake of a concurrently available, less costly commodity. Equation 1 can be used to quantify this relationship. One can compute the ratio of relative changes in consumption of the alternative, $\Delta q/q$ (sucrose or saccharin), to relative changes in the unit price of food, $\Delta p/p$ (food). The ratio of these relative changes, e_c, is the cross-price elasticity of demand for sucrose or saccharin, and economic substitution is said to occur when e_c is positive. In all three experiments, as increases in the FR reduced Δq for food, $e_{\text{c-sucrose}}$ and $e_{\text{c-saccharin}}$, the cross-price elasticities of demand for sucrose and saccharin, increased, because Δq increased for both alternatives. Sucrose and saccharin were therefore economic substitutes for food. In contrast, increases in the FR for food reduced the water intake of Monkey 4 in the food+H_2O condition and, thus, $e_{\text{c-water}}$ was negative. This means that for Monkey 4 water was a complement for food, whereas for Monkey 5 water was neither a complement nor a substitute, because this monkey's water intake remained remarkably constant across the entire range of FRs.

Despite the cross-price increases in sucrose and saccharin, only the intake of sucrose reduced demand for food. In particular, over a wide range of FRs, the intake of sucrose in Experiments 1 and 2 reduced the intake of food without systematically affecting the slope of the demand curve for food in logarithmic coordinates. In terms of the quantity (q) of food consumed at successive FRs, this means that $\ln(q_{\text{no sucrose}, i+1}/q_{\text{no sucrose}, i}) = \ln(q_{\text{sucrose}, i+1}/q_{\text{sucrose}, i})$, which implies that the elasticity of demand for food in the no-sucrose condition and the elasticity of demand in the sucrose condition were equal, because the elasticity of demand is equivalent to the slope of the demand curve in logarithmic coordinates. (Hursh & Winger, 1995, describe a normalization method that permits direct comparison of elasticities between commodities that differ in level of consumption.) In Experiment 3, $q_{\text{no saccharin}}$ and $q_{\text{saccharin}}$ were similar

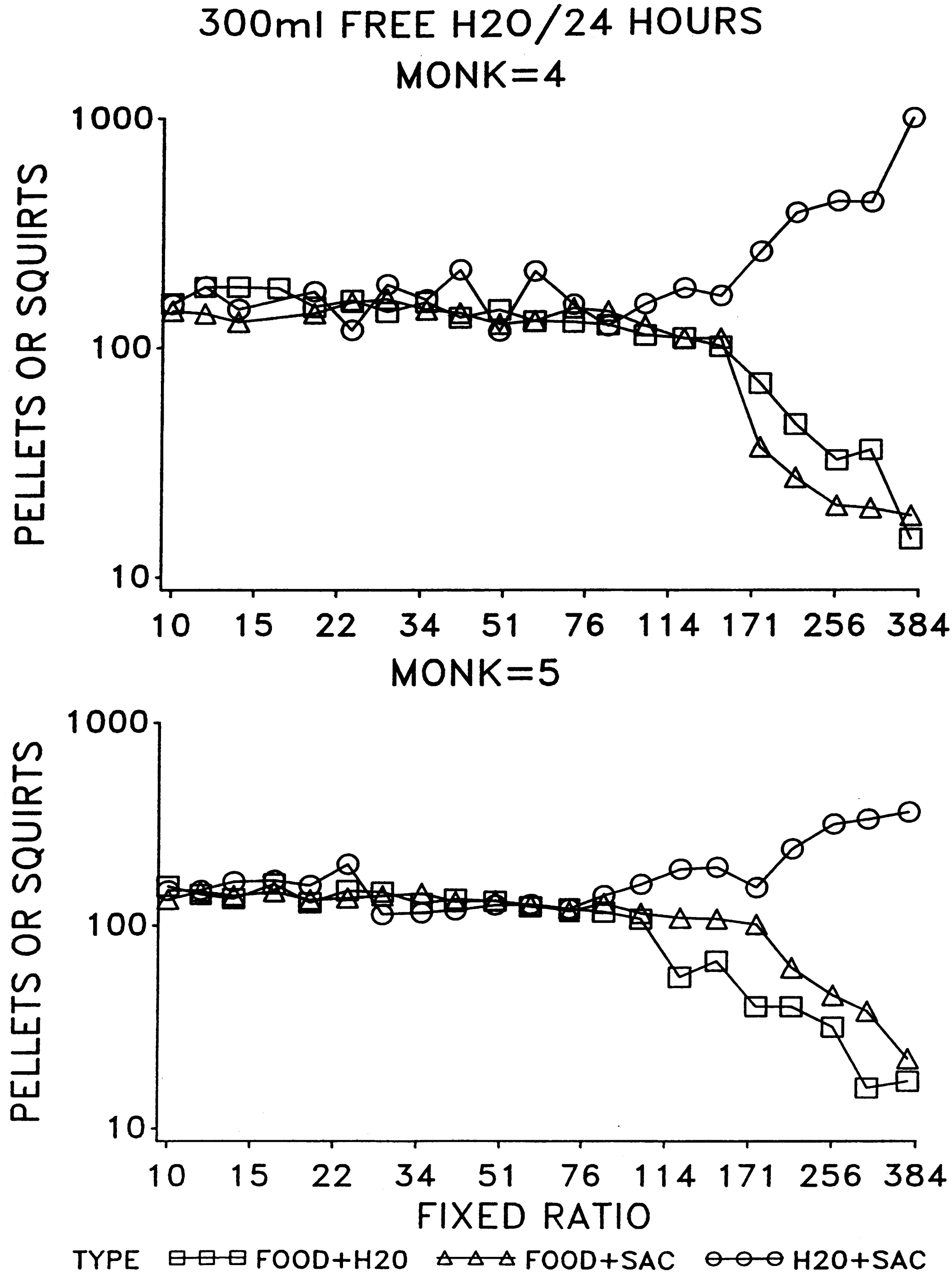


Fig. 8. Pellets of food (triangles) and squirts of saccharin-sweetened water (circles) for Monkeys 4 and 5 are shown at each FR in the food+sac+H_2O condition. The squares represent food intakes in the food+H_2O condition.

over a wide range of FRs, because the intake of saccharin-sweetened water did not systematically affect demand for food (as shown in Figures 7 and 8). As a consequence, the elasticity of demand for food in the absence of saccharin and the elasticity of demand for food in the presence of saccharin were approximately equal.

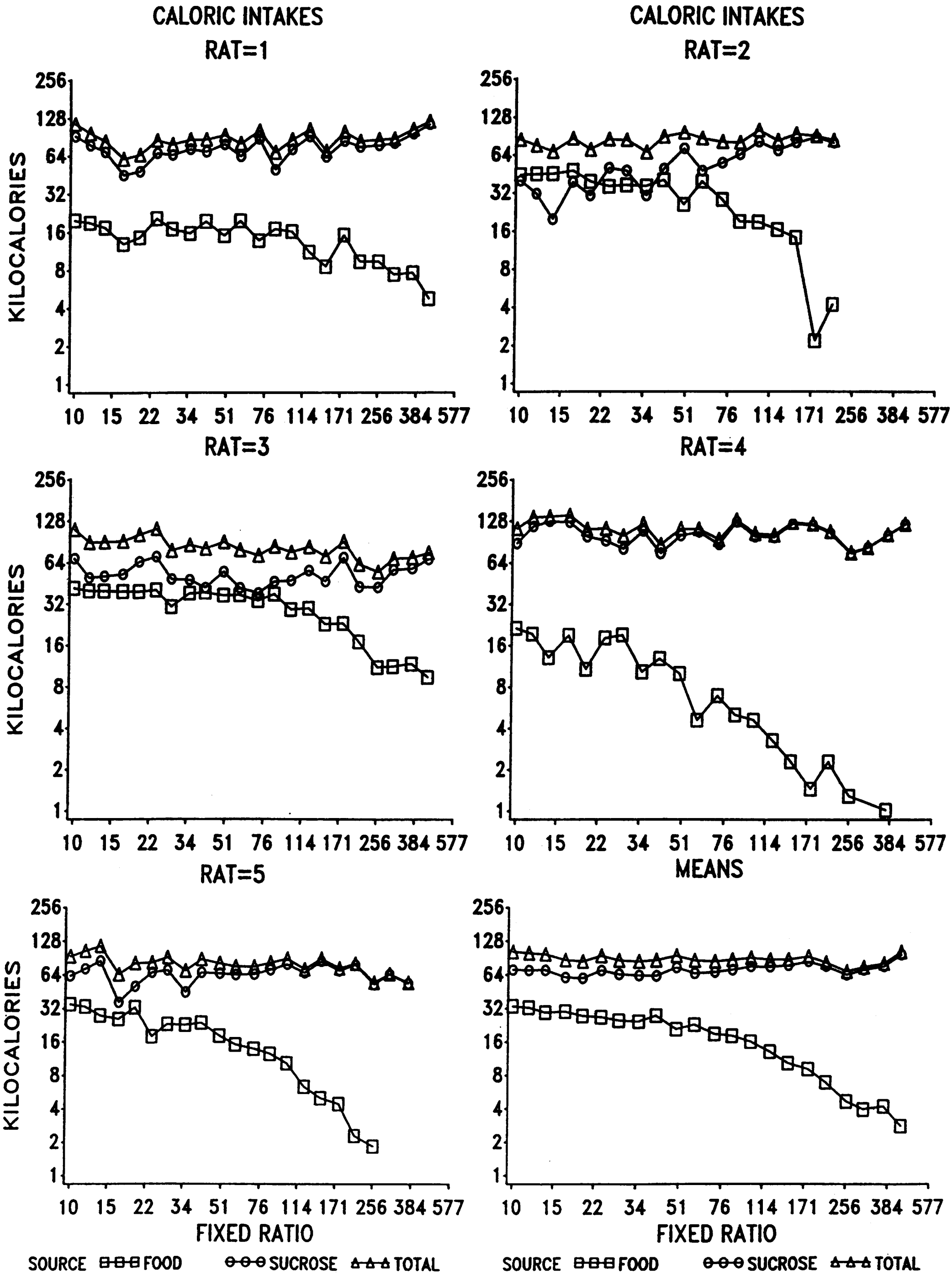
Sucrose is therefore an economic substitute that has metabolic consequences, because increases in the FR increased sucrose intake, which minimized weight loss and proportionally reduced food intake. In contrast, saccharin intake did not reduce demand for food nor did it systematically affect the elasticity of demand for food. It was, however, a substitute for food, because increases in the FR reduced food intake and increased the intake of saccharin. Therefore, saccharin is an economic substitute that does not have metabolic consequences.

GENERAL DISCUSSION

The rats in Experiments 1 and 2 and the monkeys in Experiment 3 defended their daily food intake at the smallest FR against progressive increases in the unit cost of food by increasing their daily output of presses. However, an inverse relationship between FR size and operant output does not imply that an animal is actively regulating its intake of food or some correlated quantity such as calories. It was only by reducing a rat's food intake while it had free access to a caloric substitute for food that it was possible to determine whether caloric intake would be regulated. In an effort to directly evaluate whether and the extent to which caloric intake was regulated, the number of kilocalories for food and sucrose were calculated for each rat in Experiments 1 and 2. This was done by multiplying the number of grams of food and sucrose at each FR by the caloric densities of food (3.8 kcal/g) and sucrose (4.0 kcal/g).

Figure 9 shows the individual and mean caloric intakes in kilocalories for food, sucrose, and the food + sucrose total at each FR in Experiment 1. The individual caloric intakes for food, sucrose, and the total at each FR in Experiment 2 are shown in Figure 10. There are two general features of the plots in Figures 9 and 10. First, as the FR increased and the intake of calories from food decreased, the intake of calories from sucrose occupied an increasingly larger fraction of the rat's total caloric intake until, at the largest FR, total caloric intake and intake of calories from sucrose were almost identical. (In each plot, this is implied by the convergence of the triangles and circles.) Second, the intake of sucrose greatly minimized the reduction of total caloric intake across a wide range of FRs, although total caloric intakes in Experiment 1 appeared to be reduced at the very largest FRs and perhaps total caloric intakes were reduced more in Experiment 2, within which the daily increases in the FR were relatively large. The minimal nature of this reduction is most apparent when compared to the necessarily larger reductions of caloric intake and body weight that were incurred in the no-sucrose condition of Experiments 1 and 2. (In Experiments 1 and 2, the food intake and corresponding caloric intake curves for the no-sucrose condition are identical in shape, because, in the absence of sucrose, total caloric intake at each FR is directly proportional to food intake at that FR.) Taken together, these two general findings are consistent with the possibility that rats in the present study (a) were affected by relatively short-term variations in caloric deficit (perhaps on a meal-to-meal basis, as suggested by Campfield & Smith, 1990; Johnson, Ackroff, Peters, & Collier, 1986; Kanarek, 1976; Louis-Sylvestre & Le Magnen, 1980); (b) compensated, albeit imperfectly, for the declining intake of a more costly source of calories by substituting the intake of a less costly source of calories (Castonguay et al., 1985); and (c) tended to regulate total daily caloric intake (Booth, 1972a, 1972b; Nicolaidis & Rowland, 1976). Although a caloric substitute for food was not used in Experiment 3, it is likely that if one had been available, the monkeys in that experiment also would have compensated for the intake of a relatively inexpensive caloric substitute for food by reducing their intake of food (Foltin & Shuster, 1984; Hansen, Jen, & Kribbs, 1981; McHugh, Gibbs, Falasco, Moran, & Smith, 1975; McHugh & Moran, 1978; McHugh, Moran, & Barton, 1975).

If regulation is indeed responsible for the data shown in Figures 9 and 10, then one might legitimately ask, what is regulated? Mrosovsky (1986) and Mrosovsky and Powley (1977) persuasively argued that body-fat regulation in the rat is an empirically supportable assumption but is extremely complex be-



CALORIC INTAKES RAT=1

CALORIC INTAKES RAT=2

RAT=3

RAT=4

RAT=5

MEANS

Fig. 9. In the left column and in the top and middle panels of the right column, caloric intake in kilocalories from food (squares) and sucrose (circles) and total (food + sucrose) caloric intake are shown at each FR in Experiment 1. Mean caloric intakes are displayed in the bottom right plot.

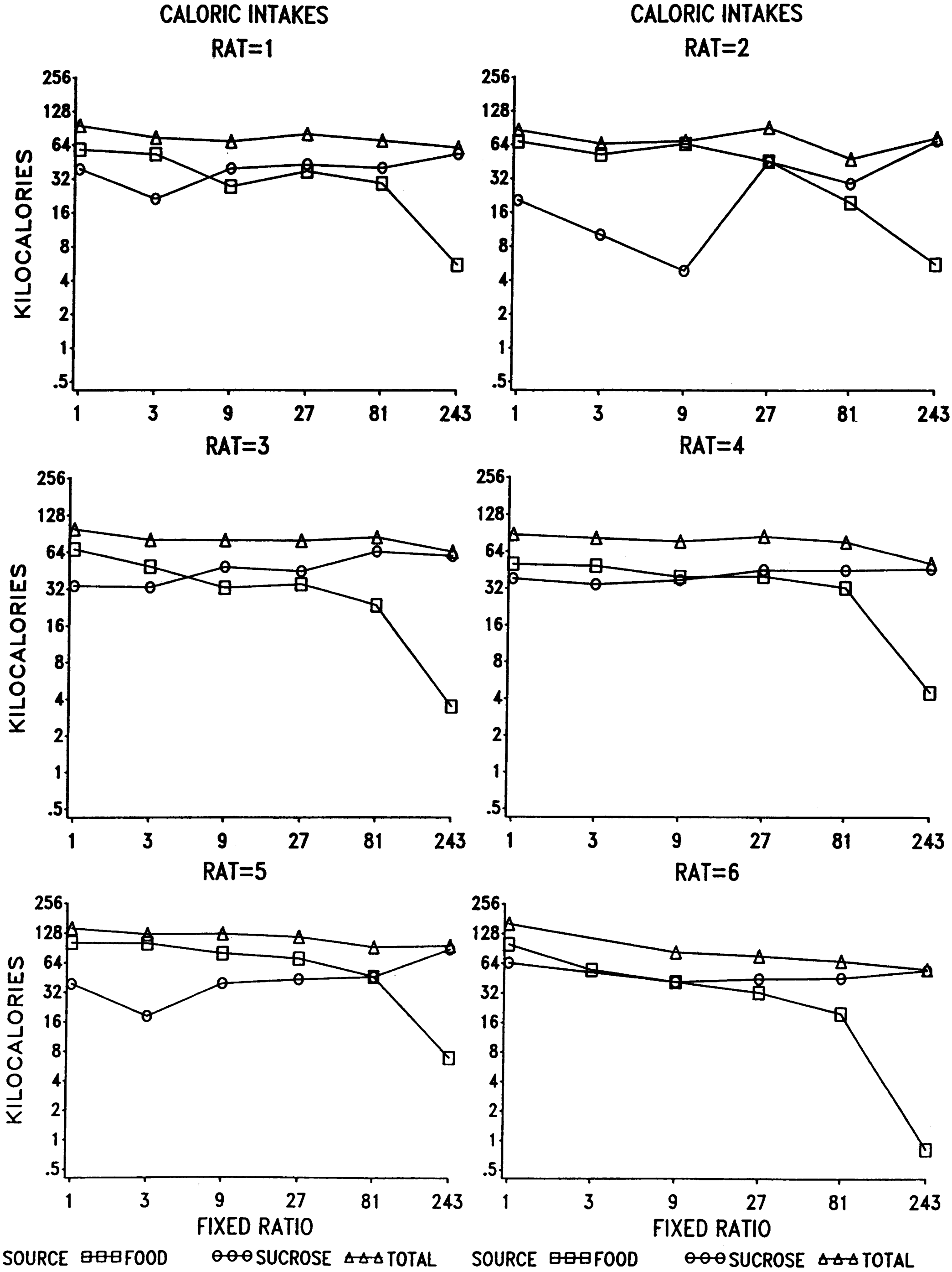


Fig. 10. Caloric intakes in kilocalories for individual rats are shown at each FR in Experiment 2. The format for this figure is identical to that of Figure 9.

cause the adipose mass of the rat is not unitary. It consists of different depots (e.g., subcutaneous, retroperitoneal, and epididymal) that are subject to individualized central nervous system control and that consist of different cell sizes that are site specific and differentially sensitive to manipulations such as deprivation, high-fat diets, and exposure to cold. The complexity of this issue notwithstanding, the relative constancy of caloric intake and body weight in Experiments 1 and 2 is consistent with the possibility that a rat's body fat or some correlate of body fat (e.g., adipose cell size) was the quantity that was regulated. This conclusion does not imply that body fat is the only quantity that might be regulated (Martin, White, & Hulsey, 1991) nor does it follow from the data of the present series of studies that there exists a fixed, immutable body-weight set point (Collier, 1983; Peck, 1976, 1978, 1980; Van Itallie & Kissileff, 1990; Wirtshafter & Davis, 1977).

Regardless of what might be regulated, it is clear from the present data that in the absence of a substitute for food, rats' and monkeys' demands for food were inelastic over a wide range of FRs. Although sucrose intake reduced the food intake of rats but saccharin intake did not reduce the food intake of monkeys, neither sucrose intake nor saccharin intake systematically altered the slopes of the demand curves that characterized food consumption in the absence of a substitute for food. As a consequence, increases in the FR resulted in corresponding increases in monkeys' and rats' daily output of presses, which enabled them to defend their intake of those nutritionally unique elements of food that complemented those in sucrose and saccharin. When sucrose and food intakes were rescaled in terms of calories, it was clear that over a wide range of ratios, as increases in the FR reduced caloric intake from food, caloric intake from sucrose occupied an increasingly larger fraction of total caloric intake and total caloric intake was reduced relatively little. These findings suggest that rats compensated for lost food calories and tended to regulate total caloric intake.

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