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THE CURRENCY OF PROCUREMENT COST

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As the number of instrumental responses required to procure access to food is increased, animals decrease the frequency of initiating meals and increase meal size, conserving total intake while limiting the increase in the overall cost of feeding. In two studies, one using wheel turns and one using bar presses as the instrumental response, we asked whether freely feeding laboratory rats measure cost according to the energy or the time they expend. In each study we varied both the price (i.e., number of wheel turns or bar presses) and the force required to make a response (i.e., torque on the wheel or weight of the bar). Price affected both procurement time (from the first to the last procurement response) and procurement work, whereas torque and bar weight affected work without altering time in most cases. Meal patterns were altered by all manipulations of price, but changes in torque and bar weight had little effect on meal patterns, except in the conditions in which they altered procurement time. These results suggest that time is a critical currency of procurement cost in rats.

Key words: foraging cost, time, effort, meal patterns, wheel running, bar pressing, rats

In a seminal paper, Schoener (1971) stated that an optimal forager would maximize the rate of return, that is, the net energy (energy gained minus energy spent) relative to the time spent in each foraging episode, or more generally, benefits relative to costs. Over the last 25 years, we have studied this relation using a closed-economy operant simulation of foraging in which animals perform an operant response for access to meals or for food portions within meals. The assumption has been that operant responding is a cost because it involves both time and effort. In our foraging paradigm, animals live continuously and earn all of their food in the experimental chambers. This allows them to use various strategies to optimize their intake. They are required to press a bar, peck a key, or run in a wheel to procure access to food and then may eat any amount; the meal ends when the animal does not eat for 10 consecutive minutes. The operant requirement per meal initiation is called the procurement price. Foraging animals (and their nonforaging controls who have ad libitum no-cost access to food) eat meals that are relatively random in onset and size but result in a regulated, constant daily caloric intake (Collier, Hirsch, & Kanarek, 1977; Collier, Johnson, Hill, & Kaufman, 1986; Johnson, Ackroff, Peters, & Collier, 1986; Richter, 1927). It seems unlikely that each feeding episode is optimal; rather, it is more likely that the animal optimizes over a sequence of meals.

All species that have been tested in this paradigm, including rats, cats, chickens, blue jays, guinea pigs, agoutis, degus, and ferrets, have used a common strategy in response to increasing procurement price: They gradually reduce the number of meals they initiate while increasing the size of their meals compensatorily (Collier & Johnson, 1990). As a result of the change in meal patterns, total intake (the benefit) is conserved and the number of responses (the cost) is limited as price increases. We hypothesize that a procurement price is a cost that affects the net energy gained by increasing energy expenditure or the time spent gaining it, that is, the numerator and denominator of the optimality function, respectively. In our paradigm we do not directly measure the actual energy gained or spent; instead, we determine the calories consumed and the number of procurement responses made.

To compute a benefit–cost ratio, it is necessary to specify currencies for both benefits and costs, which may differ as a function of activity, physiological state, species, niche, and habitat (e.g., Collier, Johnson, CyBulski, & McHale, 1990; McNamara & Houston,

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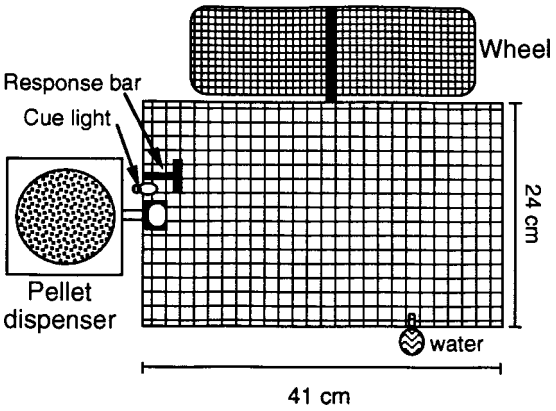

Fig. 1. Diagram of the foraging cage in Experiment 1 (top view).

1986). In a study of cats working for access to food, we attempted to assess the relative contributions of time and work to cost by factorially increasing the access price from 10 to 640 bar presses per meal and increasing bar weight from 1 to 12 N. These manipulations resulted in progressive decreases in meal frequency accompanied by compensatory increases in meal size, with the greatest effects occurring with combinations of high prices and heavy weights. Time and work were confounded as currencies, however, because increasing bar weight also resulted in a decrease in average rate of responding, thus increasing time spent as well as work done obtaining a meal. The change in average rate was due in part to increases in pauses and partial responses (bar touching) (Collier, Kaufman, Kanarek, & Fagen, 1978).

The present studies were designed to address further the issue of cost currency. Pressing a bar is an arbitrary response with dimensions of effort, time, and topography, any or all of which may vary and may contribute to the putative cost of responding. Previous results have shown that rats will run in a wheel to gain access to a meal (Kanarek & Collier, 1979). Because the topography of wheel running is relatively fixed (Collier, Hirsch, Levitsky, & Leshner, 1975), we used this less arbitrary response in the first experiment to parcel out the contributions of the potential currencies of time and work to procurement cost. We varied cost by changing both the number of wheel turns (price) required for access to each meal (more turns require more time and more work) and the torque of the wheel (higher wheel torques require more work but not necessarily more time). If increases in wheel torque do not change the running speed, then we could manipulate work independent of time required to gain access to a meal. This would allow us to determine whether energy expended is a critical currency in this paradigm by noting whether meal patterns are altered as a function of torque. To determine the generality of the findings, we conducted the second experiment using bar pressing as the operant and varied both procurement price and the force required to press the bar.

EXPERIMENT 1

METHOD

Subjects

Eight naive Sprague-Dawley-derived male rats (Camm Research Institute), weighing approximately 280 to 305 g at the start of the experiment, were used. Four rats were assigned to a foraging group, and 4 were assigned to a free-feeding control group matched for levels of spontaneous wheel running.

Apparatus

Each rat was housed in a Wahman LC-34 running wheel with an attached double-sized cage (41 cm by 24 cm by 18 cm; see Figure 1). A drinking tube was mounted on the front of the cage. The control cages contained a large cup of powdered Purina chow (5001). The experimental cages were fitted with a T-shaped bar, the consumption bar, in the center of one end wall, 6 cm above the floor. The bar required 0.35 N to press. A 1.5-cm cue-light was mounted above the bar. A pellet dispenser (BCS, Piscataway, NJ) delivered 45-mg food pellets (rodent chow formula, BioServ, Frenchtown, NJ) into a food cup located on the cage floor under the bar. Wheel movement was monitored by two microswitches positioned 180° apart, and when both switches were activated in sequence, we counted a wheel turn. The apparatus was controlled and the data were recorded by a computer.

The apparatus was located in a room maintained at 72 ± 2 °F with lights on from 8:00 a.m. to 8:00 p.m. Throughout the study the

rats lived continuously in their cages except for a daily maintenance period of about 30 min when they were weighed and placed together in holding cages while the data were recorded, the food and water were replenished, and the equipment was cleaned and tested. Any changes in response contingencies were made at this time.

The experimental rats' wheel torques were varied from 0.5 newton-meters (Nm) to 32.0 Nm by means of a brake on the wheel. A drum (8.9 cm in diameter and 2.1 cm wide) was attached to the axle of the wheel. A 2-cm strap was wrapped around the drum and the ends brought together and attached to a string that passed over a pulley that was fastened to the upper corner of the wheel frame. A weight was attached to the string, and different wheel torques were achieved by varying the weight. The torque was calibrated by attaching a lump of Play Doh® to the outer edge of the wheel, 90° from the top. The amount of Play Doh® was varied until it just caused the wheel to rotate, and its weight times the radius of the wheel provided a measure of the torque required to turn the wheel. The drum was cleaned with alcohol, and the torque was recalibrated frequently (Collier et al., 1975). The control rats' wheel turns were monitored by a mechanical counter attached to the wheel; the wheel torque was 0.5 Nm throughout.

Procedure

Training phase. Rats in the foraging group were adapted gradually to their apparatus. Unless otherwise noted, each condition during training remained in effect for 2 days or until a given rat lost no weight from one day to the next. First, the response bar was removed for 3 days, and the pellet dispenser automatically delivered pellets at random intervals varying from 15 to 90 s during alternate hours for 24 hr. The cuelight was on during the hours when pellets were delivered. Next, the bar was installed, the cuelight remained on continuously, and each bar press produced one pellet. The pellet price was raised to 5 and then to 10 bar presses per pellet. Finally, the wheel-running procurement requirement was added such that during intermeal intervals, the cuelight was off, and consumption bar presses were ineffective. When the rat completed the required number of wheel turns (the procurement price), the light came on, indicating that pellets could be earned by bar pressing. Any number of pellets could be earned. The meal ended when the rat earned no pellets for 10 consecutive minutes. A rat could begin another meal at any time by completing the procurement price again. The 10-min meal-end criterion was established in prior experiments by log-survival functions of the length of interfeeding intervals (Collier et al., 1990). Initially, the procurement price was 1 wheel turn; it was increased to 5 and then to 10 wheel turns.

Experimental phase. The pellet price was 10 bar presses throughout the remainder of the experiment. The procurement price was initially set at 10 wheel turns, and the torque was increased from 0.5 to 16 Nm by successive doubling. Each torque remained in effect for at least 7 days and until the wheel turns and meal parameters stabilized (usually 7 to 10 days). Next, these six torques, plus a torque of 32 Nm, were repeated in a random order. The order was different for each rat. After this, the procurement price was raised to 40 turns, and three torques (0.5, 4, and 32 Nm) were presented in a different random order to each rat. Finally, the procurement price was raised to 160 turns, and the three torques were repeated in a random order.

Data Analysis

Data from the last 5 days of each condition were included in the analyses. We determined the mean daily intake (in grams), meal frequency, and the mean meal size (in grams) for each rat during each experimental condition. Because rats run spontaneously, it was possible for them to complete a procurement wheel-running requirement and not feed. These wheel turns, as well as any that occurred during a meal (hence did not contribute to the completion of a procurement requirement) were scored as extra turns. We determined both the total number of turns and the total number of extra turns made daily. In addition, we computed the average procurement rate (procurement price divided by median time from the first to the last wheel turn) and the local running rate within running bursts. A burst was defined as two or more wheel turns that were separated from other turns by 15 s. Thus the local rate was

calculated at the procurement price divided by the time from the first to last turn minus any pauses of 15 s or longer during completion of the price.

The effect of torque at a procurement price of 10 was examined by means of a two-factor (6 torques × 2 presentation orders) repeated measures analysis of variance (ANOVA). The 32-N torque was not included in this analysis. The interaction of torque and price was examined via a two-factor (3 torques × 3 prices) repeated measures ANOVA. Data for the three torques (0.5, 4, and 32 N) at a price of 10 were taken from the random presentation of torques; data for these torques at prices of 40 and 160 were from the last two experimental phases. The alpha level was set at $p < .05$. Only analyses that met this criterion are presented below.

Results

The means for the noted measures, from the last 5 days of each condition, are given for individual subjects in Appendixes A through C. During their initial exposure to the ascending series of torques at a fixed procurement price, rats in both the foraging group and the free-feeding control group (whose torque remained fixed at 0.5 Nm) decreased their daily wheel running (total turns), $F(5, 30) = 12.35$. Although the means of free-feeding rats were higher than those of the foraging rats, the difference was not statistically significant, nor was the Group × Torque interaction (Figure 2). Free-feeding rats ate more than foraging rats, $F(1, 6) = 8.53$, and the food intake of both groups decreased somewhat over this phase, $F(5, 35) = 2.71$; again, the Group × Torque interaction was not significant (Figure 2).

In contrast to the results during the ascending series of torques, when the torques were presented in a random order there were no significant changes in the foraging rats' daily intake, total wheel turns, or extra turns (Figure 3). Similarly, the rats decreased meal frequency and within-burst running speed during the ascending, but not during the random, series of torques: meal frequency, $F(5, 15) = 3.00$; running speed, $F(5, 15) = 3.38$. The average procurement rate was higher during the ascending series than during random exposures, $F(1, 3) = 12.34$, and, although there is a suggestion of an inverted-U-shaped function in the ascending phase, there was no significant effect of torque during either ascending or random exposures (Figure 3). Because these changes during the initial ascending exposure appeared to be related primarily to the rats' growth, we will limit the remaining presentation to the analyses of the three torques presented at three procurement prices.

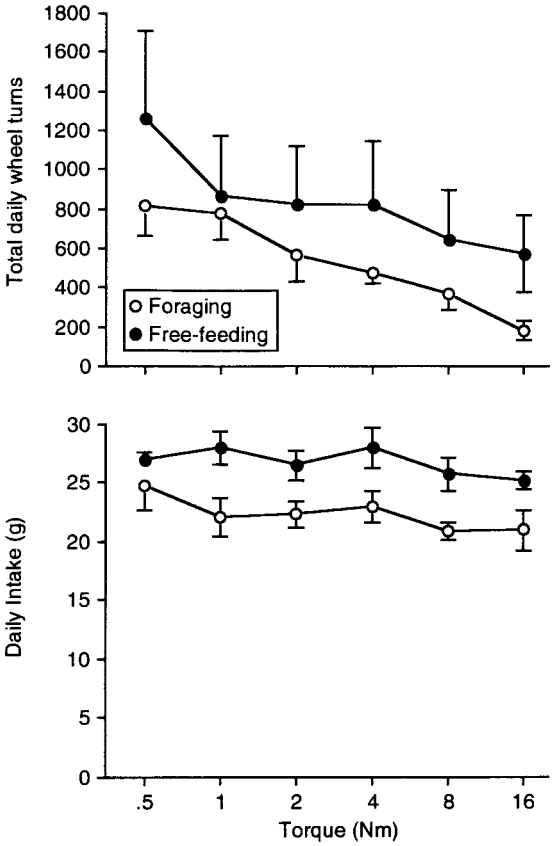

Fig. 2. Mean (±*SE*) daily wheel turns (top panel) and food intake (bottom panel) of 4 foraging and 4 control rats as a function of the foraging rats' wheel torque.

Meal frequency (i.e., meals per day) was strongly affected by procurement price, declining as price increased in all of the rats (Figure 4, top graph). There was also a decrease in meal frequency at the highest torque, but only at higher prices, $F(4, 12) = 5.61$. Price and torque also interacted as they affected meal size (i.e., grams per meal), $F(4, 12) = 5.77$ (Figure 4, middle graph). All of the rats ate larger meals at the highest procurement price and at the highest torque when it was combined with the higher prices.

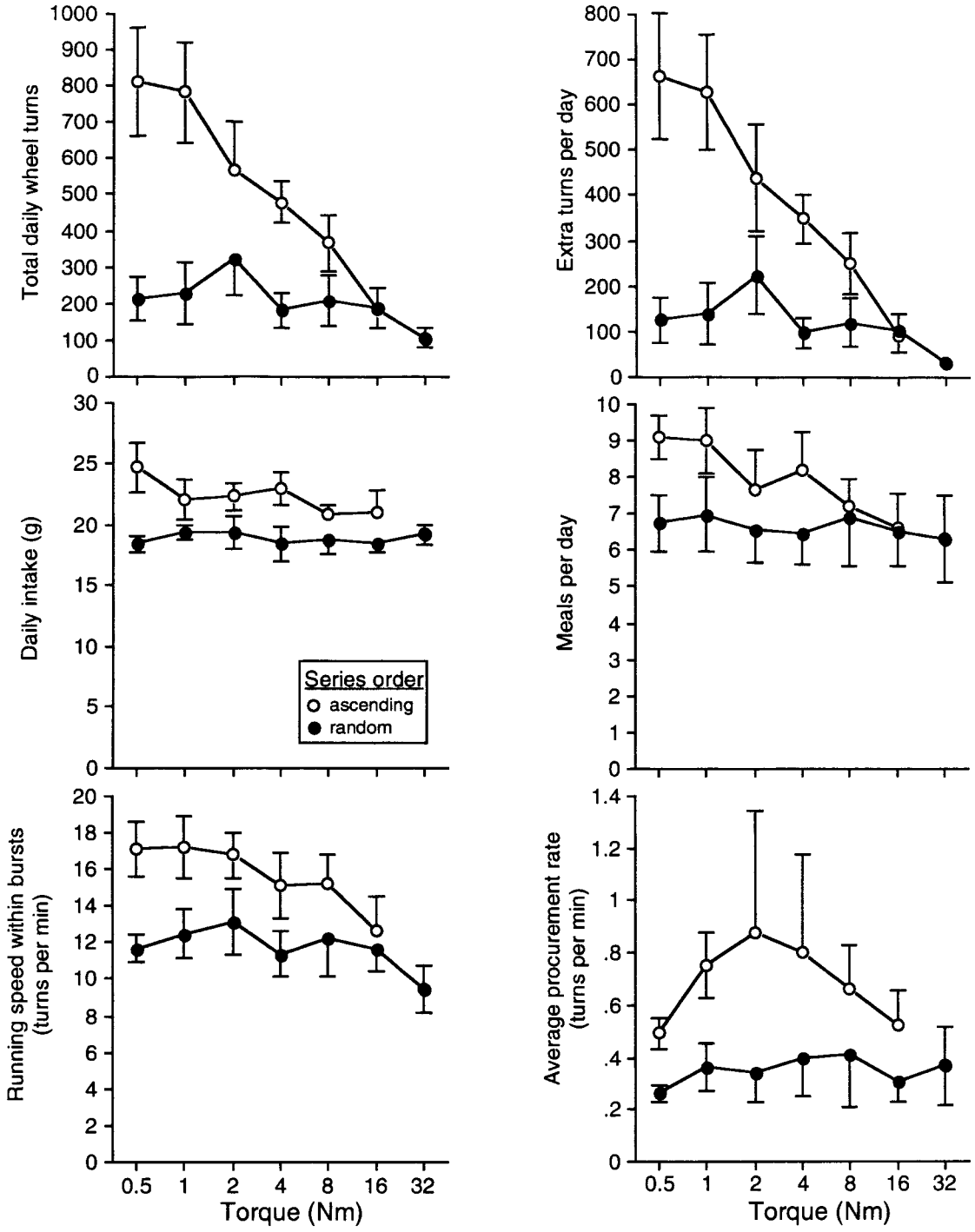

Fig. 3. Mean (±*SE*) running and feeding measures for 4 foraging rats during an ascending and random presentation of wheel torques at a procurement price of 10.

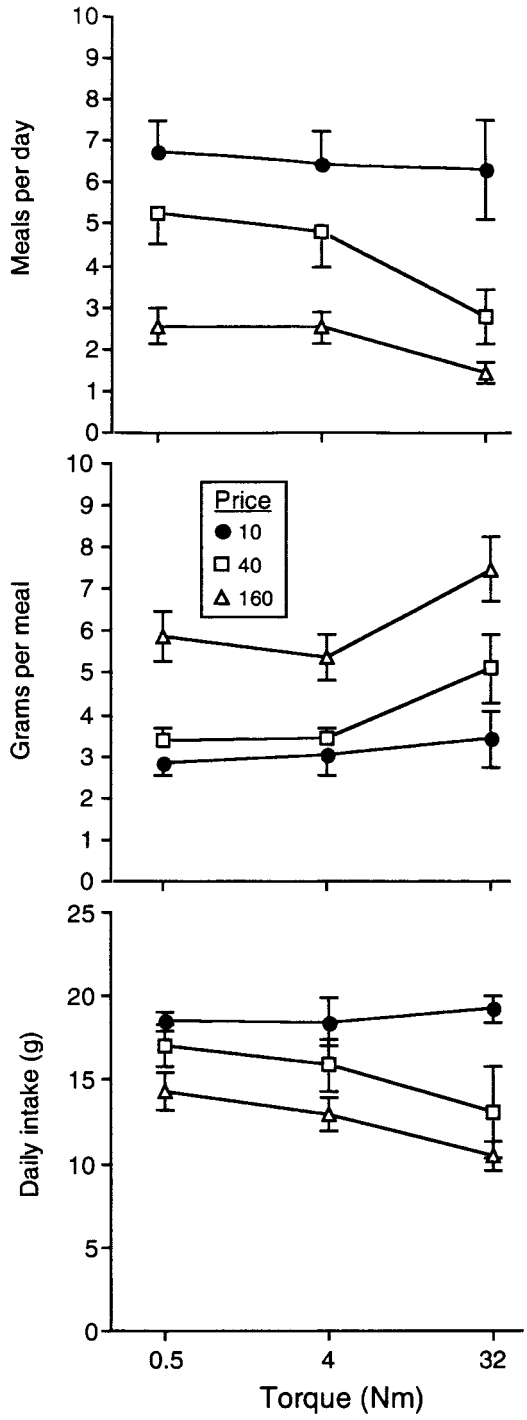

Fig. 4. Mean (±*SE*) feeding measures for 4 foraging rats as a function of wheel torque and procurement price. Note that only three of the seven torques presented at a price of 10 are plotted.

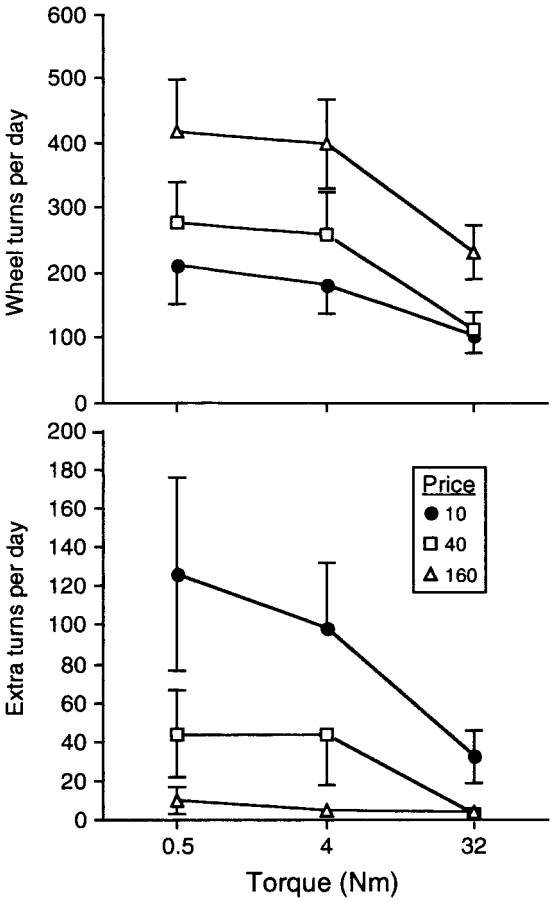

Fig. 5. Mean (±*SE*) daily wheel turns (top panel) and extra wheel turns (bottom panel) of 4 foraging rats as a function of wheel torque and procurement price. Note that only three of the seven torques presented at a price of 10 are plotted.

These changes produced a decline in daily intake as a function of both price, $F(2, 6) = 10.35$, and torque, $F(2, 6) = 10.35$, but there was no significant interaction (Figure 4, bottom graph).

Total daily wheel turns increased with procurement price and decreased at the highest torque (see Figure 5, top graph). Both the fewest wheel turns and the smallest increase as a function of price occurred at the highest torque, $F(4, 12) = 6.96$. Extra wheel turns, in contrast, declined with increases in both price and torque. At the highest price, virtually every turn occurred during procurement. The fewest extra turns occurred at the highest torque for all procurement prices, $F(4, 12) = 5.32$ (Figure 5, bottom graph).

At the highest torque, rats decreased both running speed within bursts, $F(2, 6) = 7.30$ (Figure 6, top graph), and average procurement rate, $F(2, 6) = 16.10$ (Figure 6, middle graph). The time spent completing the procurement requirement increased with its price for all the rats, and although torque had no effect on procurement time at the low price, at the higher prices, procurement took longer at the highest torque, $F(4, 12) = 6.04$ (Figure 6, bottom graph).

Finally, to compare the relative effect of work and time spent on control of meal patterns, we performed multiple linear regressions of meal frequency and meal size with procurement work (price × torque) and median procurement time (interval between the first and last wheel turns) in each condition for each rat. For Rat 3, a variance inflation factor greater than 4 (SigmaStat statistical software) indicated that work and time were highly correlated, making it impossible to parcel out the individual contributions of each. For the other 3 rats, however, only procurement time—not work—contributed significantly to the variance of meal frequency and meal size (see Table 1).

Discussion

By independently varying the wheel torque and the price (number of wheel turns) required for rats to initiate a meal, we determined whether the currency of procurement cost is the energy expended, the time spent, or some combination of these. When the torque was held constant and the price was increased, rats' frequency of initiating meals declined and the size of their meals increased compensatorily, thereby restricting the increase in the total number of wheel turns performed. These results are in accord with previously reported studies (see Collier & Johnson, 1990, for a review). When the wheel torque initially was increased in an ascending series, wheel turns and meal frequency decreased; however, because the control rats, whose wheel torque was not changed, also decreased their running at this time, we believe these changes in both groups were due to age effects (Collier, 1970). In the following phases of the study, when the price was held constant and the torque was varied, meal frequency and meal size were not significantly affected by torque except at the highest price,

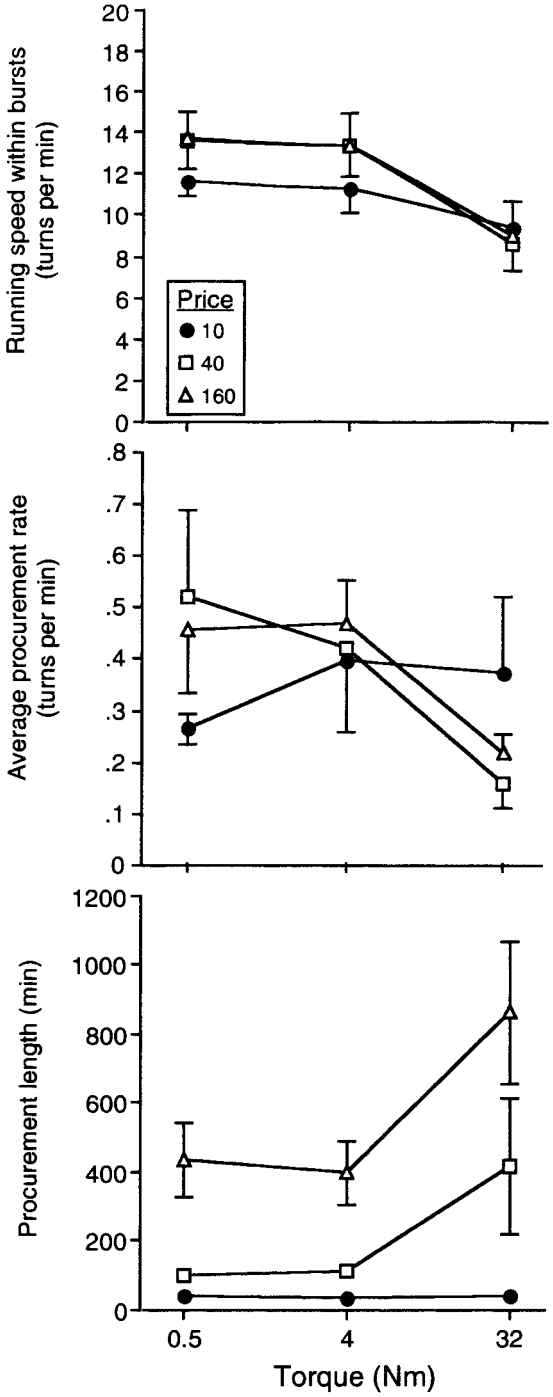

Fig. 6. Mean (±*SE*) running speed (local rate excluding pauses longer than 15 s, top panel), procurement rate (average rate including all pauses, middle panel), and procurement length (bottom panel) for 4 foraging rats as a function of wheel torque and procurement price. Note that only three of the seven torques presented at a price of 10 are plotted.

Table 1

Coefficients for procurement time and procurement work from the multiple linear regression equations relating meal frequency and meal size to these measures in Experiment 1. Also shown is a measure of collinearity of time and work (VIF).

	Meal frequency		Meal size		
Rat	Time	Work	Time	Work	VIF
1	−0.0115*	−0.0008	0.1780*	−0.0061	1.183
2	−0.0258*	−0.0006	0.2300*	−0.0081	1.862
3	−0.0003	−0.0023	−0.0403	−0.0915	13.084[a]
4	−0.0111*	0.0005	0.1910*	−0.0036	3.307

[a] High collinearity.
* $p < .05$.

when meal frequency declined and meal size increased compensatorily. The conditions in which torque affected meal patterns were also those in which increases in torque caused increases in the time to complete procurement. These results suggest that time may be a significant underlying currency of procurement cost.

EXPERIMENT 2

Experiment 1 used wheel running as an operant and modified the force required to turn the wheel and the number of turns required to initiate meals. To extend the generality of the results, we conducted a similar study using bar pressing as the operant and again modifying both the force required to press the bar and the number of presses required to initiate meals.

METHOD

Subjects

Eight naive Sprague-Dawley-derived male rats (Camm Research Institute), weighing approximately 280 to 305 g at the start of the experiment, were used.

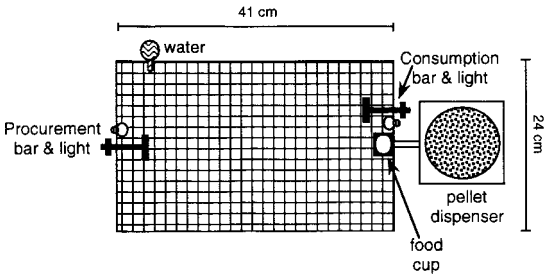

Fig. 7. Diagram of the foraging cage in Experiment 2 (top view).

Apparatus

Each of four experimental cages was equipped with a response bar (the consumption bar) centered on the cage wall 6 cm above a food cup, and a 1.5-cm cuelight mounted 2 cm above the bar (see Figure 7). A pellet dispenser (Med Associates, St. Albans, VT) delivered 45-mg food pellets (BioServ, rodent chow formula) into a food cup located on the cage floor under the bar. An identical response bar (the procurement bar) and cuelight were mounted at the opposite end of the cage. Two microswitches were mounted on each bar; one reported the depression, and one the release, of the bar. For a response to be counted, the bar had to be depressed through a throw of 1 cm and then released, equating distance pressed at all weights. Counterweights on the lever arm of each bar determined the force required to depress the bar. Water was freely available from a graduated cylinder attached to the front of the cage. The cages were interfaced to a computer (Commodore® 128D) that detected bar presses and operated the lights and pellet dispenser.

Procedure

The rats were tested in two squads of 4 rats each. Throughout the study they lived continuously in their cages except for a daily maintenance period of about 30 min when they were weighed and placed in holding cages while the data were recorded, the food and water were replenished, and the equipment

was cleaned and tested. Any changes in response contingencies were made at this time.

Training phase. Except as noted, each condition during training remained in effect for 2 days or until a given rat lost no weight from one day to the next. First, both bars were removed for 3 days, and the pellet dispenser automatically delivered pellets at random intervals varying from 15 to 90 s during alternate hours for 24 hr. The cuelight was on during the periods of pellet delivery. The consumption bar was then installed with a force requirement of 0.25 N. The consumption light was on continuously, and every bar response delivered one pellet. The pellet price was raised to 2, then 5, and finally 10 responses per pellet. The procurement bar was then installed with a force requirement of 0.25 N, the procurement force. Now during intermeal intervals the procurement cuelight was on, the consumption light was off, and responses on the consumption bar were ineffective. The procurement price was one response: When the rat pressed the procurement bar once, the procurement light went out, the consumption light came on, and pellets could be earned as before. When no pellets were earned for 10 consecutive minutes, the resting state was resumed, and to eat again, the rat again had to complete the procurement price. The procurement price was increased to 2, 5, and finally 10 responses per meal initiation.

Experimental phase. The pellet price was constant at 10 responses per pellet, and the consumption force was 0.25 N. The procurement cost was manipulated by varying both the procurement price and the procurement force. In each squad the rats were divided into two groups of 2 rats. For one group, ''price within force'' or P-F, the procurement force remained at 0.25 N, and the price was increased by doubling from 10 to 2,560 responses or until the rat lost more than 20% of its body weight. Then the price was returned to 10, the force was increased to 0.50 N, and the series of increasing prices was presented again. This pattern was repeated with forces of 0.75, 1.00, 1.25, 1.50, and 1.75 N. For the other group, ''force within price'' or F-P, the procurement price remained at 10, and the force was increased in 0.25-N increments from 0.25 to 3.25 N or until the rat lost more than 20% of its body weight. Then the force was returned to 0.25 N, the price was increased to 20, and the series of increasing forces was presented again. This pattern was repeated with prices of 40, 80, and 160. Each cost condition (one force–price combination) was in effect for at least 7 days and until there were no trends in any feeding measures (usually 7 to 10 days). If a rat met the 20% weight-loss criterion during a condition, its data from that condition were not included in the analysis.

Table 2

The highest force (in newtons) at which each rat in Group F-P successfully maintained its body weight at each price.

	Price				
Rat	10	20	40	80	160
1	3.25	3.25	3.25	0.50	
2	3.25	3.25	3.25	3.25	0.50
5	3.25	3.25	3.25	3.25	0.50
6	3.25	3.25	3.25	3.25	1.25

Data Analysis

Data from the last 5 days of each condition were included in the analyses. We analyzed each group's data with two-factor repeated measures ANOVAs (Price × Force). Due to the weight-loss criterion, some rats did not complete all cost conditions; only the conditions completed by at least 2 rats are presented. Some cost conditions (prices of 10 to 80 with forces of 0.25 to 1.75 N) were experienced by both groups of rats. For these conditions the data were analyzed with three-factor ANOVAs (Group × Price × Force) with repeated measures over the latter two factors. The alpha level was set at $p < .05$. Only analyses that met this level are presented below.

Results

The means for the noted measures, from the last 5 days in each condition, are given for individual subjects in Appendixes D through J. One rat in the P-F group died before completing the Force 0.50 conditions; its data are not included in the analyses. The highest price–force conditions completed by each of the other 7 rats are shown in Tables 2 and 3. Note that, due to our 20% weight-loss criterion, the P-F rats could not be tested over the same range of bar weights as the F-

Table 3

The highest price at which each rat in Group P-F successfully maintained its body weight at each force.

	Force (N)							
Rat	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00
4	640	320	160	160	80	160	80	
7	320	1,280	2,560	1,280	2,560	1,280	640	320
8	2,560	1,280	2,560	1,280	1,280	320	20	

P rats, and, similarly, the F-P rats could not be tested over the same range of prices as the P-F rats.

Meal Patterns

All of the rats ate fewer meals as procurement price increased (Figure 8, top graphs). This effect was significant in both groups: P-F, $F(6, 12) = 50.28$; F-P, $F(3, 9) = 53.76$. Although there was a suggestion of a decline in meal frequency at the higher bar forces in the P-F group, $F(6, 12) = 2.90$, $p = .055$, procurement bar force affected meal frequency significantly only in the F-P group, that is, the rats that were exposed to the highest forces, $F(12, 36) = 3.56$. A decrease in meal frequency with increasing bar force was seen in all 4 rats at a price of 10, 3 rats at prices of 20 and 40, and 2 rats at a price of 80.

Meal size (grams per meal) tended to change in the opposite direction from meal frequency; that is, when meal frequency declined with price or force, meal size increased (Figure 8, middle graphs). In the F-P group, the differences were not statistically significant. In the P-F group, there was a significant interaction of price and force on meal size, $F(36, 72) = 1.95$: Although meal size increased with procurement price at every force, force affected meal size only at the highest prices.

Over the cost conditions experienced by both groups, the effect of price was significant for both meal frequency, $F(3, 15) = 17.20$, and meal size, $F(3, 15) = 8.67$, but there were no effects of force or group and no interactions. That is, there were no significant differences between the groups in their responses to the ranges of prices and forces they both experienced.

Daily intake (Figure 8, bottom graphs) is the product of meal frequency and size. Because meal size did not always increase enough to compensate for the decline in meal frequency with price, intake declined as a function of price. This effect was statistically significant only in the P-F group, $F(6, 12) = 15.03$. In the F-P group, intake declined as a function of force, $F(12, 36) = 2.82$. Body weight reflected both growth and intake (Figure 9).

Procurement Responding

The local procurement bar-press rate (Figure 10, top graphs) of the rats in the P-F group was between 25 and 35 responses per minute, except that at high prices the rats responded faster (35 to 50 responses per minute) when the bar force was low, $F(36, 72) = 2.51$. Surprisingly, in the F-P group, response rate increased and then decreased as bar force increased, $F(36, 108) = 2.16$; price had no effect. For Rat 5, the response rate did not decline at the highest forces, but rather continued to increase. The rats often paused during completion of the procurement price; thus, the average response rate (Figure 10, bottom graphs) was slower and more variable than the local rate. In the P-F group, the average rate decreased as price increased, $F(6, 12) = 5.15$, but force had no effect. In the F-P group, the average rate showed the same pattern as the local rate, with higher rates at intermediate forces, $F(12, 36) = 2.90$.

Procurement length was composed of time spent bar pressing and time spent pausing (waiting more than 15 s between responses), with pause time making up the majority. The bar-pressing time (Figure 11, top graphs) was unaffected by force and increased with price for all the rats in both the P-F group, $F(6, 12) = 14.95$, and the F-P group, $F(3, 9) = 36.75$. Total procurement length (i.e., including pauses; Figure 11, bottom graphs) tended to increase with price, but in the P-F group, although the effect was seen in all 3 rats, the variability of the data rendered the differences not statistically significant; force had no effect in this group. In the F-P group, the increase in procurement length with price was significant, $F(3, 9) = 11.89$, and there was also an effect of bar force: Procurement was shorter, because

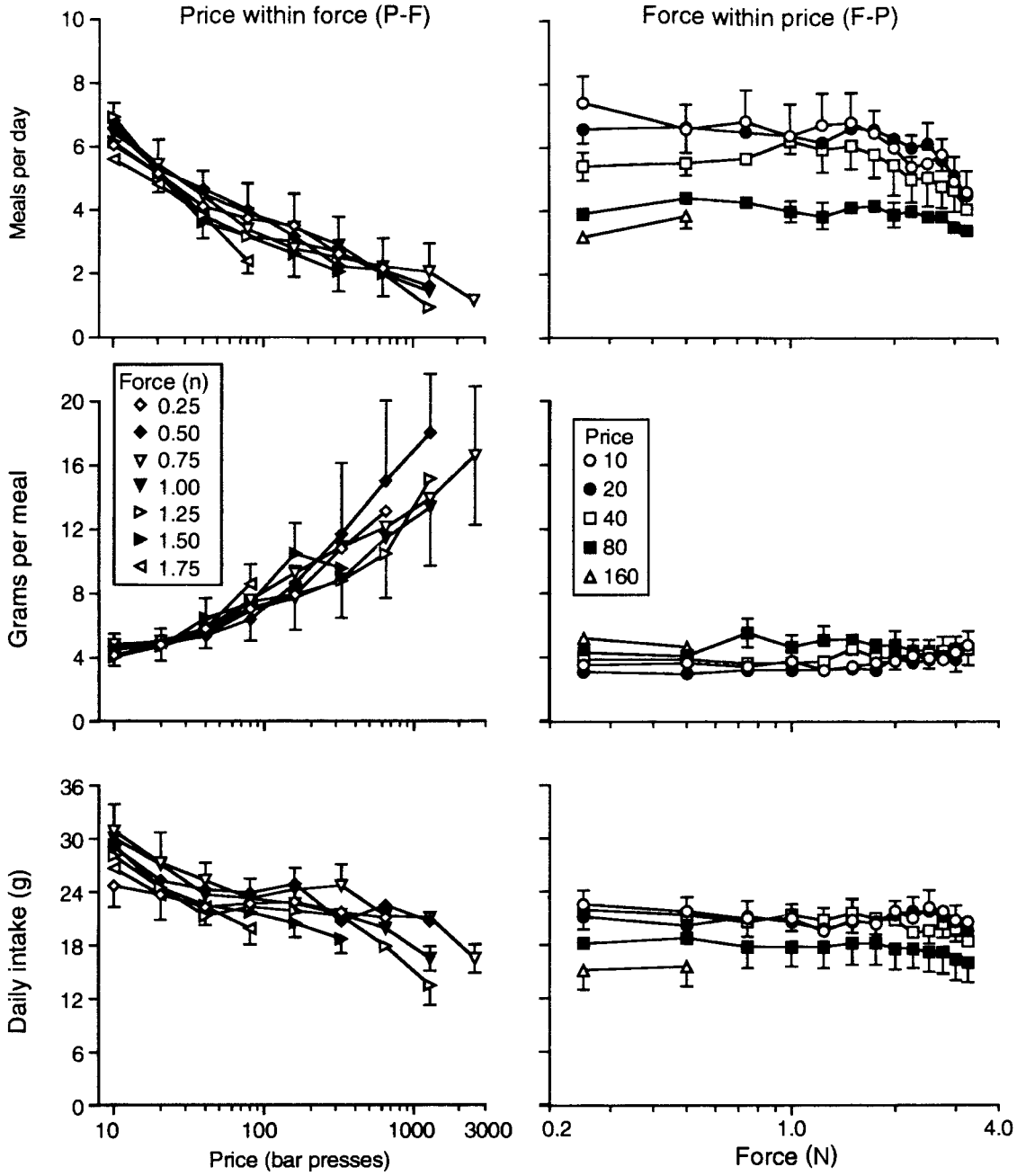

Fig. 8. Mean (±*SE*) meal frequency (top panels), meal size (middle panels), and daily intake (bottom panels) of 3 rats in the P-F group and 4 rats in the F-P group as a function of bar force and procurement price in Experiment 2. Note logarithmic scale on *x* axis.

the rats paused less, as force increased to between 1.5 and 2.5 N, $F(12, 36) = 15.48$. As force increased further, the effect on procurement length was inconsistent.

Cost: Work or Time?

Work and time are correlated over changes in price because more bar presses take both

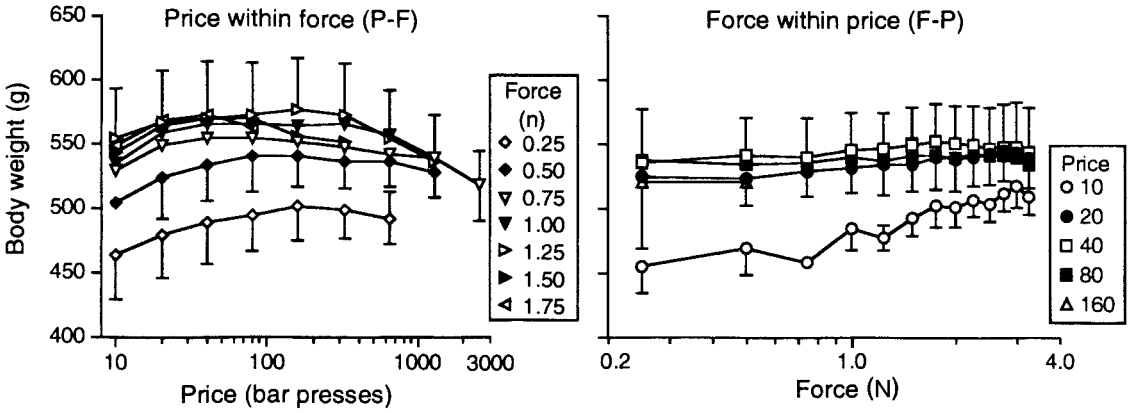

Fig. 9. Mean (±*SE*) body weights of 3 rats in the P-F group and 4 rats in the F-P group as a function of bar force and procurement price. Note logarithmic scale on *x* axis.

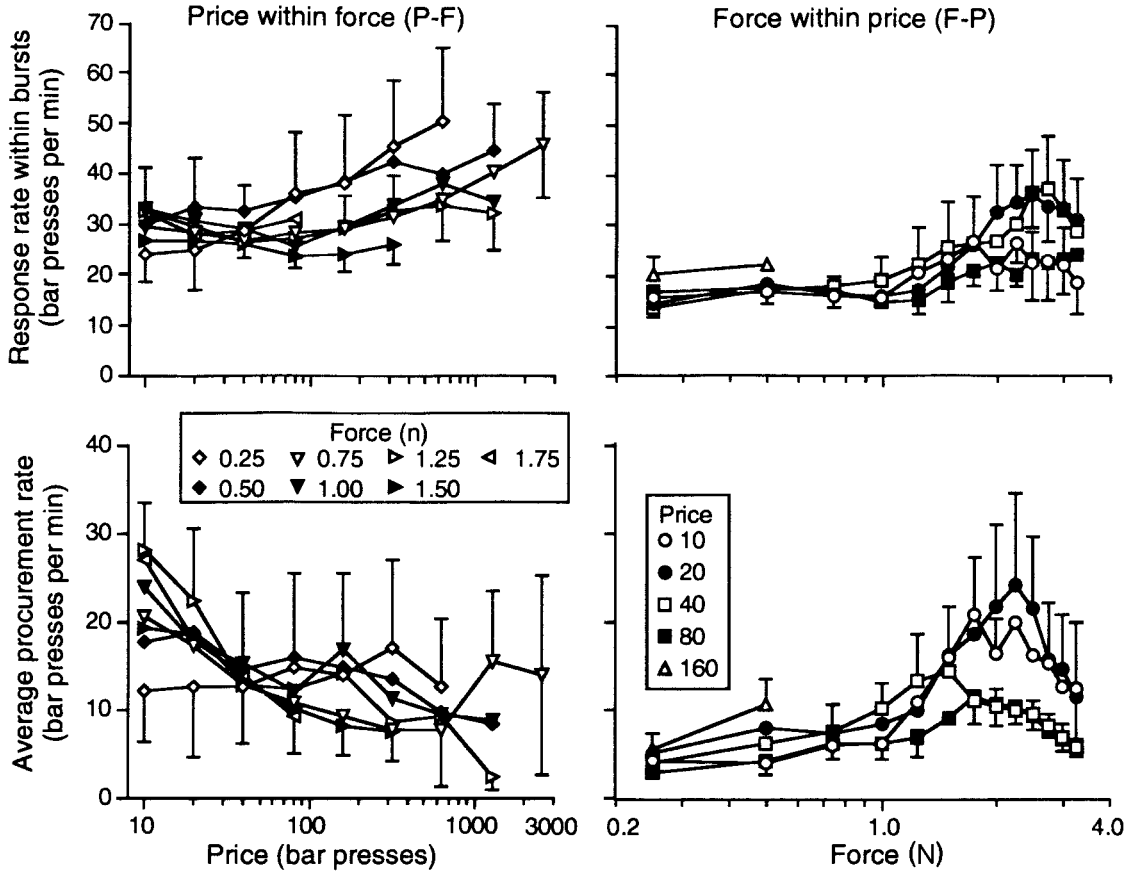

Fig. 10. Mean (±*SE*) procurement rate within bursts of responding (top panels) and average procurement rate (bottom panels) for 3 rats in the P-F group and 4 rats in the F-P group as a function of bar force and procurement price. Note logarithmic scale on *x* axis.

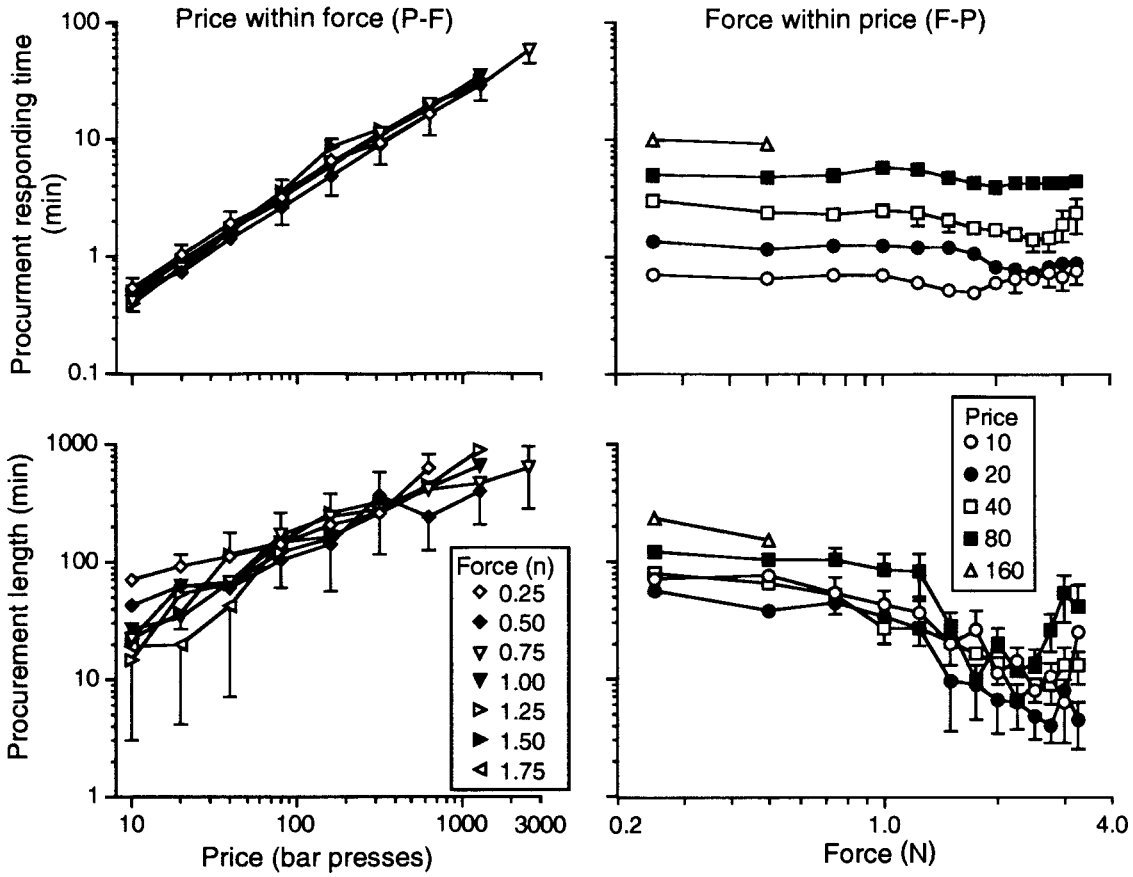

Fig. 11. Mean (±*SE*) time responding in procurement (top panels) and procurement length (bottom panels) for 3 rats in the P-F group and 4 rats in the F-P group as a function of bar force and procurement price. Note logarithmic scale on *x* and *y* axes.

more time and more work. But work and time were not correlated over changes in bar force. We performed multiple linear regressions of meal frequency and meal size with procurement work (force × bar excursion × price) and procurement length for each rat. There was no clear pattern in the results (Table 4).

Discussion

Due to the weight-loss criterion, the two groups of rats were exposed to different ranges of price and force. The P-F rats, exposed to a wide range of prices at each constant force, did not maintain their body weights at high bar forces. Similarly, the F-P rats, which were exposed to a wide range of forces at each constant price, did not maintain their weights at high prices. Note that at the highest force, these rats were pressing bars weighted with 325 g—more than half each rat's own body weight. Although bar force did not appear to have clear effects on meal patterns, the fact that none of the rats maintained its body weight at combinations of high price and high force suggests that work can interact with time as a cost.

Over the relatively low prices and forces experienced by both groups, there was an effect of price, but not force, on meal patterns. The effects of the higher prices seen by the P-F group were those seen in many previous studies—decreasing meal frequency and increasing meal size with increasing price. As in Experiment 1, increases in procurement price had little effect on response rate in this group, so higher prices took more time as well as more work.

At the higher forces seen by the F-P group, meal frequency did decline as force increased; however, the change was not as dra-

Table 4

Coefficients for procurement time and procurement work from the multiple linear regression equations relating meal frequency and meal size to these measures in Experiment 2. Also shown is a measure of the collinearity of time and work (VIF).

		Meal frequency		Meal size		
Group	Rat	Time	Work	Time	Work	VIF
F-P	1	−0.013	0.739*	0.017	−15.163*	1.18
	2	−0.017*	−1.306*	0.341*	15.787*	1.00
	5	−0.006*	−0.950*	0.096	−2.919	1.14
	6	0.001	−0.647*	−0.034	17.970*	1.10
P-F	4	−0.006*	0.166*	0.475*	−1.703	3.93
	7	−0.007*	−0.026	0.389	2.507	5.84[a]
	8	−0.006*	−0.107*	0.103	1.822	2.38

[a] High collinearity.
* $p < .05$.

matic as that seen as a function of price (see Figure 8). It is surprising that the decreases in meal frequency were not accompanied by increases in meal size. There were nonmonotonic effects of bar force on procurement time for the F-P rats: They took less time to complete procurement at intermediate forces than the lowest or highest forces (see Figure 11, bottom right graph). These changes in procurement time were not related, however, to the changes in meal patterns in the expected way; that is, meals were not more frequent when procurement time was shortest. It is intriguing that over the range of bar forces from 0.25 to 2.5 N, the work required for procurement increased, but, because the rats paused less, procurement time decreased. The fact that these two potential cost components changed in opposite directions may have been responsible for the relatively stable meal frequency and size seen over this force range. In any case, for the rats in this group, neither procurement time nor procurement work alone was a good predictor of meal frequency, and neither can be said to be the more likely currency of procurement cost.

GENERAL DISCUSSION

In two studies, we varied procurement price concurrently with procurement work in an attempt to determine the currency of procurement cost. In both cases, procurement price had the systematic orderly effects on meal patterns that we have reported previously. Because making more responses requires both more time and more energy, this manipulation does not help to distinguish between these two currencies. Increasing the wheel torque or the bar force increased the procurement work requirement but had little effect on procurement time, and, in general, had relatively minor effects on meal patterns. Because changes in procurement time reliably produced orderly changes in meal patterns, except in one case when procurement work concurrently changed in the opposite direction, time appears to be more likely than work to be a currency of procurement cost.

Prior results from our laboratory support the importance of time. When the procurement cost was defined in terms of an imposed interval (from 0 s to 23 hr) between a single bar press and access to a large cup of food, meal frequency declined and meal size increased with the length of the interval in a fashion parallel to that seen when the procurement cost was altered by changing the number of bar presses (Mathis, Johnson, & Collier, 1995). In this study, waiting time was a cost in the absence of explicit work.

Other data, however, suggest that work can be a currency of procurement cost. In a recent study in which mink had to push open doors to gain access to resource compartments, procurement work was manipulated by weighting the doors, and heavy doors resulted in less frequent openings and longer periods in the chambers each time (Cooper & Mason, 2000). The authors did not report whether the mink took longer to open heavy doors, so we cannot determine if time could have been a currency in this study. Also, in Experiment 2 of the present study, the fact

that the rats did not tolerate combinations of high price and high bar force suggested that work is a factor.

The minimal effects of wheel torque and bar force are counterintuitive. Doing work should be costly because energy must be expended. Work should enter into the feeding optimization equation as a factor that reduces net energy gain. Because procurement work occurs against a background metabolic state, however, it may or may not be significant to the animal. The metabolic cost of locomotion, for example, has been measured in studies of episodes of forced treadmill activity. Oxygen consumption is an increasing function of running speed, and the minimum cost of running (the slope of the curve relating oxygen consumption to running speed) is a declining function of body weight (Taylor, Schmidt-Nielsen, & Raab, 1970). The ecological significance of this metabolic cost, however, has been characterized as the energetic cost of transport, that is, as the percentage of an animal's daily energy expenditure that is devoted to traveling through the habitat. For small mammals, this cost is on the order of only 1% of their daily energy expenditure, and for large mammals, it is only 5% to 15% and includes many nonfeeding activities (Garland, 1983). Also, Rashotte (in press) recently has reported that the oxygen consumption of pigeons key pecking for food is no greater when the food cost is high than when the cost is low.

In the studies reported here, the rats' daily intake amounts provided no strong evidence that any increased effort expended at higher costs was significant in the animal's overall energy budget. When additional energy is expended, additional energy should need to be consumed to allow maintenance of body weight. Thus, one might expect the rats to have consumed more calories to maintain body weight as price, torque, or force increased. Consistent with previous reports, we found no such increase in total intake as a function of cost. At different forces or torques, for example, the rats' net energy gain varied for the same amount of time and number of responses spent foraging, and yet their body weights were stable.

Thus, the metabolic cost of procurement behavior may be relatively trivial relative to the total metabolic cost and may not vary significantly in closed economies over the normal range of foraging efforts expended by animals such as rats, especially in the laboratory, where episodes of feeding are infrequent and the time spent feeding is small (only 1 to 2 hr per day; Collier et al., 1990; Squibb & Collier, 1979). In natural settings, animals engage in multiple activities (defense of territory, establishment and defense of hierarchies, predation avoidance, reproduction, etc.) in addition to foraging, and time spent on any activity is a cost because it cannot be spent on a different activity. Thus, time is a likely common cost currency across multiple activities, and we would expect animals to be biologically prepared to be sensitive to time spent foraging in competition with other activities with different priorities, continuing to conserve time even in relatively undemanding habitats.

A complication for this hypothesis is that laboratory animals do not always alter their foraging behavior in ways that could save time. For example, as the procurement price increases, time spent procuring access to a meal could be reduced if animals increased their rate of responding, but they do not; the procurement response rate remains relatively low and is insensitive to price. This is in contrast to the increase in rate of bar pressing with increasing *consumption* price in closed economies (Collier et al., 1986; Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988). Further complicating the analysis of effort is the fact that activity per se apparently has benefits as well as costs. Rats (and other animals) run voluntarily in wheels or on treadmills even when there is no externally imposed contingent benefit for doing so (Collier, 1969; Kavanau, 1964; Sherwin, 1998). Activity also appears to be reinforcing, as evidenced by the fact that rats will pay an instrumental cost to gain access to a wheel (Collier & Hirsch, 1971). Voluntary running, however, is a decreasing function of the torque of a wheel or the slope of a treadmill (Collier et al., 1975). This effect also was seen in Experiment 1 of the present study in the decline in extra turns as torque increased. The amount of work done increases as torque increases, however, indicating that voluntary activity is not a simple regulatory process (Collier et al., 1975). Further illustrating the complex relation between voluntary running

and energy balance is the fact that both food-deprived and water-restricted rats run more as a linear function of log percentage body-weight loss, and the highest rate of running is at the point of metabolic crisis (Collier, 1964, 1969). If running involves a significant energy cost, then deprived animals are expending their reserves. Of course, expending energy searching for food when deprived could be adaptive in some circumstances; but we do not know whether finding food is a motivation for a rat running in a wheel (Collier, 1970).

In conclusion, the results of the present experiments support the hypothesis that time is an important currency of cost in a cost–benefit analysis of foraging in a closed economy. The effect of work on foraging appears to be indirect, via its impact on the time required to complete effortful responses.

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APPENDIX A

Daily wheel turns and food intake for the foraging rats (1–4) and the free-feeding control rats (5–8) during the initial presentation of torques in ascending order to the foraging rats in Experiment 1. Control rats' wheel torque was 0.5 Nm throughout.

		Foraging rats' torque (Nm)					
	Rat	0.5	1	2	4	8	16
Wheel turns per day	1	533	449	197	361	207	131
	2	971	1,052	828	596	492	291
	3	587	676	585	401	262	75
	4	1,154	942	659	555	502	232
	5	331	274	272	204	192	215
	6	1,572	1,474	1,420	1,428	1,237	1,066
	7	757	431	370	341	259	279
	8	2,373	1,306	1,236	1,321	877	734
Grams per day	1	27.0	25.4	21.3	26.4	20.0	21.7
	2	28.4	17.8	21.1	23.1	21.3	23.1
	3	19.2	21.3	21.0	20.0	19.6	15.8
	4	24.5	23.9	25.8	22.6	22.8	23.4
	5	27.0	25.0	23.0	25.0	24.0	24.0
	6	26.0	26.0	26.0	25.0	23.0	24.0
	7	28.0	30.8	29.0	31.0	29.0	27.0
	8	27.0	30.2	28.0	31.0	27.0	26.0

APPENDIX B

Mean behavioral measures in Experiment 1 for 4 foraging rats as a function of wheel torque. The torques were presented in an ascending, and then in a random, series.

		Ascending series					
		Wheel torque (Nm)					
	Rat	0.5	1	2	4	8	16
Wheel turns per day	1	533.2	448.5	196.8	361.2	207.4	131.1
	2	970.6	1,051.7	827.6	596.1	491.6	290.9
	3	587.1	675.8	585.4	401.0	262.2	74.8
	4	1,153.9	941.5	659.0	555.3	502.3	232.2
Extra turns per day	1	402.2	318.5	115.8	232.2	111.4	48.1
	2	802.0	890.5	670.9	466.1	367.3	178.7
	3	468.6	534.5	465.4	291.0	162.2	19.2
	4	985.3	774.0	506.1	409.6	368.0	122.2
Grams per day	1	27.0	25.4	21.3	26.4	20.0	21.7
	2	28.4	17.8	21.1	23.1	21.3	23.1
	3	19.2	21.3	21.0	20.0	19.6	15.8
	4	24.5	23.9	25.8	22.6	22.8	23.4
Meals per day	1	9.4	9.9	6.8	9.4	7.6	7.4
	2	10.0	9.5	10.2	9.9	8.4	8.7
	3	7.3	6.4	5.3	5.3	5.0	4.2
	4	9.7	10.3	8.4	8.3	7.9	6.2
Running speed within bursts (turns per minute)	1	17.2	16.3	18.2	14.0	13.4	12.2
	2	23.3	22.4	21.0	22.2	23.8	22.3
	3	19.7	20.1	21.4	18.9	20.3	16.4
	4	20.8	19.8	18.7	19.4	20.9	17.8
Procurement rate (turns per minute)	1	0.6	0.4	0.5	0.3	0.5	0.5
	2	0.6	0.8	2.3	1.9	1.2	0.8
	3	0.4	1.0	0.4	0.5	0.5	0.2
	4	0.4	0.8	0.4	0.4	0.5	0.6

APPENDIX B

(*Extended*)

Random series						
Wheel torque (Nm)						
0.5	1	2	4	8	16	32
174.4	132.4	234.0	168.1	150.6	179.6	109.0
370.8	454.4	565.4	289.1	397.9	298.8	162.4
85.3	80.3	98.0	69.4	73.4	52.7	31.4
219.4	245.3	401.2	200.5	220.0	228.1	116.0
93.0	52.4	138.0	88.1	66.3	92.4	27.3
266.5	331.9	440.4	185.1	272.1	185.0	64.1
29.6	31.7	40.9	18.0	29.1	4.1	0.0
116.6	141.5	279.2	101.9	117.1	128.1	39.3
17.3	20.7	18.6	15.6	19.4	16.9	19.9
19.7	18.0	20.2	16.8	19.6	19.4	19.9
17.9	19.1	16.1	19.6	15.3	17.7	16.8
19.0	19.9	22.7	21.8	20.9	20.1	20.4
6.6	7.4	6.2	5.8	5.9	5.3	6.5
8.7	9.3	8.4	8.4	10.0	8.5	9.0
5.0	4.3	4.3	4.6	3.9	4.6	3.1
6.7	7.0	7.3	7.0	7.9	7.8	6.7
12.1	13.5	14.0	12.4	12.1	12.0	10.3
17.1	18.3	19.2	18.3	23.5	17.6	12.2
11.7	11.3	9.9	10.9	11.6	9.4	6.4
13.5	13.5	16.0	12.6	15.2	20.4	18.2
0.2	0.4	0.3	0.2	0.2	0.3	0.3
0.3	0.6	0.7	0.8	1.0	0.5	0.8
0.2	0.1	0.1	0.2	0.2	0.2	0.2
0.3	0.4	0.3	0.4	0.2	0.2	0.2

APPENDIX C

Data in Experiment 1 from 4 rats foraging at three procurement prices (10, 40, and 160 wheel turns), each combined with three wheel torques (0.5, 4, and 32 Nm).

		Procurement price (wheel turns)								
		10			40			160		
		Wheel torque (Nm)								
Measure	Rat	0.5	4	32	0.5	4	32	0.5	4	32
Meals per day	1	6.6	5.8	6.5	5.0	4.0	2.6	2.3	2.3	1.3
	2	8.7	8.4	9.0	7.2	7.0	3.7	3.7	3.4	2.0
	3	5.0	4.6	3.1	3.4	3.3	1.0	1.6	1.6	0.9
	4	6.7	7.0	6.7	5.5	5.0	3.9	2.6	2.7	1.6
Grams per meal	1	2.6	2.7	3.1	3.2	3.7	3.9	5.6	5.3	7.3
	2	2.3	2.0	2.2	2.6	2.7	4.0	4.3	4.0	5.5
	3	3.6	4.3	5.4	4.1	3.7	7.4	7.2	6.6	9.2
	4	2.8	3.1	3.1	3.6	3.6	5.1	6.3	5.7	7.9
Daily intake (g)	1	17.3	15.6	19.9	16.0	14.8	10.0	12.8	12.0	9.7
	2	19.7	16.8	19.9	18.3	18.6	14.8	16.1	13.6	10.9
	3	17.9	19.6	16.8	14.2	12.0	7.4	11.8	10.8	8.7
	4	19.0	21.8	20.4	19.7	18.2	19.8	16.3	15.5	12.5
Wheel turns per day	1	174.4	168.1	109.0	225.7	187.8	106.0	369.1	368.1	213.9
	2	370.8	289.1	162.4	417.5	432.1	153.5	625.0	563.0	330.4
	3	85.3	69.4	31.4	138.6	131.9	40.0	239.2	232.9	134.9
	4	219.4	200.5	116.0	330.4	289.0	156.4	440.8	436.9	253.7
Extra turns per day	1	93.0	88.1	27.3	20.0	12.8	3.1	3.4	2.4	2.2
	2	266.5	185.1	64.1	104.2	117.9	5.0	30.7	14.4	12.8
	3	29.6	18.0	0.0	1.4	1.9	0.0	0.3	0.1	0.1
	4	116.6	101.9	39.3	50.4	43.3	2.1	6.5	2.6	2.3
Running speed within bursts (turns per minute)	1	12.1	12.4	10.3	12.7	12.1	9.9	13.8	14.1	10.5
	2	17.1	18.3	12.2	18.9	20.0	11.3	17.8	17.8	13.3
	3	11.7	10.9	6.4	12.7	13.2	6.3	12.8	12.6	9.4
	4	13.5	12.6	18.2	15.2	14.3	12.4	15.0	14.0	10.4
Procurement rate (turns per minute)	1	0.2	0.2	0.3	0.3	0.3	0.1	0.4	0.5	0.2
	2	0.3	0.8	0.8	1.0	0.7	0.2	0.8	0.7	0.3
	3	0.2	0.2	0.2	0.3	0.3	0.0	0.2	0.3	0.1
	4	0.3	0.4	0.2	0.5	0.3	0.3	0.4	0.5	0.2
Procurement length (in minutes)	1	42.7	79.2	30.1	121.4	139.9	263.7	405.3	335.1	703.6
	2	32.4	13.1	12.5	40.1	53.6	214.6	186.8	242.9	510.1
	3	51.9	47.4	66.3	159.2	137.3	1,007.0	676.2	680.6	1,429.1
	4	32.0	30.6	53.4	79.3	115.4	156.0	376.9	336.4	706.3

APPENDIX D

Mean behavioral measures for the 4 rats in Experiment 2, Group F-P, as a function of bar force at a procurement price of 10 bar presses.

		Procurement price 10 (bar presses)												
		Bar force (N)												
Measure	Rat	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25
Meals per day	1	6.4	5.9	5.8	5.6	6.0	5.0	4.3	6.3	4.8	5.1	6.5	5.2	5.5
	2	8.3	8.8	9.4	7.9	9.2	8.8	9.0	6.2	5.9	6.7	5.5	3.8	2.8
	5	9.2	6.8	7.5	8.2	7.2	7.8	7.1	6.5	5.9	5.7	6.6	6.0	5.8
	6	5.8	4.6	4.7	3.8	4.6	5.5	5.3	5.0	5.0	4.5	4.5	4.8	4.3
Grams per meal	1	3.3	3.8	3.0	3.6	2.7	3.6	4.1	3.0	3.6	3.8	3.0	3.5	3.4
	2	2.8	2.6	2.7	3.1	2.3	2.7	2.4	3.7	3.8	3.7	4.3	5.4	6.9
	5	3.6	3.6	3.5	3.5	3.3	3.5	4.0	3.5	4.2	3.2	3.0	3.4	3.7
	6	4.1	4.4	4.0	4.7	4.5	3.7	4.1	4.5	4.3	4.7	4.7	5.0	5.3
Daily intake (g)	1	20.8	22.4	17.2	20.2	16.3	18.0	17.7	19.2	17.5	19.6	19.3	18.2	18.8
	2	23.2	22.7	25.6	24.0	21.0	23.5	21.4	23.2	22.7	25.1	23.5	20.8	19.7
	5	19.8	19.8	19.2	19.3	18.3	19.2	18.7	19.0	19.9	17.7	19.6	18.8	20.5
	6	23.6	20.4	18.7	18.2	20.6	20.5	21.7	22.3	21.5	21.0	21.3	24.0	22.8
Body weight (g)	1	475.9	489.5	470.9	496.5	479.3	491.0	493.2	489.7	497.5	492.4	502.5	501.3	503.7
	2	504.9	515.8	463.8	520.0	491.8	523.2	543.7	524.4	526.6	518.7	534.2	539.7	502.8
	5	403.8	420.0	435.5	446.3	449.8	454.0	460.6	464.7	474.1	470.0	476.8	479.0	481.8
	6	440.2	451.9	462.3	474.3	491.6	504.7	515.7	524.7	531.0	535.0	538.0	553.4	552.8
Procurement local rate (bar presses per minute)	1	12.7	15.3	14.5	17.7	29.2	31.0	46.4	33.0	62.1	44.2	44.8	37.1	38.0
	2	16.4	12.0	13.5	12.1	14.7	15.6	19.8	21.5	14.2	18.0	22.0	26.0	13.2
	5	19.3	22.7	17.1	16.3	19.9	22.7	20.0	15.5	14.0	11.5	12.5	15.5	15.4
	6	15.0	17.6	20.1	17.6	19.1	25.1	22.4	16.1	17.0	16.6	13.0	10.6	9.4
Procurement average rate (bar presses per minute)	1	3.7	5.5	5.3	8.3	13.3	24.6	40.0	26.8	56.0	37.1	36.2	32.5	35.4
	2	7.7	4.4	9.7	5.8	11.9	11.5	15.9	19.4	8.1	11.1	11.2	7.2	2.6
	5	2.0	3.6	2.5	4.4	10.2	11.9	11.2	9.0	5.1	4.1	4.2	3.7	4.4
	6	4.5	3.6	7.7	7.4	9.1	16.8	17.3	11.4	11.7	13.7	10.6	7.8	7.8
Procurement response time (in minutes)	1	0.8	0.7	0.8	0.7	0.4	0.4	0.3	0.4	0.2	0.3	0.3	0.4	0.3
	2	0.7	0.9	0.8	0.9	0.7	0.7	0.6	0.6	0.8	0.7	0.6	0.5	0.7
	5	0.6	0.5	0.7	0.6	0.6	0.5	0.6	0.8	0.9	1.0	1.1	0.9	0.9
	6	0.7	0.6	0.6	0.6	0.6	0.5	0.5	0.7	0.7	0.7	0.9	1.0	1.1
Procurement length (in minutes)	1	58.7	83.8	38.2	68.7	33.4	4.2	61.0	30.2	7.1	6.9	13.4	3.6	0.6
	2	32.3	41.8	16.4	45.2	8.9	2.7	1.9	3.5	20.2	9.2	19.3	17.3	91.4
	5	93.3	97.6	77.0	60.0	49.7	42.7	28.4	11.0	5.9	16.5	8.2	3.7	2.9
	6	114.7	97.9	97.1	5.2	59.8	33.1	15.7	1.4	24.7	0.9	1.7	1.5	9.3

APPENDIX E

Mean behavioral measures for the 4 rats in Experiment 2, Group F-P, as a function of bar force at a procurement price of 20 bar presses.

		Procurement price 20 (bar presses)												
		Bar force (N)												
Measure	Rat	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25
Meals per day	1	5.5	4.8	5.3	4.8	6.1	6.3	7.5	6.5	6.3	7.8	6.5	6.8	6.3
	2	7.7	8.5	8.0	8.2	7.2	7.8	7.7	6.7	7.0	6.4	5.7	5.0	3.2
	5	6.7	7.0	7.2	6.5	6.4	7.0	5.3	6.3	5.3	5.4	5.4	4.6	5.2
	6	6.3	6.0	5.5	6.0	5.0	5.3	5.7	5.7	5.2	4.7	4.9	4.0	3.3
Grams per meal	1	3.4	3.7	3.3	3.7	2.8	2.8	2.4	2.8	3.0	2.6	2.7	2.6	2.7
	2	2.8	2.3	2.5	2.5	2.7	2.6	2.7	3.1	3.0	3.2	3.9	4.3	5.8
	5	3.8	3.4	3.8	3.5	4.1	4.0	3.5	6.0	3.6	4.4	5.3	2.8	3.7
	6	2.7	2.8	3.0	2.8	3.0	4.3	4.2	4.2	5.0	5.3	5.0	6.2	7.0
Daily intake (g)	1	18.7	18.0	17.5	18.0	16.8	17.4	17.8	18.3	19.2	20.0	17.8	17.8	16.8
	2	21.7	19.7	20.3	20.2	19.5	20.3	20.3	20.8	21.0	20.3	22.0	21.6	18.5
	5	20.8	18.7	21.2	19.2	19.4	22.2	19.2	24.8	19.8	20.9	22.0	18.8	24.2
	6	24.2	23.8	24.0	23.2	21.7	32.0	23.7	28.4	29.1	24.7	24.3	34.8	23.3
Body weight (g)	1	496.5	491.3	492.8	498.7	496.9	497.7	490.0	492.8	498.0	501.0	498.3	498.0	497.9
	2	550.0	549.2	553.3	553.5	553.2	556.3	561.2	550.5	566.8	569.0	568.7	569.0	550.8
	5	491.0	486.0	497.7	498.2	496.8	502.3	500.8	507.0	505.8	507.6	516.8	510.4	509.8
	6	564.2	570.3	574.5	575.5	592.8	581.4	599.5	607.2	591.4	592.7	597.4	598.0	600.3
Procurement local rate (bar presses per minute)	1	11.6	13.1	13.6	17.6	26.8	43.5	55.2	60.6	56.0	47.4	42.5	42.4	35.0
	2	14.5	17.8	14.8	13.1	13.2	16.1	18.4	28.6	32.7	35.9	19.3	17.7	15.8
	5	10.7	13.6	12.8	12.8	12.8	15.7	16.5	22.2	30.0	44.3	49.6	55.8	52.4
	6	22.1	29.9	24.4	21.2	17.1	13.2	15.5	20.5	20.4	18.1	25.2	18.4	22.0
Procurement average rate (bar presses per minute)	1	2.3	3.5	4.1	5.0	13.9	33.0	41.2	48.7	52.1	40.7	34.6	32.6	28.3
	2	5.2	5.3	3.8	6.2	6.1	10.5	13.0	21.7	29.5	30.6	13.4	14.6	8.3
	5	2.9	6.2	4.7	6.4	6.4	12.8	10.5	8.3	7.6	8.9	7.8	8.8	7.5
	6	10.5	17.5	17.7	17.3	14.3	9.9	11.2	9.1	8.6	7.3	8.6	3.7	3.2
Procurement response time (in minutes)	1	1.6	1.5	1.5	1.2	0.8	0.5	0.5	0.4	0.4	0.5	0.5	0.6	0.7
	2	1.5	1.2	1.4	1.6	1.5	1.3	1.2	0.8	0.7	0.6	1.2	1.3	1.5
	5	1.7	1.5	1.6	1.6	1.7	1.4	1.3	1.1	0.8	0.6	0.5	0.5	0.5
	6	0.7	0.5	0.6	0.7	0.9	1.6	1.4	1.1	1.2	1.2	1.0	1.2	0.9
Procurement length (in minutes)	1	63.1	54.3	29.4	43.6	24.8	1.4	7.4	5.5	9.7	6.1	7.5	22.7	1.8
	2	37.7	28.2	28.8	25.8	16.0	29.0	4.4	2.4	0.9	0.9	2.3	1.8	2.9
	5	80.0	41.3	67.0	47.0	54.5	3.3	2.7	16.9	3.3	3.3	3.8	2.0	3.2
	6	50.0	35.7	61.9	25.4	19.4	6.8	22.3	3.0	12.1	9.6	2.8	7.0	10.6

APPENDIX F

Mean behavioral measures for 4 rats in Experiment 2, Group F-P, as a function of bar force at a procurement price of 40 bar presses.

		Procurement price 40 (bar presses)												
		Bar force (N)												
Measure	Rat	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25
Meals per day	1	4.7	4.4	5.9	7.1	8.2	8.2	7.9	8.2	6.9	7.6	6.5	6.3	5.5
	2	6.7	6.0	5.5	6.2	5.6	5.2	5.3	4.0	4.5	3.5	3.7	3.6	2.9
	5	5.0	5.5	6.0	6.5	5.4	6.1	5.6	5.3	5.0	5.2	5.0	5.0	4.2
	6	5.2	6.0	5.3	5.2	4.7	4.8	4.3	4.3	3.6	4.0	3.8	3.7	3.7
Grams per meal	1	3.4	2.9	2.8	2.5	2.4	2.4	2.4	2.4	2.2	2.3	2.6	2.6	2.6
	2	3.8	3.6	4.0	3.5	3.8	4.2	4.1	5.0	4.3	5.4	4.3	5.4	6.4
	5	3.9	3.9	3.5	3.9	3.7	6.3	3.9	3.4	3.8	3.4	3.5	3.6	3.3
	6	5.0	4.3	4.5	4.6	5.1	5.3	5.4	5.5	6.1	5.8	6.1	6.1	6.1
Daily intake (g)	1	16.1	15.9	16.4	17.6	19.5	19.4	19.0	19.8	17.8	17.1	16.6	16.5	14.4
	2	25.0	21.9	22.0	21.7	21.6	21.7	21.8	20.0	19.4	18.9	22.6	19.3	18.1
	5	25.8	21.7	19.3	21.3	17.6	19.0	18.6	18.7	17.9	18.5	19.2	20.0	18.2
	6	30.8	31.2	23.8	24.0	23.7	25.7	23.5	23.8	21.9	23.1	23.3	22.5	22.5
Body weight (g)	1	487.3	478.1	472.4	478.9	484.2	489.2	489.2	488.7	484.4	480.4	473.0	468.2	461.0
	2	533.7	553.7	559.2	562.6	566.9	563.2	564.0	559.1	557.6	545.6	548.6	552.4	451.3
	5	516.0	520.7	518.8	522.3	522.9	526.4	532.9	531.8	529.0	531.0	534.7	536.8	539.2
	6	606.0	615.2	613.3	617.3	615.2	623.2	625.7	628.0	630.7	632.1	637.2	635.7	634.2
Procurement local rate (bar presses per minute)	1	12.0	14.4	21.0	33.0	43.3	52.1	43.4	44.5	47.9	56.7	51.5	52.8	46.9
	2	16.3	19.5	17.6	12.4	13.2	14.5	19.0	18.7	19.5	19.9	19.6	14.7	10.0
	5	12.2	14.6	15.1	12.5	12.7	15.2	18.6	19.5	28.1	44.9	59.8	51.1	46.7
	6	14.3	20.6	18.3	18.8	20.5	22.0	25.1	25.6	27.4	24.9	19.7	13.9	12.6
Procurement average rate (bar presses per minute)	1	2.5	2.9	6.9	18.6	29.5	32.0	19.2	16.5	13.0	10.5	8.2	5.5	5.9
	2	5.3	6.4	5.5	5.7	6.1	7.2	9.5	9.7	12.1	10.2	9.2	8.0	4.7
	5	2.2	6.2	8.5	8.5	9.5	10.9	10.0	9.8	10.5	13.2	11.5	10.9	9.3
	6	7.1	10.2	10.0	8.9	8.7	8.5	7.0	6.3	5.6	5.0	4.8	4.3	4.2
Procurement response time (in minutes)	1	3.5	2.7	2.0	1.3	1.0	0.8	1.0	0.9	0.9	0.8	0.9	0.9	1.0
	2	2.6	2.1	2.3	3.3	3.2	2.8	2.2	2.2	2.1	2.1	2.2	2.9	4.1
	5	3.1	2.9	2.7	3.3	3.3	2.8	2.3	2.2	1.6	1.0	0.8	1.0	1.0
	6	2.8	2.0	2.3	2.3	2.1	2.0	1.7	1.6	1.5	1.7	2.1	3.0	3.4
Procurement length (in minutes)	1	80.1	82.1	64.9	18.5	21.6	38.7	25.7	24.4	6.2	17.2	18.4	29.6	17.2
	2	45.0	58.0	72.6	30.2	30.4	31.1	11.3	15.4	3.9	5.9	6.7	6.7	9.7
	5	117.8	69.4	40.9	16.5	13.6	10.7	12.1	8.8	9.9	4.9	3.7	4.1	4.0
	6	85.8	67.8	40.8	48.7	47.4	5.3	18.4	7.1	7.8	9.6	8.8	13.1	22.9

APPENDIX G

Mean behavioral measures for the 4 rats in Experiment 2, Group F-P, as a function of bar force at procurement prices of 80 and 160 bar presses.

		Procurement price (bar presses)						
		80						
		Bar force (N)						
Measure	Rat	0.25	0.50	0.75	1.00	1.25	1.50	1.75
Meals per day	1	3.9	4.4					
	2	4.3	4.2	3.8	3.2	2.8	3.7	4.2
	5	3.4	4.5	4.5	4.8	4.9	4.8	4.9
	6	3.8	4.3	4.3	4.0	3.8	3.8	3.4
Grams per meal	1	3.0	2.6					
	2	4.6	5.4	5.5	6.6	7.2	5.7	5.0
	5	3.4	3.1	7.9	3.2	3.6	4.9	3.9
	6	6.1	5.2	4.8	5.2	5.6	5.5	6.3
Daily intake (g)	1	11.8	11.6					
	2	20.0	22.7	21.0	20.8	20.5	20.8	20.7
	5	16.1	16.8	17.3	17.3	17.0	17.9	18.6
	6	23.5	22.7	20.7	20.8	21.5	21.2	21.3
Body weight (g)	1	436.3	418.3					
	2	538.3	544.8	543.3	541.2	53.02	538.0	540.5
	5	537.0	538.8	542.8	551.0	551.0	547.0	545.6
	6	636.7	637.5	640.0	646.3	650.8	656.2	657.8
Procurement local rate	1	11.7	14.5					
(bar presses per minute)	2	15.5	18.8	15.0	10.9	11.2	13.9	16.3
	5	19.2	13.7	14.9	16.3	14.3	16.3	20.2
	6	20.7	23.8	25.6	20.8	23.4	29.2	30.7
Procurement average rate	1	1.4	3.2					
(bar presses per minute)	2	2.9	2.2	4.0	2.5	1.9	7.0	10.9
	5	1.2	3.5	7.1	7.1	10.4	9.0	14.1
	6	6.6	9.2	9.1	11.1	10.9	11.1	8.9
Procurement response time	1	6.7	5.5					
(in minutes)	2	55.	4.2	5.4	7.5	6.9	5.9	5.1
	5	4.1	6.0	5.5	5.1	5.7	5.1	4.1
	6	3.8	3.5	3.3	4.0	3.5	2.8	2.8
Procurement length	1	143.2	72.4					
(in minutes)	2	96.2	125.9	94.9	180.3	188.3	47.2	10.5
	5	178.6	151.7	191.6	65.1	49.0	37.2	6.3
	6	94.0	82.1	73.9	42.4	43.5	7.5	9.7

APPENDIX G

(*Extended*)

Procurement price (bar presses)										
80						160				
Bar force (N)										
2.00	2.25	2.50	2.75	3.00	3.25	0.25	0.50	0.75	1.00	1.25
3.7	4.7	4.2	4.0	3.3	3.2	3.3	3.1			
4.8	4.0	4.0	3.8	3.7	3.8	2.7	4.8			
3.0	3.2	3.2	3.5	3.3	3.0	3.3	3.3	4.2	3.7	3.3
3.9	4.4	4.8	4.6	5.3	5.6	4.9	4.8			
3.2	3.2	3.2	3.2	2.9	2.8	5.4	3.6			
6.8	6.4	6.1	6.3	6.6	7.1	6.2	6.1	5.5	5.8	6.1
20.2	20.5	20.0	18.4	17.4	17.7	15.8	14.8			
17.8	17.7	17.5	17.3	16.0	15.5	14.6	17.5			
20.3	20.3	19.5	22.2	21.8	21.2	20.7	20.3	23.0	21.3	19.8
535.1	546.8	546.0	540.2	534.6	526.0	498.8	495.6			
547.2	545.3	544.2	545.3	542.0	536.8	521.9	525.5			
656.8	655.7	653.7	657.5	662.3	659.0	656.0	654.5	659.2	658.2	650.5
18.3	15.5	14.5	14.1	14.3	13.8	15.7	20.7			
23.2	22.7	39.3	39.6	42.0	46.6	15.2	19.3			
29.7	25.8	20.8	18.7	18.6	16.8	30.1	25.0	23.7	25.5	27.6
8.4	11.9	11.2	7.3	6.3	5.7	3.4	3.3			
14.1	10.0	10.4	9.2	8.3	7.3	1.9	10.0			
8.9	8.5	5.8	5.5	4.8	4.9	10.3	12.0	15.5	15.2	13.5
4.6	5.4	5.8	5.9	5.7	5.9	9.8	7.6			
3.6	3.6	2.2	2.1	2.0	1.8	10.2	8.5			
2.9	3.2	3.9	4.4	4.4	2.8	5.5	7.0	7.2	6.8	6.2
39.5	7.4	7.9	11.9	39.5	48.3	172.5	210.2			
6.1	8.0	7.5	27.7	7.9	7.3	335.4	90.9			
9.7	10.1	15.0	16.3	51.5	18.0	178.2	129.1			

APPENDIX H

Mean behavioral measures for 3 rats in Experiment 2, Group P-F, as a function of procurement price at bar forces of 0.25 and 0.50 N.

		Bar force (N)								
		0.25								
		Procurement price (bar presses)								
Measure	Rat	10	20	40	80	160	320	640	1,280	2,560
Meals per day	4	5.6	4.1	3.0	2.2	2.0	1.3	1.0		
	7	5.8	5.2	3.9	3.7	3.3	2.2			
	8	6.8	6.3	5.5	5.3	5.2	4.3	3.8	3.0	1.6
Grams per meal	4	4.4	6.1	8.2	10.7	12.4	16.4	20.0		
	7	4.7	5.1	4.4	6.2	6.9	10.7			
	8	2.8	2.7	3.3	3.4	3.5	4.0	4.9	6.2	11.6
Daily intake (g)	4	24.8	24.9	24.5	23.8	24.8	21.8	19.0		
	7	27.7	26.2	19.4	22.8	23.0	23.2			
	8	19.0	17.3	18.0	18.3	18.2	17.2	18.6	18.5	18.3
Body weight (g)	4	530.9	542.3	549.0	546.5	550.8	538.7	529.0		
	7	446.5	467.2	476.6	484.2	494.5	495.3			
	8	413.5	426.7	441.0	452.7	458.0	461.0	457.8	461.7	435.3
Procurement local rate	4	13.9	13.6	10.9	12.0	11.4	19.8	22.3		
(bar presses per minute)	7	24.7	21.1	27.4	42.1	47.8	51.6			
	8	33.9	40.0	47.8	53.5	54.9	64.6	71.5	67.5	52.1
Procurement average rate	4	5.9	1.9	0.8	0.9	1.0	1.2	0.8		
(bar presses per minute)	7	6.9	7.8	14.0	21.8	14.9	14.1			
	8	23.5	28.1	23.4	21.9	25.7	35.8	27.1	25.6	12.6
Procurement response time	4	0.4	1.4	2.8	5.7	13.2	15.0	27.3		
(in minutes)	7	0.5	1.0	1.7	2.1	3.5	7.0			
	8	0.5	0.6	1.1	1.6	3.1	5.1	9.0	18.6	45.9
Procurement length	4	81.0	111.4	232.4	307.3	392.6	500.4	809.7		
(in minutes)	7	75.6	122.0	58.3	91.9	162.5	225.8			
	8	55.1	40.8	43.7	27.3	67.5	36.2	193.6	192.9	465.4

APPENDIX H

(*Extended*)

Bar force (N)							
0.50							
Procurement price (bar presses)							
10	20	40	80	160	320	640	1,280
5.5	4.2	3.5	2.7	2.0	1.0		
7.7	5.7	5.2	4.5	3.4	2.5	1.7	1.3
6.5	6.0	5.3	4.8	4.2	3.2	3.8	3.0
3.0	4.9	6.0	8.5	12.5	20.3		
4.1	5.3	5.5	5.9	6.9	9.6	13.9	14.3
4.3	3.6	3.9	4.1	5.0	5.5	5.7	6.1
23.3	20.6	20.8	22.7	25.0	20.3		
31.2	30.2	28.2	26.5	25.5	24.0	23.2	23.8
28.0	21.7	20.7	20.0	20.8	17.3	25.2	18.2
577.0	579.8	581.0	586.5	576.0	556.2		
493.8	519.3	534.8	543.7	550.1	556.3	552.0	545.4
442.7	469.5	483.8	489.2	494.5	494.7	497.6	488.0
16.0	19.2	25.5	24.9	23.6	24.1		
43.8	51.8	42.9	52.3	58.4	68.0	54.7	59.9
29.7	29.4	29.2	28.3	33.0	35.3	41.4	46.9
2.7	5.7	5.8	1.9	1.5	0.4		
25.3	34.2	24.0	33.9	28.2	29.5	7.5	3.4
24.9	16.7	14.3	12.1	14.5	10.3	21.3	21.4
0.7	0.9	1.5	3.2	6.5	12.5		
0.4	0.5	1.1	1.6	2.9	4.8	10.4	19.1
0.5	0.8	1.5	3.0	4.9	9.2	14.8	26.1
111.8	124.7	83.0	191.0	304.8	779.3		
6.4	35.5	86.2	50.2	98.7	102.0	357.9	567.9
8.7	28.5	12.5	72.2	17.2	201.3	123.6	206.4

APPENDIX I

Mean behavioral measures for 3 rats in Experiment 2, Group P-F, as a function of procurement price at bar forces of 0.75 and 1.00 N.

		Bar force (N)								
		0.75								
		Procurement price (bar presses)								
Measure	Rat	10	20	40	80	160	320	640	1,280	2,560
Meals per day	4	5.5	4.0	3.3	2.0	1.8				
	7	6.7	6.0	4.8	3.5	3.0	2.3	1.4	1.2	1.0
	8	7.2	6.4	5.3	4.7	3.6	3.7	4.0	3.8	1.7
Grams per meal	4	5.6	5.5	6.8	10.0	13.5				
	7	5.3	5.6	6.0	7.9	9.5	12.4	13.0	18.9	18.7
	8	3.4	3.7	4.1	4.4	5.3	5.5	5.1	5.1	8.1
Daily intake (g)	4	30.7	22.2	22.7	20.0	24.8				
	7	35.0	33.7	28.5	27.5	28.5	28.8	22.8	22.0	18.7
	8	24.3	24.1	21.7	20.3	19.3	20.3	20.6	19.7	13.9
Body weight (g)	4	572.8	584.5	575.2	567.5	559.8				
	7	528.3	560.8	576.0	582.8	586.2	587.5	577.4	568.8	560.0
	8	487.2	499.1	509.8	512.2	507.7	498.6	498.2	500.3	466.4
Procurement local rate	4	22.4	25.4	21.4	18.8	18.0				
(bar presses per minute)	7	39.9	32.2	31.1	35.7	38.9	46.9	50.0	55.7	65.0
	8	25.9	27.6	28.2	29.8	30.7	27.9	33.1	40.6	44.2
Procurement average rate	4	8.2	6.2	3.2	0.8	1.0				
(bar presses per minute)	7	35.4	28.3	21.9	19.5	15.8	9.5	1.6	12.5	2.7
	8	18.2	17.2	13.4	12.5	10.9	12.9	20.8	30.6	36.6
Procurement response time	4	0.5	0.8	1.8	4.1	8.2				
(in minutes)	7	0.3	0.7	1.4	2.3	4.0	6.7	12.2	14.9	39.3
	8	0.5	0.9	1.6	2.8	5.3	11.4	19.4	31.7	51.4
Procurement length	4	17.5	130.6	138.0	350.8	425.9				
(in minutes)	7	41.5	41.8	42.1	108.6	172.4	235.5	452.4	552.9	958.5
	8	8.4	15.4	25.9	57.0	128.4	111.6	100.8	96.7	279.3

APPENDIX I

(*Extended*)

Bar force (N)							
1.00							
Procurement price (bar presses)							
10	20	40	80	160	320	640	1,280
5.3	4.5	3.3	2.2	1.8			
6.7	6.0	4.8	4.0	3.2	2.5	1.8	1.3
8.0	5.8	5.3	5.5	5.4	4.7	3.2	2.4
5.3	5.8	6.9	10.2	10.9			
5.4	5.0	5.4	6.5	8.0	9.7	12.1	14.9
3.0	3.6	3.8	3.6	3.8	4.1	5.4	6.2
28.5	26.0	22.8	22.0	20.0			
35.7	30.2	26.2	26.0	25.3	24.3	22.2	18.7
23.7	21.2	20.2	19.7	20.6	19.2	17.4	15.0
536.3	569.2	576.2	559.3	539.2			
577.8	599.7	611.2	621.1	625.5	625.7	625.8	604.7
491.0	504.5	507.3	515.5	526.7	528.3	510.8	496.3
24.6	28.9	25.2	18.9	19.1			
46.8	34.5	39.3	32.1	43.8	50.1	58.8	44.3
27.3	28.4	22.8	25.3	25.7	29.5	30.7	35.8
8.1	7.2	4.6	1.0	1.1			
40.0	33.0	31.0	18.5	30.8	10.4	8.3	2.6
23.6	12.9	10.1	16.9	18.5	22.8	19.6	23.1
0.5	0.7	1.6	3.9	8.3			
0.3	0.7	1.3	2.7	3.7	6.5	10.6	22.3
0.5	0.9	1.9	3.2	6.3	11.0	19.6	35.5
57.6	61.3	122.3	307.9	360.5			
10.7	14.3	57.8	111.1	119.9	253.2	395.0	602.0
11.9	24.7	24.4	24.1	12.8	17.0	74.3	120.8

APPENDIX J

Mean behavioral measures for 3 rats in Experiment 2, Group P-F, as a function of procurement price at bar forces of 1.25, 1.50, and 1.75 N.

		Bar force (N)								
		1.25								
		Procurement price (bar presses)								
Measure	Rat	10	20	40	80	160	320	640	1,280	2,550
Meals per day	4	6.8	4.8	3.2	2.0					
	7	6.7	5.7	4.1	3.8	3.3	2.7	1.7	1.0	1.0
	8	7.3	5.2	4.2	3.8	3.8	3.8	3.1	1.3	
Grams per meal	4	4.6	5.1	5.8	10.8					
	7	4.0	4.4	5.4	6.4	7.8	9.1	11.1	17.1	17.8
	8	3.3	4.2	4.5	4.8	4.3	4.5	5.0	6.9	
Daily intake (g)	4	31.3	24.5	18.7	21.5					
	7	26.7	24.7	22.3	24.0	26.0	24.2	18.5	17.1	17.8
	8	24.0	21.8	18.8	18.3	16.3	17.1	15.7	9.2	
Body weight (g)	4	543.7	555.2	552.7	543.3					
	7	625.4	637.7	640.6	648.9	655.5	650.7	616.0	615.4	580.6
	8	492.7	504.8	515.6	522.0	525.2	522.0	517.7	483.7	
Procurement local rate	4	23.1	23.6	19.9	16.9					
(bar presses per minute)	7	37.8	38.7	28.5	36.5	41.0	44.9	46.1	45.4	38.7
	8	36.4	26.4	30.5	27.6	28.2	32.6	34.3	31.2	
Procurement average rate	4	17.7	10.0	4.6	1.1					
(bar presses per minute)	7	35.4	37.9	16.4	21.5	25.8	10.5	10.2	1.9	2.8
	8	31.3	19.5	17.6	14.4	15.2	14.7	16.6	5.0	
Procurement response time	4	0.5	0.9	1.9	4.8					
(in minutes)	7	0.3	0.7	1.5	2.4	4.2	7.6	13.0	22.8	31.8
	8	0.4	0.8	1.4	2.9	5.8	10.1	18.5	27.1	
Procurement length	4	38.0	82.2	111.6	261.2					
(in minutes)	7	4.5	67.2	77.5	97.8	133.1	247.5	390.8	710.0	859.5
	8	1.5	12.3	5.8	7.7	74.7	106.9	153.9	484.8	

APPENDIX J

(*Extended*)

Bar force (N)											
1.50								1.75			
Procurement price (bar presses)											
10	20	40	80	160	320	640	1,280	10	20	40	80
5.8	5.0	2.7	2.2	1.3				5.8	5.0	3.3	1.8
6.2	5.0	4.0	3.2	2.7	2.0	1.3	1.0	5.7	4.5	4.2	3.0
6.5	5.6	4.2	4.2	3.8	3.2			5.3	5.0		
5.0	4.8	8.6	9.8	13.6				4.3	4.2	6.2	10.9
5.6	5.6	6.2	7.9	8.7	10.6	14.8	18.7	5.6	6.6	6.4	7.7
3.2	3.4	4.2	4.2	8.0	5.1			3.8	3.8		
29.2	23.8	22.8	21.3	18.2				25.3	21.0	20.7	19.0
34.8	28.2	24.7	25.2	23.2	21.2	19.7	18.7	31.5	29.5	26.5	23.0
21.0	18.9	17.3	17.5	17.3	16.0			20.5	19.2		
517.2	540.2	540.4	528.3	497.2				513.5	524.8	525.5	513.0
607.2	633.0	646.5	655.3	649.5	642.5	626.8	608.7	623.8	645.5	653.3	646.7
502.1	519.0	521.5	523.2	517.2	516.3			508.8	534.2		
20.8	19.8	24.2	21.3	16.9				22.2	26.7	21.4	23.1
21.4	22.3	23.0	25.0	29.0	31.8	36.9	44.1	24.5	18.4	24.4	26.2
38.4	37.6	31.2	24.1	26.8	28.0			49.9	38.1		
13.2	8.1	5.0	1.7	1.9				17.6	17.0	8.2	1.9
17.0	19.5	17.2	17.6	13.0	9.6	5.5	1.7	19.9	15.9	17.1	16.4
27.4	28.1	17.6	11.4	9.4	11.0			43.8	21.1		
0.5	1.1	1.7	3.7	9.6				0.6	0.8	2.0	3.3
0.6	1.1	2.0	3.4	5.1	10.0	15.8	28.6	0.6	1.3	1.8	3.2
0.4	0.6	1.4	3.5	10.6	11.2			0.2	0.7		
38.5	50.0	244.3	345.2	484.3				26.5	52.2	113.9	356.6
11.9	41.4	63.3	37.2	191.5	252.0	342.8	756.7	18.8	4.1	6.3	38.2
16.4	18.7	33.6	59.7	85.2	105.6			11.9	4.0		