*FOOD AND WATER INTAKE AS FUNCTIONS OF
RESOURCE CONSUMPTION COSTS IN A CLOSED ECONOMY*

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In two experiments, rats living in a closed economy were offered continuous, concurrent access to four resources: food, water, a nest, and a running wheel. Costs of consuming food and water were imposed with bar-press requirements, and the price of either one or both resources was raised. As the consumption cost increased, less was consumed in each bout of resource use. Bout frequency increased, but not sufficiently to compensate for the fall in bout size, and total intake fell. Food and water tended to be complementary resources, in that as intake of one fell with its price, intake of the other also decreased. This interaction was accounted for by the defense of the ratio of body water to lean body mass. As amount consumed decreased, increases in feed efficiency (weight gain per unit of food ingested) and the use of stored calories compensated for the reduced energy intake. There was evidence of competition between feeding and drinking at the higher costs: When both commodities were expensive, the decline in the intake of each one was greater than when only one commodity was expensive. Although the time spent nesting, running, and in unmonitored activity was adjusted when feeding or drinking took more of the rat's day, there was no particular activity that was sacrificed.

Key words: food intake, water intake, consumption cost, behavioral economics, closed economy, lever press, rats

In a world of limited resources and the need to satisfy multiple requirements, an animal must efficiently allocate its time and effort among resources and activities. Each of the activities involved in the use of a resource (i.e., discovery, selection, procurement, and consumption) is constrained by (a) the animal's behavioral repertoire, (b) the costs associated with using that resource, (c) the animal's regulatory requirements for that resource, and (d) requirements for other resources (e.g., food, water, nest sites, etc.) and other activities (e.g., mating, territorial defense, antipredator behavior, etc.). Through natural selection, animals have developed behavior and physiology that are sensitive to these constraints, and, together, these tend to result in the efficient satisfaction of their requirements (McFarland, 1977). The present research addresses the behavioral processes that respond to these constraints in a paradigm that naturalizes the laboratory environment: Animals are housed continuously in environments in which varying work require-

ments are placed on gaining access to and using different resources. Our results extend our understanding of how environmental costs and benefits affect animals' allocation of time and effort among available resources.

When exploiting resources that are discontinuously distributed, an animal's behavior is characterized by bouts of different activities. In previous experiments we have examined how the behavioral rules for bout initiation, bout cessation, and choice among patches of a single resource (food or water) are affected by the costs of access to and consumption of that resource (Collier & Johnson, 1990). In addition, we have explored possible competition and linkages among activities by varying the cost of access to food, water, a nest, and a running wheel that were simultaneously available (Collier, Johnson, CyBulski, & McHale, 1990). We found that the functions relating the cost of access to a resource to the frequency and size of bouts of using that resource were similar for all four activities and were not affected by the availability of the other resources: Bout frequency declined, and bout size and duration increased as the cost of resource access increased. Furthermore, the activities appeared to be independent rather than linked in some way: Changes in the pattern of one activity did not affect patterns of the other activities. Finally, there

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was no evidence of competition among the four activities for the rat's time in our experiment (Collier *et al.*, 1990). This was because the total amount of time spent in each activity was constant (feeding and drinking) or decreased (running and nesting) as resource access cost increased, and, at all costs, time spent in unmonitored activities was a substantial part of the rat's time budget.

In the present study, we continue this exploration of behavioral linkage and competition by examining the effects of a different cost, that of resource consumption, on the use of multiple resources. Changes in resource-consumption costs are likely to affect the time budget because, in contrast to resource-access cost, as the cost of consuming a commodity increases, the time spent consuming the daily requirement also increases (Collier, Johnson, Hill, & Kaufman, 1986; Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988). Thus, increases in consumption cost should increase the competition among activities for an animal's time. This proved to be the case in a study of rats living at either 0 or 24 °C with access to food, water, a nest site, and a running wheel (Collier, Johnson, Naveira, & Cybulski, 1989). The rats spent more time feeding and nesting in the cold, and when high food consumption cost further increased the time needed to attain the daily food requirement, the rats sacrificed food intake for nesting time. When a cost was placed on nest access as well as on food consumption, the opposite result was found (Schultz, 1993): Rats living in the cold sacrificed costly nesting for feeding even when food consumption cost was high.

Another effect of increasing the cost of consuming a resource is to decrease intake of that resource (Collier *et al.*, 1986; Hursh *et al.*, 1988). We asked how high costs of consuming both food and water would influence a rat's intake, bout patterns, and time budget. Is there an upper limit on the amount of time (or effort) a rat is willing to devote to feeding or drinking, and, if so, does intake fall when cost is high because the limit is reached before the rat can fulfill its requirement? Further, is a limit for one activity influenced by the time or bar presses required to perform other activities? If so, one would predict, for example, that the intake of water would be

lower when both food and water were expensive than when only water was expensive.

We performed two experiments that differed only slightly: Subjects in Experiment 1 were selected to be rats with high nest use, but no selection was performed in Experiment 2. There was a cost on access to the nest and running wheel in Experiment 1 but not in Experiment 2; and in Experiment 2, we recorded the time rats spent sitting, as well as running, in the wheel.

METHOD

Subjects

In Experiment 1, the subjects were 4 male 60-day-old Sprague-Dawley rats. These individuals were selected from a group of 9 rats as those that spent the most time nesting during 6 days of preliminary housing in cages fitted with a running wheel and nest box. In Experiment 2, we used 4 naive rats of the same age and strain from the same supplier; they were not subjected to any selection criteria. During the experiments, the rats were individually housed in galvanized steel cages (60 cm by 60 cm by 80 cm) in a room at 22 °C with lights on from 8:00 a.m. to 8:00 p.m. daily. They lived in these cages continuously except for a daily maintenance period of approximately 60 min starting at 11:30 a.m., during which they were weighed, food and water were replenished, and the apparatus was cleaned and tested.

Apparatus

Each experimental cage was equipped with a pellet feeder, a drinking tube, a running wheel, and a nest box (Figure 1). Resource stations for feeding, drinking, and nesting consisted of a platform (15 cm by 20 cm) mounted 13 cm above the cage floor, with a custom-made T-shaped response bar requiring 0.35 N applied through a throw of 15 mm mounted 6.5 cm above each platform. The crosspiece of the bar (0.5 cm diameter, 5 cm long) protruded 4 cm into the cage. A cue-light (1.5 cm diameter) (Sylvania 28PSB) was located 3 cm to one side of the response bar, 6.5 cm above the feeding and drinking platform. A custom-made pellet feeder dispensed 45-mg Bioserv pellets into a food cup on the feeding platform, 10 cm to the right of the food bar. A retractable drinking tube entered

Fig. 1. The experimental apparatus (top view).

the cage 7.5 cm above the drinking platform, 9 cm to the left of the water bar. When retracted, the tube was 1 cm away from the cage. A custom-made drinkometer retracted and extended the drinking tube, and licking was monitored by a Grason-Stadler lickometer connected to the drinking spout. A black Plexiglas nest box (20 cm by 16 cm by 14 cm) containing a bedding tray filled with corncob bedding was mounted outside the cage behind the nesting platform. An entrance hole (6 cm diameter) was located 28 cm to the right of the nest bar and 4 cm above the platform. An infrared light source and photocell (Microswitch Models TLS3C and TPC4LF, respectively) mounted across the nest from each other, 2 cm above the nest bedding, detected the rat's presence in the nest box. Access to a Wahmann running wheel was via an opening (8 cm by 6.5 cm) in the cage wall 11 cm above the cage floor, and a response bar was mounted 6 cm above the floor, 25 cm to the right of this opening. The wheel was mounted outside the cage on a lever arm with a counterweight adjusted so that when the rat was in the wheel a microswitch on the arm was deflected. A microswitch on the outside of the wheel monitored wheel turns. In Experiment 1, entry into the running wheel and nest box were controlled by motor-operated sliding doors engineered to prevent trapping the rat. In Experiment 2, these doors were

always open and the nest and wheel response bars were absent. A 40-W houselight was centered on the cage ceiling and was illuminated from 8:00 a.m. to 8:00 p.m. daily. All equipment was controlled, and the rats' activities were recorded, by Commodore® 128 computers interfaced to the cages via interfaces made in the Rutgers Psychology shop and programmed in Basic by the second author.

Procedure

Initial training. The response bars were removed from the cage, a cup of Purina® chow was mounted next to the pellet cup, the drinking tube was extended into the cage, and the wheel and nest doors were open. After 2 days, the cup of chow was removed and for 2 days a surfeit of food pellets was delivered on a variable-time ($M = 2$ min) schedule from 2:00 p.m. to 9:00 a.m. The food bar was then installed, the food cue light was on continuously, and every response earned one food pellet. All animals began to bar press without a shaping procedure. The criterion for subsequent changes in contingencies was 2 days without loss in body weight.

Delivery of each pellet continued to be contingent on bar pressing on a fixed-ratio (FR) schedule of reinforcement; the number of bar presses required per pellet is the food consumption cost or pellet price. The pellet price was raised to five and then to 10 bar presses. Then a food procurement cost was imposed at one bar press. This means that in the resting state, the food cue light was off and the pellet dispenser was not operational. When the rat completed the food procurement cost on the food response bar, the food cue light was illuminated, indicating that the pellet feeder was operational and that further responses would earn pellets. The pellet price remained at 10 bar presses. The rat could earn any number of pellets; the feeding bout ended when the rat did not earn a pellet for 10 consecutive minutes. At that time, the cue light was turned off. The rat had to complete the food procurement cost to begin another feeding bout. The food procurement cost was raised to five and then to 10 bar presses.

Next, the water bar was installed, the water cue light was on continuously, and the water tube was retracted. The rat could earn brief presentations of the drinking tube, called sips, lasting 5 s or until 20 licks occurred,

whichever came first. Delivery of each sip was contingent on bar pressing on an FR schedule of reinforcement; the number of bar presses required per sip is the water consumption cost or sip price. The initial sip price was one bar press; it was raised to five and then to 10 bar presses. Then a water procurement cost of one bar press was imposed: In the resting state, the water cuelight was off. When the rat completed the water procurement cost, the water cuelight was illuminated, indicating that the drinkometer was operational and that further responses would earn sips. The sip price remained at 10 bar presses. The rat could earn an unlimited number of sips. A drinking bout ended when the rat did not earn a sip for 15 consecutive minutes. At that time, the cuelight was turned off; to begin another drinking bout, the rat had to complete the water procurement cost. The water procurement cost was raised to five and then to 10 bar presses.

In Experiment 1 only, the nest door was then closed, and the nest bar was installed with a nest procurement cost of one bar press. When the rat completed the nest procurement cost, the nest door was opened. A nesting bout ended when the rat remained out of the nest for 15 consecutive minutes, at which time the nest door closed. The nest procurement cost was raised to five and then to 10 bar presses.

Finally in Experiment 1, the wheel door was closed and the wheel bar was installed with a wheel procurement cost of one bar press. When the rat completed the wheel procurement cost, the wheel door was opened. A running bout ended when 20 consecutive minutes elapsed with no wheel turns, at which time the wheel door closed. The wheel procurement cost was raised to five and then to 10. There were no consumption costs on nesting or running.

Training in Experiment 2 was as in Experiment 1 except that no response bars for the nest or wheel were installed, and the doors on these resources were never closed. We recorded a new activity in this experiment: wheel sitting. This is the time the rat spent in the wheel when a running bout was not in progress.

Experimental conditions. After use of all resources had stabilized (i.e., when the rats were exhibiting normal weight gain and

there was no obvious trend in any behavioral measure) at a price of 10 for both pellets and sips and resource procurement costs of 10, a series of cost conditions was imposed. There were three experimental phases.

Experiment 1. In the pellet price phase, the sip price was fixed at 10 and the pellet price was increased from 10 to 20, 40, 60, 80, 100, 120, and 140 bar presses per pellet. Next, in the sip price phase, the pellet price was fixed at 10, and the sip price was increased from 10 to 20, 40, 60, 80, and 120 bar presses per sip. In the final both prices phase, the pellet and sip prices were increased simultaneously from 10 to 20, 40, 80, and 100.

Experiment 2. The three experimental phases were presented in a different order: The both prices phase was first, and the pellet and sip prices were simultaneously increased from 10 to 20, 40, 80, and 160. Next, in the sip price phase, the same price series was presented for sips while the pellet price was fixed at 10. Finally, in the pellet price phase, the same price series was presented for pellets while the sip price was fixed at 10.

Each price condition was in effect for at least 10 days and until there had been no obvious trend in any behavioral measure nor loss of body weight for at least 7 days. The number of days that each subject was exposed to each condition varied from 10 to 15, not including days that the equipment failed to operate properly. There was no relationship between price and number of days exposed to a condition. If a rat's weight dropped below 80% of its previously stable weight, the data were not included in the analysis for that condition and the rat was not exposed to higher prices.

Data Analysis

A brief explanation of the definition of *bouts* of behavior is in order here; a more complete discussion is presented by Collier *et al.* (1990). When examined over a time frame of days, feeding and drinking (and many other activities) occur in bouts of relatively closely spaced bursts of activity separated from other bouts by relatively long interbout intervals. To define a bout, one must distinguish between intrabout intervals (between bursts) and interbout intervals (between bouts). An objective way to make this distinction is to plot the distribution of interval lengths as a

log survivor function, usually a double negative exponential curve, and to select as the criterion interval length the point at which the slope changes: Longer intervals are interbout intervals, and shorter intervals are intrabout intervals (Clifton, 1987; Slater, 1974). The bout-ending criterion interval without activity for each behavior in our experiments (10 min for feeding, 15 min for drinking, 15 min for nesting, and 20 min for running) was selected by inspection of log survivor functions of the lengths of interbehavior intervals in several groups of rats in our laboratory (not the subjects in the current experiments) with no operant contingencies on resource use (Collier et al., 1990). Bouts of different activities were not mutually exclusive.

The last 7 days of each exposure to each price condition were analyzed. Some days were excluded because of occasional equipment failure. For each condition, we measured the bout frequency, bout duration, and daily time spent for all activities; the amount of food and water consumed daily and per bout; and the consumption rates for feeding and drinking (grams or milliliters per minute, calculated by dividing daily intake by daily time). The daily time includes only the time actually spent in a behavior; intrabout intervals longer than 30 s without behavior were excluded. Other time (i.e., time not accounted for by the four measured activities) was calculated by subtraction. Local response rates within bouts of feeding and drinking were calculated as total bar presses separated by 30 s or less divided by the summed interresponse intervals of those bar presses.

The data were analyzed separately for each experiment with two-way (Phase $\times$ Price) analyses of variance (ANOVA) with repeated measures and a priori contrasts between pellet, sip, and both prices phases at each price. The alpha level was 0.05. In Experiment 1, because prices increased only to 100 in the both prices phase, data for Prices 10, 20, 40, 60, 80, and 100 in all three phases were analyzed. Values for missing conditions Sip Price 100 and Both Prices 60 were estimated as the mean of the values for the surrounding conditions, that is, (Sip Price 80 + Sip Price 120)/2 and (Both Prices 40 + Both Prices 80)/2, and the degrees of freedom were adjusted appropriately. In Experiment 2, because of the weight-loss criterion, not all rats

completed all price conditions. Three rats completed the Pellet Price 160 condition, 3 rats completed the Sip Price 160 condition, 3 rats completed the Both Prices 80 condition, and 2 rats completed the Both Prices 160 condition; all 4 rats completed the other conditions. For the statistical analyses, missing data points were estimated using the method described by Winer (1971, p. 489). Significant contrasts are indicated in the figures, which present the data as means for all rats in each condition. Data for individual subjects are shown in the Appendixes.

RESULTS

Rates of Consumption Within Bouts

In both experiments, there were significant interactions of phase and price in the effects on the rate of eating: Experiment 1, $F(8, 24) = 6.83, p < .01$, Experiment 2, $F(8, 24) = 9.83, p < .01$; the rate of bar pressing for pellets: Experiment 1, $F(8, 24) = 4.85, p < .01$, Experiment 2, $F(8, 24) = 18.09, p < .01$; the rate of drinking: Experiment 1, $F(8, 24) = 5.18, p < .01$, Experiment 2, $F(8, 24) = 9.22, p < .01$; and the rate of bar pressing for sips: Experiment 1, $F(8, 24) = 8.96, p < .01$, Experiment 2, $F(8, 24) = 50.51, p < .01$. As pellet price increased, the rate of bar pressing for pellets increased (Figure 2) and the rate of eating decreased. The rates were the same whether pellet price was changed alone or in combination with sip price; but these rates did not change as a function of sip price alone. Exactly comparable results were found for the rate of bar pressing for sips and the rate of drinking (Figure 3), which changed as a function of sip price but not pellet price. Thus, the rate at which food or water was consumed was affected only by the cost of the resource itself and not by the cost of the other resource.

Daily Intake

In both experiments, there was a significant effect of price on food intake: Experiment 1, $F(5, 15) = 9.25, p < .05$, Experiment 2, $F(4, 12) = 41.29, p < .01$. The amount of food consumed each day decreased as the cost of either pellets, sips, or both increased (Figure 4). At the highest price (100 in Experiment 1 and 160 in Experiment 2), less food was consumed when both pellets and

Fig. 2. The rate of eating (top) and rate of responding for pellets (bottom) as a function of the price of pellets, sips, and both pellets and sips in two experiments. The values are the mean ($\pm$ SE) for 4 rats except for the following conditions in Experiment 2: Pellet Price 160 (3 rats), Sip Price 160 (3 rats), Both Prices 80 (3 rats), and Both Prices 160 (2 rats). Asterisks indicate a significant difference ($p < .05$) from the value for the both prices phase at that price.

sips were costly than when only pellets were costly. In Experiment 1 (but not Experiment 2), there was also an effect of phase, $F(2, 6) = 6.27$, $p < .05$. Food intake was greatest during the sip price phase.

Water intake fell as sip price or both prices increased. In Experiment 1, the Phase $\times$ Price interaction was significant, $F(8, 24) = 4.77$, $p < .01$. Pellet price alone had no effect on water intake, and the rate of decline in water intake was greater when both prices were increased than when sip price alone was increased. In Experiment 2, the interaction was not significant; increases in either or both prices reduced water intake, $F(4, 12) = 81.79$, $p < .01$.

Thus, although the daily consumption of food or water was affected primarily by the

cost of the resource itself, intake was not independent of the cost of the other resource. The effect of sip price on food intake was more robust than the effect of pellet price on water intake, which was seen in only one experiment. The ratio of water intake to food intake ranged from 1.2 to 1.9 ml/g and was unaffected by the price manipulations except in Experiment 1 in the both prices phase, when it fell from 1.4 to 1.0 ml/g.

The rats' body weights declined when food intake declined with price, that is, in every phase except when sip price alone was increased in Experiment 1 (Figure 4). However, although food intake decreased by about 50% from the lowest to highest price, body weight declined only about 12%. The interaction effects were significant in both exper-

Fig. 3. The rate of drinking (top) and rate of responding for sips (bottom) as a function of the price of pellets, sips, and both pellets and sips in two experiments. Details as in Figure 2.

iments, Experiment 1, $F(8, 24) = 6.20$, $p > .01$, Experiment 2, $F(8, 24) = 3.05$, $p < .05$, but for different reasons. In Experiment 1, there was no change in weight in the sip price phase; in Experiment 2, the weight loss was greater when both prices increased than when only one price increased.

Bout Patterns

The amount consumed in bouts of feeding (Figure 5) decreased as price increased: Experiment 1, $F(5, 15) = 11.25$, $p < .01$, Experiment 2, $F(4, 12) = 30.92$, $p < .01$. In Experiment 1, the main effects of phase and price, but not their interaction, were significant. Feeding bout sizes were smallest when both prices increased and largest when only sip price increased, $F(2, 6) = 22.50$, $p < .01$. In Experiment 2, the Phase $\times$ Price interaction was significant, $F(8, 24) = 2.41$, $p < .05$: In

the Price 160 conditions, feeding bouts were smaller when both resources were expensive than when only one was expensive.

These changes were mirrored by changes in feeding bout frequency (Figure 5). The number of daily feeding bouts increased as price increased: Experiment 1, $F(5, 15) = 5.22$, $p < .01$, Experiment 2, $F(4, 12) = 12.47$, $p < .01$. In Experiment 1, feeding bouts were more frequent in the both prices phase than in the pellet price phase. In Experiment 2, the Phase $\times$ Price interaction was significant, $F(8, 24) = 3.72$, $p < .01$: More feeding bouts occurred when both prices were 160 than when only one price was 160.

Drinking bouts decreased in size as the sip price or both prices increased (Figure 6). In Experiment 1, there was no systematic effect of pellet price on drinking bout size; the Phase $\times$ Price interaction was significant, $F(8,$

Fig. 4. The daily food intake (top), daily water intake (middle), and body weight (bottom) as a function of the price of pellets, sips, and both pellets and sips in two experiments. Details as in Figure 2.

24) = 9.21, $p < .01$. In Experiment 2, the interaction was not significant; in all phases, increasing price resulted in a decrease in drinking bout size, $F(4, 12) = 53.39$, $p < .01$. In both experiments, drinking bouts were smaller when both prices were 160 than when only the sip price was 160.

Drinking bout frequency (Figure 6) increased when sip price or both prices, but not pellet price, increased in Experiment 1, $F(8, 24) = 6.11$, $p < .01$. In Experiment 2, bout frequency increased with pellet or both prices but not with sip price, $F(8, 24) = 3.52$, $p < .01$. In both experiments, there were more

Fig. 5. The feeding bout size (top), bout frequency (upper middle), bout length (lower middle), and responses per bout (bottom) as a function of the price of pellets, sips, and both pellets and sips in two experiments. Details as in Figure 2.

Fig. 6. The drinking bout size (top), bout frequency (upper middle), bout length (lower middle), and responses per bout (bottom) as a function of the price of pellets, sips, and both pellets and sips in two experiments. Details as in Figure 2.

drinking bouts when both prices were high (80 or 160) than when sip price alone was high.

Despite the decreases in bout size, there were increases in both the amount of time, Experiment 1, $F(8, 24) = 2.57, p < .05$, Experiment 2, $F(8, 24) = 7.47, p < .01$, and number of bar presses, Experiment 1, $F(8, 24) = 5.12, p < .01$, Experiment 2, $F(8, 24) = 8.39, p < .01$, spent in each feeding bout as pellet price or both prices increased, but there was no effect of sip price (Figure 5). Similarly, the amount of time, Experiment 1, $F(8, 24) = 3.60, p < .01$, Experiment 2, $F(8, 24) = 16.83, p < .01$, and number of bar presses, Experiment 1, $F(8, 24) = 11.39, p < .01$, Experiment 2, $F(8, 24) = 27.11, p < .01$, spent in each drinking bout increased with increases in sip price or both prices but not with increases in pellet price (Figure 6). The time and responses per feeding or drinking bout were lower when both resources were expensive than when only food or water, respectively, was expensive.

Response Budget

The number of bar presses made daily for food increased with pellet or both prices but not with sip price, Experiment 1, $F(8, 24) = 20.20, p < .01$, Experiment 2, $F(8, 24) = 81.72, p < .01$; the number of bar presses for water increased with sip or both prices but not with pellet price, Experiment 1, $F(8, 24) = 11.67, p < .01$, Experiment 2, $F(8, 24) = 40.64, p < .01$ (Figure 7). In both experiments, at the highest price, more responses were made for a resource when it alone was expensive than when both resources were expensive. The combined number of daily bar presses for the two resources was greater when both pellets and sips were costly than when either one alone was costly in Experiment 2, $F(8, 24) = 29.31, p < .01$. In Experiment 1, however, this was true only when comparing the sip price and both prices phases; the rats made no more total daily responses when both resources were expensive than when pellets alone were expensive, $F(8, 24) = 14.27, p < .01$.

Time Budget

As the price of pellets or sips increased, the decrease in the rate of intake resulted in an increase in consumption time for that re-

source (Figure 8). The accompanying decrease in amount consumed and increase in instrumental rate counteracted this change to some extent, but, overall, daily time spent feeding increased with pellet price or both prices, Experiment 1, $F(8, 24) = 7.91, p < .01$, Experiment 2, $F(8, 24) = 38.24, p < .01$, and time spent drinking increased with the sip price or both prices, Experiment 1, $F(8, 24) = 6.70, p < .01$, Experiment 2, $F(8, 24) = 20.35, p < .01$. In Experiment 1, at the highest prices the rats spent more time consuming food or water when only the resource itself was costly than when both resources were costly; in Experiment 2 this was true only for feeding.

The combined daily feeding and drinking time (Figure 8) was greater when both resources were costly than when only one was costly in Experiment 2, $F(8, 24) = 8.54, p < .01$. In Experiment 1, this was true for the sip price versus both prices phases; however, there was no difference between the pellet price and the both prices phases in daily feeding plus drinking time, $F(8, 24) = 2.65, p < .05$.

The rats generally spent less time in the nest or the wheel when they spent additional time feeding and drinking, but there was no systematic pattern to these changes except in Experiment 2, when running time decreased across all price phases, $F(4, 12) = 4.86, p < .05$ (Figure 9). Time spent in unknown activity was reduced in Experiment 2 compared to Experiment 1 due to increased time in the nest and wheel (which were free), but it was still a substantial portion of the rat's day (4 hr or more), even at the highest prices.

DISCUSSION

The present experiments offered rats simultaneous access to four resources while the costs of consuming two of the resources, food and water, were manipulated. Our results confirm that as the consumption cost increases for a resource, intake of that resource decreases (Collier & Johnson, 1990; Collier et al., 1986). Food and water were complementary resources (Hursh, 1980): A decline in intake of one was accompanied by a decline in intake of the other. When water intake fell as a function of sip price, food intake simultaneously decreased. When food intake fell as

Fig. 7. The daily pellet bar presses (top), daily sip bar presses (middle), and combined daily bar presses (bottom) as a function of the price of pellets, sips, and both pellets and sips in two experiments. Details as in Figure 2.

pellet price increased, water intake either was unaffected or decreased. This classic relationship between food and water intake results from the defense of the ratio of body water to lean body mass in a closed economy (Adolph, 1947; Collier & Knarr, 1966; Collier

& Levitsky, 1967; Wolf, 1958). The effect of food intake on water intake is usually less rigorous, because excess water can be excreted as an alternate way of regulating body water (Collier, 1964; Oatley & Tonge, 1969). Thus, we believe that the effect of the cost of one

Fig. 8. The daily feeding time (top), daily drinking time (middle), and combined feeding plus drinking time (bottom) as a function of the price of pellets, sips, and both pellets and sips in two experiments. Details as in Figure 2.

resource on intake of the other is indirect; that is, food intake fell as a function of the reduction in water intake with sip price, not because of the sip price per se.

This linkage between food and water intake complicates somewhat the interpretation of the effects of the cost of food or water on

patterns of intake of the other resource. That is, we cannot know from our data why bouts of food or water intake decreased in size or frequency as the cost of the other resource increased. The simplest explanation is that the cost of one resource only secondarily affected the patterns of using the other re-

Fig. 9. Mean time spent daily feeding, drinking, nesting, running, and, in Experiment 2, sitting in the running wheel, as a function of the price of pellets, sips, and both pellets and sips. Time unaccounted for by these activities (other) was calculated by subtraction from 23 hr (1,380 min).

source as a result of changing the daily intake of that other resource. For example, when food intake decreased as water intake decreased with sip price, either the size or frequency of feeding bouts had to decrease. There need not have been a direct effect of either sip price or the pattern of drinking on the pattern of eating. Rather, the effect of the cost of water on the pattern of intake of food was indirect, through a cascade of events: Increased water cost resulted in decreased water intake, the decreased water intake resulted in reduced food intake, and the reduction in food intake resulted in smaller feeding bouts. This conclusion is strengthened by the results of Collier *et al.* (1990) showing that feeding and drinking patterns were independent of one another despite even more dramatic changes in bout patterns than were seen here.

Several models of choice between simultaneously available resources have been based on economic principles. Usually these models describe the behavior of animals offered two foods or food and water. One arose from the

examination of the spontaneous alternation between eating and drinking as food- and water-deprived animals repleted themselves within a session (i.e., in an open economy) and describes the path of repletion (McFarland & Lloyd, 1973). This model does not generate specific predictions for the present paradigm because our rats were self-regulating and were never seriously depleted. In this respect, our study differed from most concurrent-choice paradigms (e.g., Fantino, 1985). Because the rats lived continuously in the experimental environment, no constraint was placed on the time they spent or the bar presses they made, and they were allowed to determine bout frequency, size, and distribution as well as daily food and water intake and within-bout consumption rates. Although at any given moment the rat might choose one resource instead of another, this choice did not preclude or constrain the use of the others.

However, although less than the competition between feeding and nesting in rats in cold environments (Collier *et al.*, 1989;

Schultz, 1993) or between feeding and social contact in chicks (Hill, Rovee-Collier, Collier, & Wasserloos, 1986), we did find some evidence of competition between feeding and drinking when the resources were costly in these studies. First, less food and water were consumed when both were expensive than when the price was high for either one alone. This was especially evident in Experiment 1, but was also true at the highest price in Experiment 2. Further, in both studies fewer rats were able to maintain their body weight over the whole range of prices in the both prices phase than in the other phases. In Experiment 1, this effect appeared to be due, at least in part, to a ceiling on the amount of time or effort the rats devoted to feeding and drinking. That is, the total amount of time and total number of responses spent feeding and drinking each day were no higher when both pellets and sips were costly than when only pellets were costly. In Experiment 2, however, the total time and bar presses reached a higher asymptote when the prices of both commodities were increased than when only one price was increased. This suggests that the decline in intake of a commodity with its price was not a result of an upper limit on the number of bar presses a rat makes or the amount of time it spends in daily ingestion. These differences between the two experiments may be the result of the order in which the conditions were presented, a hypothesis that cannot be tested without further experimentation.

If time were the constraining factor, one wonders why the rats did not sacrifice some other activity (e.g., nesting) to allow more time for ingestion. In fact, there did not appear to be any particular activity that was reduced when feeding or drinking required more of the rat's time. Time spent nesting and running varied unsystematically across conditions in both experiments. Our efforts to reduce the time we could not account for (other time) were only modestly successful. The rats in Experiment 1, selected for high nesting levels when the nest was free, did not spend more time in the costly nest than rats in previous studies (Collier et al., 1990). We did account for more of the rats' time in Experiment 2, because the rats spent additional time in the nest and the wheel when they were cost-free and because we recorded

wheel sitting, but other time remained a substantial portion of the rat's day, presumably permitting the rat to expand the time spent in an activity as it became more costly.

The possibility of competition for time was reduced because the rats increased their response rate with resource price. This rate change restricts the increase in time spent feeding or drinking as unit price increases (Collier et al., 1986). In the present study, the rate of responding for a resource was affected by the cost of that resource only. Increasing the consumption cost for both food and water simultaneously, resulting in longer times spent consuming both, did not result in additional increases in rate. That is, the rats did not respond faster for pellets and save even more time feeding when they also had to spend more time drinking. In this respect, adjustments in the time budget to accommodate increases in consumption costs were made independently for feeding and drinking.

A central tenet in economic theory is the demand law—the fall in consumption (purchase) of a commodity produced by increases in its price. This is attributed to the decline in a commodity's marginal value as it is accumulated (e.g., Samuelson, 1976). The decline in intake of food, water, drugs, and so forth shown by laboratory animals as a function of the instrumental requirement has been characterized as an analogue of the demand law (Allison, 1979; Hursh, 1980; Lea, 1978; Rachlin, Green, Kagel, & Battalio, 1976). Why does food or water intake decline as a function of consumption cost? In open economies, the animal's income is restricted by constraints on time and effort. This was not the case in our study, and yet the decline in intake with price still occurred. Allison has interpreted the decline using a conservation model, which asserts that the total amount of behavior, consummatory plus instrumental, is conserved over all prices: As the price increases and more instrumental behavior is required, the amount of consummatory behavior must fall (Allison, Miller, & Wozny, 1979). Data supporting this model has come from studies in open economies with restrictions on time, response output, or both. The data from our closed economy are not consistent with the conservation model: Total instrumental plus consummatory behavior was not

conserved in our rats, and yet intake still declined with price.

Our results replicate earlier findings (Collier *et al.*, 1986) showing that the reductions in daily intake of both food and water were accomplished by decreases in bout size without compensatory increases in bout frequency. The fact that bouts become smaller as price increases suggests that the effect of price could be a local within-bout phenomenon rather than a more global effect on daily consumption. Such a local effect could be due, for example, to a ceiling on the number of responses or amount of time a rat spends in one consumption bout. A constraint on bout duration seems to be an unlikely explanation, however, because individual bouts lasted only 20 to 30 min at the highest costs, and in previous studies bouts of an hour or more have been reported when procurement costs were high (Collier, 1983). However, a constraint on responses per bout remains a possibility.

If, for whatever reason, the primary effect of consumption cost is on bout size, the regulatory puzzle is why bout frequency does not increase enough to maintain daily intake with the smaller bouts; that is, why the rats did not initiate meals of expensive pellets more often. The failure to maintain daily intake as price increases is not seen with a different cost, that of procuring access to a resource. Procurement cost differs from consumption cost in that the animal has some control over the cost-benefit ratio. When there is a price on procuring access to a resource, the animal determines the magnitude of the consequences (i.e., the size of the ensuing bout) associated with its responses and thus can (and does) limit the increase in the overall ratio of cost to benefit by taking larger bouts as the cost increases. The animal has no such behavioral option to limit the increase in the cost-benefit ratio as consumption cost increases. Instead, the rat appears to be managing its energy balance, at least in part, using physiological strategies. At higher prices, the rats initially lost body weight, indicating that they were metabolizing alternative fuels rather than maintaining food intake. In the most extreme case, a 50% reduction in intake resulted in only a 12% body weight loss, suggesting that the rats also increased feed efficiency, that is, unit weight gained (or maintained) per unit food

consumed (Maynard & Loosli, 1969). Both of these tactics conserve caloric expenditure while limiting the increase in consumption time and effort as pellet price, sip price, or both increased.

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APPENDIX A

Data for individual rats in Experiment 1.

	Rat	Pellet price							
		10	20	40	60	80	100	120	140
Pellet response rate (bar presses per minute)	1	40.5	59.5	61.9	66.3	146.6	204.4	155.8	158.7
	2	36.4	50.2	56.5	63.9	78.2	87.0	87.2	87.8
	3	34.6	57.2	81.9	82.0	87.5	98.8	106.3	123.6
	4	27.5	38.6	53.6	64.0	68.5	67.1	77.9	64.6
Sip response rate (bar presses per minute)	1	38.8	39.4	34.8	41.2	46.8	52.5	47.7	50.6
	2	33.5	40.1	40.8	41.3	46.8	49.8	48.3	47.6
	3	41.4	38.9	42.8	39.5	40.8	42.9	45.1	47.4
	4	25.0	29.8	28.5	31.0	29.3	32.3	34.5	34.4
Daily food intake (g)	1	18.0	16.8	12.0	8.4	16.9	17.8	12.9	12.4
	2	20.0	24.3	13.6	13.1	13.3	13.1	12.2	8.3
	3	18.0	16.7	19.2	16.5	15.1	15.8	15.0	11.5
	4	17.7	17.1	15.2	15.9	12.3	9.0	12.8	6.9
Daily water intake (ml)	1	27.1	28.8	41.7	50.2	62.3	26.0	21.3	20.0
	2	24.5	31.5	27.0	25.2	24.1	25.0	22.7	20.8
	3	25.4	23.1	29.3	25.6	24.2	25.8	26.0	21.6
	4	22.8	23.6	30.8	26.4	27.3	18.6	16.5	13.5
Body weight (g)	1	438.9	445.3	428.2	393.3	393.4	400.2	388.3	380.5
	2	501.5	500.8	473.0	463.7	460.6	452.7	435.9	414.2
	3	472.4	474.7	472.2	469.6	462.7	458.8	450.4	402.1
	4	510.5	509.9	446.5	449.4	453.5	417.4	401.5	390.8
Eat bouts per day	1	10.7	10.2	13.6	12.4	11.9	11.0	14.0	13.0
	2	13.3	13.5	10.0	15.2	17.6	17.6	14.9	13.3
	3	10.0	8.7	9.8	12.1	11.2	11.5	10.6	11.3
	4	9.8	9.9	8.3	6.3	8.5	11.6	12.0	14.3
Drink bouts per day	1	12.7	12.9	9.6	12.5	13.3	12.3	11.4	11.3
	2	13.5	12.8	10.8	10.2	10.1	10.9	9.6	8.8
	3	9.4	8.1	8.3	7.9	10.0	10.1	9.8	14.4
	4	8.5	8.4	10.8	8.6	11.2	9.9	13.0	11.8
Eat bar presses per day	1	3,993	7,458	10,662	11,244	30,110	39,533	34,286	38,430
	2	4,438	10,820	12,096	17,460	23,589	29,071	32,400	25,923
	3	3,997	7,440	17,047	21,960	26,800	35,075	39,960	35,900
	4	3,935	7,610	13,550	21,189	21,840	20,050	34,110	21,385
Drink bar presses per day	1	1,628	1,740	3,011	4,405	1,425	1,357	894	995
	2	1,075	1,348	1,218	1,067	1,141	1,116	1,057	910
	3	1,393	1,237	1,725	1,321	1,423	1,340	1,538	1,453
	4	593	883	1,195	1,006	957	695	968	745
Eat minutes per day	1	130.4	131.3	183.5	167.7	212.8	218.6	222.9	244.9
	2	124.8	221.7	218.5	279.7	317.4	340.5	378.2	295.7
	3	117.4	131.7	211.7	273.4	312.1	360.0	378.3	231.9
	4	148.1	203.6	253.0	333.6	324.4	289.2	441.0	306.6
Drink minutes per day	1	46.1	47.4	89.5	121.2	33.3	29.0	20.8	24.4
	2	36.1	37.2	36.0	27.7	35.0	23.9	23.3	20.2
	3	35.5	33.3	42.1	35.3	37.3	33.1	35.5	32.5
	4	76.6	32.3	45.2	34.7	44.2	29.8	30.7	24.0
Nest minutes per day	1	114.0	244.5	341.8	488.4	150.7	135.8	208.3	326.7
	2	140.3	180.1	640.9	408.0	213.4	235.9	376.0	411.9
	3	620.6	943.4	802.1	768.7	663.0	783.1	789.7	730.8
	4	437.4	533.3	193.4	174.4	398.5	175.4	612.1	717.8
Run minutes per day	1	2.2	1.7	6.5	16.8	10.0	4.1	7.0	3.8
	2	13.9	7.4	8.0	9.6	10.1	6.4	9.2	10.2
	3	3.7	3.7	5.8	4.4	4.2	3.9	2.3	7.9
	4	3.2	0.7	2.8	0.6	1.6	2.3	1.8	3.4

APPENDIX A

(Extended)

Sip price						Both prices				
10	20	40	60	80	120	10	20	40	80	100
29.1	29.5	29.5	29.3	30.1	31.9	30.2	45.7	70.9	115.6	128.0
29.0	27.5	29.8	29.9	29.6	36.5	31.4	46.0	58.7	67.6	71.6
32.3	34.5	34.3	33.0	36.5	894.4	45.5	69.9	75.1	89.3	96.8
37.6	33.3	30.9	30.8	26.5	25.9	28.7	41.6	61.9	70.4	82.1
45.8	55.8	70.6	77.4	99.7	117.2	44.4	63.4	79.6	110.2	110.3
45.9	54.4	55.8	60.5	64.9	71.7	38.4	54.9	60.0	67.5	70.0
50.7	65.0	81.8	88.6	101.2	100.5	42.8	65.1	80.9	101.8	98.8
30.6	39.0	45.8	75.5	55.3	70.8	28.5	40.0	53.2	78.2	86.7
22.6	16.6	20.1	20.2	20.7	18.1	20.2	18.0	16.4	14.6	12.4
22.2	21.4	13.4	14.2	15.2	14.3	17.8	19.4	14.2	9.2	8.2
23.6	21.1	21.7	17.8	19.9	14.2	20.1	29.0	18.6	14.5	13.4
19.6	26.4	20.3	17.4	15.9	14.5	22.2	19.9	16.1	10.2	8.1
29.5	23.1	26.0	22.0	21.8	22.5	29.8	23.8	20.2	18.0	14.2
38.0	31.8	21.0	20.5	21.3	18.5	31.8	29.6	18.7	12.1	11.7
27.2	24.2	19.5	20.2	20.7	15.8	27.7	26.0	22.8	16.0	13.0
18.5	23.0	20.0	20.9	15.0	15.4	21.1	17.6	11.0	6.8	3.8
425.8	433.7	434.8	433.3	436.5	427.3	441.8	441.6	433.2	403.3	389.8
449.3	469.0	480.0	481.8	474.0	466.0	500.0	488.8	489.5	456.6	432.3
452.6	469.8	482.5	482.2	482.7	456.0	494.3	401.5	498.2	480.1	454.6
412.5	450.3	467.3	465.7	458.3	435.0	476.4	483.4	478.6	432.4	386.3
11.0	12.3	10.8	12.0	12.3	11.0	12.2	13.8	13.8	12.9	18.3
8.7	12.2	11.8	14.0	11.3	12.2	13.9	13.8	19.2	20.4	22.7
8.8	8.3	10.3	9.8	9.0	7.2	9.0	8.4	11.2	13.8	13.2
9.0	8.0	8.0	11.9	8.7	8.6	10.2	10.6	12.4	13.2	10.5
10.0	8.9	12.5	11.5	14.5	16.0	13.8	15.4	19.4	19.4	19.3
11.3	11.7	10.0	10.3	15.3	12.8	13.5	16.8	16.3	17.3	18.2
8.4	9.2	12.3	13.0	11.7	12.0	6.8	9.6	11.6	14.0	16.2
8.5	10.3	12.7	11.6	17.0	14.4	8.0	9.6	13.0	19.3	15.3
5,018	3,680	4,468	4,495	4,590	4,018	4,480	8,016	14,576	25,966	27,600
4,937	4,755	2,983	3,163	3,378	3,188	3,954	8,636	12,593	16,408	18,167
5,240	4,693	4,813	3,962	4,430	3,166	4,464	8,556	16,552	25,720	29,860
4,355	5,877	4,517	3,873	3,543	3,231	4,928	8,844	14,352	18,062	18,067
1,340	1,700	3,920	5,700	10,240	16,230	1,462	2,488	4,824	8,846	9,517
1,717	2,583	3,180	3,960	7,560	9,400	1,515	2,760	3,340	4,328	5,300
1,344	2,440	4,290	6,528	8,587	6,960	1,290	2,284	3,752	7,050	9,840
910	2,593	3,933	5,396	6,053	9,651	1,189	2,712	4,736	7,716	6,833
174.2	127.3	153.7	155.4	154.0	127.4	150.8	178.6	209.5	229.4	220.4
173.2	176.5	106.9	109.8	117.1	93.5	130.1	191.7	221.9	248.3	270.3
165.7	137.9	143.3	122.1	124.6	73.7	100.5	124.2	206.4	292.7	311.3
132.2	179.4	147.7	129.1	212.8	125.6	180.0	215.9	235.5	260.4	230.1
30.8	34.8	59.2	81.2	107.6	145.9	35.2	42.1	67.0	85.3	97.3
39.8	50.9	65.5	100.6	125.2	145.2	45.2	55.9	95.6	110.4	94.6
32.8	40.1	56.5	78.9	89.9	89.7	31.4	37.5	49.5	73.2	106.1
33.6	71.0	92.5	86.9	120.8	143.4	45.1	72.8	95.9	109.1	85.3
0.0	4.8	0.0	0.0	0.0	0.0	0.0	146.4	0.0	232.1	203.1
265.3	138.6	222.4	520.5	114.5	257.1	135.5	67.2	76.6	241.5	238.9
891.3	861.1	892.7	892.8	817.9	792.0	901.2	861.6	798.3	743.1	653.8
672.0	746.5	571.6	471.1	479.2	10.5	457.4	463.9	516.4	0.0	0.0
3.1	5.3	8.0	5.7	4.2	1.3	6.8	13.2	13.5	12.6	11.0
2.0	5.3	10.2	8.2	8.9	12.8	17.8	13.7	8.9	13.0	12.8
6.5	4.9	2.3	4.8	5.4	2.9	4.0	5.1	4.2	4.2	3.4
3.1	1.9	2.4	6.2	1.7	1.8	1.7	2.3	2.2	3.1	3.1

APPENDIX B

Data for individual rats in Experiment 2.

	Rat	Pellet price				
		10	20	40	80	160
Pellet response rate	1	55.3	85.5	121.8	128.0	152.5
(bar presses per minute)	2	44.2	81.4	116.6	156.2	188.2
	3	42.6	55.9	88.4	87.7	
	4	48.2	73.9	102.8	128.4	148.9
Sip response rate	1	43.0	43.5	43.5	44.9	44.9
(bar presses per minute)	2	43.6	43.6	44.5	44.7	44.5
	3	48.3	42.2	44.0	39.2	
	4	55.7	56.6	58.7	58.1	63.0
Daily food intake (g)	1	23.1	22.5	21.8	20.4	15.1
	2	27.8	19.5	20.3	17.6	14.8
	3	22.5	16.1	19.6	15.0	
	4	25.9	26.1	19.4	19.8	18.0
Daily water intake (ml)	1	31.3	32.2	30.0	26.3	23.0
	2	34.4	24.4	25.2	22.1	20.9
	3	27.3	18.9	22.0	20.6	
	4	46.3	48.7	38.6	39.1	33.6
Body weight (g)	1	530.1	537.3	535.7	512.2	493.7
	2	470.4	493.2	491.8	492.0	472.6
	3	451.9	442.7	443.9	428.7	
	4	428.3	463.3	463.1	456.4	435.9
Eat bouts per day	1	11.4	14.0	13.0	12.8	12.6
	2	11.8	12.8	12.5	12.0	16.0
	3	12.1	11.9	16.1	15.9	
	4	9.2	9.4	11.2	10.5	7.3
Drink bouts per day	1	10.4	13.5	14.5	14.6	13.9
	2	12.4	12.0	12.8	15.8	16.6
	3	12.4	12.9	15.1	13.3	
	4	14.2	13.1	13.8	17.5	18.9
Eat bar presses per day	1	5,139	9,987	19,347	36,337	53,829
	2	6,176	8,676	18,071	31,248	52,571
	3	5,005	7,147	17,383	26,583	
	4	5,748	11,606	17,249	35,120	64,069
Drink bar presses per day	1	3,598	3,803	3,555	3,500	3,106
	2	3,730	2,682	3,111	2,322	2,386
	3	3,429	4,470	4,299	3,457	
	4	4,757	4,809	3,850	3,824	3,333
Eat minutes per day	1	95.1	119.6	161.6	286.6	358.3
	2	142.0	108.7	156.3	201.4	281.6
	3	120.3	129.6	201.9	311.1	
	4	122.8	158.9	169.8	275.1	431.3
Drink minutes per day	1	85.4	89.8	84.5	81.2	71.7
	2	87.4	63.2	72.0	54.1	55.9
	3	73.8	107.5	101.7	92.1	
	4	87.8	86.9	67.3	68.3	55.9
Nest minutes per day	1	618.2	401.8	636.4	681.5	711.4
	2	581.6	389.8	612.5	490.6	555.9
	3	855.0	772.3	758.2	773.6	
	4	796.7	889.4	853.6	734.0	778.4
Run minutes per day	1	19.3	18.3	11.8	8.0	6.9
	2	2.7	2.0	2.1	1.6	1.4
	3	51.7	30.7	23.6	11.9	
	4	18.8	27.2	47.9	28.1	9.2
Wheel-sit minutes per day	1	111.0	82.4	116.3	26.7	34.9
	2	118.9	96.9	187.5	206.0	148.7
	3	15.1	21.1	14.4	0.7	
	4	106.4	78.3	82.5	87.4	7.5

APPENDIX B

(Extended)

Sip price					Both prices				
10	20	40	80	160	10	20	40	80	160
54.3	54.3	56.0	71.7	98.0	51.8	77.8	100.4	126.6	146.6
40.5	38.9	38.3	37.3	35.1	46.5	76.9	106.8	135.8	
45.9	44.0	42.5	37.3		47.3	68.1	98.0		
54.8	48.3	52.2	50.5	46.2	58.2	89.9	120.3	139.4	152.7
40.4	64.0	94.1	113.8	136.2	42.6	66.3	96.2	125.7	149.0
40.4	60.9	92.5	117.5	140.8	39.2	64.7	85.0	97.6	
48.9	76.9	93.9	112.3		47.9	70.5	99.0		
56.6	68.7	108.9	131.5	142.8	56.5	87.3	120.1	145.3	142.6
26.8	22.3	20.0	19.0	11.2	24.4	26.8	25.6	18.6	13.1
22.6	17.8	16.6	14.5	11.3	25.4	23.4	20.6	16.1	
19.1	17.9	21.3	19.1		23.2	19.6	21.0		
25.4	17.3	21.2	20.0	16.7	24.5	23.4	25.2	22.7	12.7
34.1	26.8	25.1	22.7	12.4	36.3	32.2	30.4	29.8	13.1
27.1	21.3	21.0	19.3	12.0	26.4	24.8	22.0	16.6	
23.2	26.4	24.0	17.7		22.7	21.0	20.8		
42.4	25.3	34.4	31.6	24.1	34.5	33.2	35.5	31.0	16.4
511.5	530.4	533.7	517.9	471.3	493.4	502.1	480.8	487.8	440.6
477.8	489.6	484.8	475.6	454.3	443.4	469.4	469.3	429.3	
457.0	449.5	446.3	437.6		457.3	449.4	448.3		
468.9	456.8	463.5	461.0	435.3	455.2	464.8	460.5	440.3	404.0
8.5	10.2	10.4	10.3	10.4	11.1	12.3	13.2	17.5	17.7
10.6	11.6	12.0	11.6	9.9	8.3	11.1	11.1	11.7	
12.0	11.4	13.7	12.0		12.7	13.5	12.4		
7.5	9.8	10.5	9.2	7.4	8.1	10.1	10.4	12.7	14.8
11.4	12.0	13.2	13.6	13.6	11.9	12.2	13.1	16.0	16.3
12.3	11.5	10.9	10.6	9.4	11.6	11.1	11.1	12.4	
11.8	14.9	12.3	12.3		12.0	12.1	11.9		
12.4	12.0	12.8	11.8	10.7	11.7	12.9	13.7	13.8	15.9
5,953	4,958	4,439	4,231	2,486	5,422	11,915	22,756	33,072	46,580
5,024	3,954	3,697	3,231	2,509	5,647	10,398	18,342	28,540	
4,252	3,974	4,741	4,241		5,160	8,732	18,678		
5,644	3,848	4,709	4,446	3,707	5,448	10,389	22,431	40,280	45,100
3,981	7,660	15,711	26,994	37,349	5,972	9,122	15,664	23,780	34,480
2,676	4,264	9,004	16,994	26,423	4,523	6,456	10,458	18,969	
4,021	10,250	13,183	21,231		4,211	8,666	13,007		
4,601	6,165	14,502	27,169	52,000	4,785	9,120	15,723	26,632	38,700
112.5	93.6	82.3	62.5	28.2	108.4	155.8	218.3	266.1	323.6
125.6	103.5	98.2	88.2	73.2	125.8	138.2	175.2	211.5	
95.0	91.4	114.3	116.3		111.5	131.0	194.5		
106.2	78.7	91.9	89.3	80.8	95.8	117.4	188.6	291.6	297.9
100.6	121.9	171.5	242.3	280.3	142.5	139.9	167.2	194.0	237.6
68.1	71.9	98.8	146.7	190.4	118.5	101.5	125.5	196.2	
84.5	133.4	143.0	191.0		91.8	125.6	133.9		
83.3	79.5	135.0	208.6	367.1	86.9	106.4	133.0	186.0	275.3
651.5	520.3	622.8	662.0	607.2	555.4	649.7	683.1	621.8	592.7
383.4	361.3	337.5	292.2	373.3	528.9	544.6	549.9	565.3	
892.6	616.2	785.0	654.8		822.0	823.4	808.1		
900.2	772.0	667.8	729.0	657.7	804.4	830.7	742.7	662.9	630.2
9.3	11.8	10.7	8.5	5.0	21.0	21.1	15.4	9.6	4.4
2.7	2.7	3.0	2.2	1.3	4.5	5.5	3.4	2.2	
44.3	38.0	34.3	24.8		54.1	45.5	32.2		
44.0	58.5	48.2	23.3	8.5	60.6	61.1	39.3	30.7	20.6
76.6	139.6	90.2	124.5	68.1	89.8	79.6	37.1	36.3	4.2
187.5	185.5	131.3	197.3	272.4	160.1	182.0	166.1	73.7	
9.4	8.1	16.3	13.3		24.8	18.9	6.9		
81.3	98.2	109.0	78.2	119.2	82.0	77.6	35.3	40.3	19.8