DRINKING IN A PATCHY ENVIRONMENT: THE EFFECT OF THE PRICE OF WATER

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Rats in a laboratory foraging paradigm searched for sequential opportunities to drink in two water patches that differed in the bar-press price of each "sip" (20 licks) of water within a bout of drinking (Experiment 1) or the price and size (10, 20, or 40 licks) of each sip (Experiment 2). Total daily water intake was not affected by these variables. The rats responded faster at the patch where water was more costly. However, they accepted fewer opportunities to drink, and thus had fewer drinking bouts, and drinking bouts were smaller at the more costly patch than at the other patch. This resulted in the rats consuming a smaller proportion of their daily water from the more costly patch. The size of the differences in bout frequency and size between the patches appears to be based on the relative cost of water at the patches. The profitability of each patch was calculated in terms of the return (in milliliters) on either effort (bar presses) or time spent there. Although both measures were correlated with the relative total intake, bout size, and acceptance of opportunities at each patch, the time-based profitability was the better predictor of these intake measures. The rats did not minimize bar-press output; however, their choice between the patches and their bout sizes within patches varied in a way that reduced costs compared to what would have been expended drinking randomly. These data accord well with similar findings for choices among patches of food, suggesting that foraging for water and food occurs on the basis of comparable benefit-cost functions: In each case, the amount consumed is related to the time spent consuming.

Key words: foraging, drinking, benefit-cost, currency, consumption rate, profitability, bar press, rats

The present experiments explore the behavior of rats "foraging" for water in a laboratory environment. Water, like other resources, is generally distributed patchily, requiring animals to travel among different potential water sources, or patches, deciding whether and how much to exploit each patch. Optimality models assume that these decisions are based at least partly on an attempt to minimize costs relative to benefits. For example, desert herbivores sometimes rely on water holes far from their grazing or browsing areas. There are costs of discovering, traveling to, and using the water hole (the last because of competition and predation). Schmidt-Nielsen, Schmidt-Nielsen, Houpt, and Jarnum (1956) showed that camels reduce the costs of using distant water holes by traveling to them infrequently, thus reducing their travel times, and, once there,

by consuming 20% to 30% of their body weight in 15 to 20 min, limiting their exposure at the water site. This example illustrates two classes of resource costs that may differ among patches: those costs arising in gaining access to the resource and those costs arising in utilizing or consuming the resource. The latter costs are the subject of interest here.

Consumption cost for food resources has been studied in the laboratory by varying the price of each small unit of food, such as a pellet or brief presentation of a food hopper (e.g., Collier, Johnson, Hill, & Kaufman, 1986). Foraging rats are sensitive to these costs as they select among food patches. When two different-price patches are sequentially encountered, rats eat more and larger meals at the patch with the lower consumption cost. Daily intake from both patches combined is constant regardless of the pattern of patch exploitation. The price metric (currency) that best describes their feeding behavior at a patch is the rate of calorie intake (calories per minute) at that patch relative to the other patch (Johnson & Collier, 1987, 1989, 1991). This supports the notion that net energy gain per unit time, or profitability, is an important parameter for foraging decisions (Schoener, 1971; Stephens & Krebs,

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1986). It raises the question, however, as to what the comparable parameter would be for other resources. For example, energy gain is not an appropriate currency for the benefit gained from water.

In our laboratory simulation, rats were offered opportunities to drink in patches that differed in the consumption cost of water. The cost was manipulated by varying both the bar-press price and the size of portions that the rats could earn (Marwine & Collier, 1979). Time and energy spent foraging and drinking seem to be appropriate currencies for cost in this situation. The currency we chose for benefit was amount of water ingested. We computed the water benefit-cost ratio in two ways—as milliliters per bar press and as milliliters per minute—and compared these cost measures in their ability to predict the rats' behavior.

EXPERIMENT 1

METHOD

Subjects and apparatus. Four male Sprague-Dawley rats, weighing approximately 275 g at the outset, were housed individually, 23 hr a day, in stainless steel cages (43 cm by 25.5 cm by 17.5 cm) located in a room at 22 °C with lights on from 8 a.m. to 8 p.m. The subjects were removed from their cages for approximately 1 hr a day (at 11:00 a.m.) and were placed together in a holding cage for the maintenance period. During this time, the rats were weighed, food and water were replenished, the apparatus was cleaned and tested, the data were recorded, and any changes in the experimental contingencies were made.

The experimental cages were fitted with T-shaped response bars requiring 0.35 N to depress and 1.3-cm cue lights. A "search bar," 3.5 cm above the floor, and a "search light," 12 cm above the bar, were located in the center of one end wall of the cage. On the opposite end wall of the cage, another response bar, the "water bar," was centered 3.5 cm above the floor. A cuelight was located on each side of the water bar; these "patch lights" represented two water sources. A single bar was used to avoid the position preferences sometimes seen in rats. A third, "consumption," light was located 10.5 cm above the water bar. An opening (1.75 cm diameter), 1 cm above the water bar,

gave access to a drinking tube. The water bottle was mounted in a cam-operated device that moved the tube in and out of the rat's reach. The "in" position of the tube was adjusted so that the rat had to lick in order to drink and so that the lick size was approximately the same for all rats. Contact with the tube was monitored by a Gerbrands lickometer. Food (ground chow, Purina® 5001) was freely available in round metal feeding cups, filled daily with approximately 95 g of chow, mounted on the floor in the center of one long cage wall. A microprocessor (Commodore® 128D) controlled the experimental equipment and recorded the data.

The cages operated as follows: During intervals between drinking bouts, the search light was illuminated and the rat could search for a patch of water by pressing the search bar five times. This caused the search light to go out and one of the two patch lights, chosen at random, to come on, indicating that a water patch had been encountered. The rat could either reject or accept this drinking opportunity. The patch could be rejected in two ways: The rat could make no responses on the water bar for 1 min or could press the search bar three times. In both cases, the patch light went out, the search light came on, and the rat could continue to search. To accept an opportunity, the rat procured access to the patch by completing 10 responses (the procurement price) on the water bar. This caused the consumption light to come on, indicating that further responses would produce short periods of access to the water tube, called "sips," on a fixed-ratio (FR) schedule. Each completion of the FR, or sip price, caused the tube to move into the rat's reach for 5 s or 20 licks, whichever came first. Any number of sips could be earned per bout. A drinking bout ended when 15 min elapsed with no sip earned. At that time, the patch and consumption lights went out and the search light came back on.

Procedure. The rats were adapted to their cages and the response contingencies over a period of about 3 weeks. First, both response bars were removed, and for 2 days the water bottles moved into the cage at random intervals, remaining in reach for 5 s each time. On the 3rd day, the water bar was installed, with a sip price of one bar press. The rats quickly began to bar press; shaping was not necessary. The following steps were taken after 2 days

of normal water and food intake and body weight gain. If a problem arose, the training schedule returned to the previous stage. The sip price was raised to two bar presses and then to five presses. The procurement price was raised from zero to five and then to 10 presses. The search bar was then installed. The search price was raised from one to two bar presses and then to five presses with no reject options available. Finally, the rejection contingencies were added.

During the experimental phases, the search price was constant at five bar presses and the procurement price was constant at 10 bar presses for both the left and right patches. Sip prices were presented so that one patch light indicated a low sip price of five presses and the other light indicated a sip price of five, 10, 20, 40, or 80 presses. Each price combination was presented twice, once in order of ascending high price and then in random order. The left-right positions of the low- and high-priced patches were alternated between conditions. Each condition was in effect for at least 9 days (sometimes longer because of equipment failures), and data from the last 7 days of each condition were analyzed. Although the rats generally adapted to new schedules during the 1st day, we did not include data from the first 2 days of any condition in our analyses. Differences between the low- and high-priced patches in acceptance of opportunities, bout frequency, bout size, daily intake, and rates of responding and of drinking were evaluated using two-factor (patch $\times$ higher price) repeated measures analysis of variance (ANOVA), with a priori contrasts specified between the two patches in each price condition and $\alpha = .05$. In all cases, statistically significant main effects were accompanied by a significant interaction term in the ANOVA, so F values for the main effects are not presented here. Statistically significant between-patches contrasts are indicated in the figures, which present data as group means. Individual-subject data are shown in Appendix B, and they generally confirm the representativeness of the group means.

RESULTS AND DISCUSSION

Data from the first and second exposures to each price condition were combined for each rat. The rats accepted nearly all (90% to 94%) opportunities to drink at the low-priced patch. Acceptance at the high-priced patch gradually

declined from 90% to 12% as the sip price increased at that patch from 10 to 80 presses (Figure 1, top panel). The patch $\times$ price interaction was statistically significant, $F(4, 12) = 46.981$, $p < .001$. The preference for the low-priced patch became statistically significant at the high price of 40 presses (indicated by asterisks in the figure). The difference in acceptance resulted in fewer bouts per day (Figure 1, second panel) occurring at the high-priced patch at high sip prices of 40 and 80 presses: patch $\times$ price $F(4, 12) = 19.217$, $p < .001$. Note that bout frequency changed at both patches, decreasing at the high-priced patch but increasing at the low-priced patch as the sip price increased.

The number of sips earned per bout (Figure 1, third panel) was similarly affected by the price of water. Bouts were larger at the low-priced patch, and the difference increased as the higher sip price increased: patch $\times$ price $F(4, 12) = 12.304$, $p < .001$. The difference between patches became statistically significant at the high price of 20. As with bout frequency, bout size decreased at the high-priced patch but increased at the low-priced patch as the price increased.

These changes resulted in the rats consuming more water per day (Figure 1, bottom panel) at the low-priced patch, and less water per day at the high-priced patch, as the high price increased: patch $\times$ price $F(4, 12) = 28.351$, $p < .001$. There was no consistent effect of high sip price on total daily water intake, $F(4, 12) = 2.817$, $p > .05$; the rats drank a mean of 33.4 mL per day. Food intake ($M = 21.6$ g per day) was also relatively unaffected by manipulations of sip price, $F(4, 12) = 1.809$, $p > .05$, and the rats grew normally. The effects of sip price on patch choice, bout size, and daily intake were identical in form to the effects of pellet price on analogous measures of food intake (Johnson & Collier, 1989).

The drinking rate (sips per minute during bouts) was calculated at each patch (Figure 2, top panel). The rate was constant at the low-priced patch, but declined gradually at the high-priced patch as price increased: patch $\times$ price $F(4, 12) = 54.367$, $p < .001$. Recall that the sip rate is a function of the sip price and the rate at which the rat presses the bar during the consumption period. The response rate was calculated as bar presses per minute during

Fig. 1. Experiment 1. Percentage of opportunities accepted (a), bouts per day (b), sips per bout (c), and milliliters per day (d) in the low- and high-priced patches as functions of the higher sip price. The low sip price was FR 5 throughout. Values are means ($\pm SE$) for 4 rats in two replications. Asterisks indicate a statistically significant between-patch contrast: * $p < .05$, ** $p < .01$.

Fig. 2. Experiment 1. Drinking rate (top) and response rate (bottom) in the low- and high-priced patches as a function of the higher sip price. The low sip price was FR 5 throughout. Details as in Figure 1.

drinking bouts (i.e., in the presence of the consumption light), as both an average rate (number of responses divided by bout time) and as a local rate (number of responses divided by bout time excluding pauses between responses greater than 15 s). Both rates showed the same patterns; the local rates are presented here (Figure 2, bottom panel). The response rate increased at the high-priced patch with increased sip price, but was not affected at the low-priced patch: patch $\times$ price $F(4, 12) = 7.575$, $p < .01$. Although the rats did not increase their response rate enough to maintain a constant drinking rate at the high-priced patch, the drinking rate was higher than it would have been if they had not increased their response rate at all. The change in rate with sip price has been reported previously (Marwine & Collier, 1979).

EXPERIMENT 2

The generality of the effects of food-consumption cost on feeding has been strength-

ened by the fact that regardless of the way cost has been manipulated, the results are the same. For example, in addition to the bar-press price of pellets, the size of the food pellet and the length of a minimum interval between pellet deliveries have also been altered to effect a cost difference, and the best predictor of patch exploitation is still the relative rate of calorie consumption at the patches (Johnson & Collier, 1989, 1991). In Experiment 2, the cost of water was varied between patches by presenting sips of different sizes at each patch. If the sip price is the same, larger sips provide water that is less expensive and is consumed at a higher rate within bouts; thus, if rats meter water cost using bar presses per milliliter or minutes per milliliter, we would expect them to adjust their choices and intake patterns in response to this type of price alteration just as was seen in the first experiment. These results should yield a broader picture of how time and energy costs affect the intake patterns and should provide a better understanding of the currency of costs and benefits for rats.

METHOD

Subjects and apparatus. Four naive male Sprague-Dawley rats were tested in the apparatus described in Experiment 1.

Procedure. The rats were adapted to the cages and contingencies as in Experiment 1. There were two experimental phases. In the first, the water patches differed in the size of the sip they offered, while the sip price was five bar presses at both patches. Recall that during a sip the water tube was accessible for a set number of licks or a set amount of time, whichever came first. We used three sip sizes: 10 licks or 2.5 s, 20 licks or 5 s (as in Experiment 1), and 40 licks or 10 s; all three pairs of these sizes, one at each patch, were presented to each rat in a random order, and then the first pair was presented again. The left-right position of the small sip was alternated between pairs. Finally, the middle sip size, 20 licks, was presented at both patches. Each condition was in effect for at least 13 days, and data from the last 10 days were analyzed.

In the second phase, the three pairs of sip sizes were presented again to each rat in the following order: 10 versus 40 licks, 20 versus 40 licks, and 10 versus 20 licks. For each pairing, the sip price began at five bar presses at both patches and then was increased at the

large-sip patch to 10, 20, 30, 40, and 60 presses, and, in some cases, to 80, 100, and 120 presses or until the rat obtained less than 10% of its daily water from that patch. Each price condition was in effect for at least 10 days, and data from the last 7 days were analyzed.

The small differences in the number of days per condition between Experiments 1 and 2, and between the phases of Experiment 2, are unrelated to the behavioral outcomes. Behavior usually stabilized in our paradigm by the 2nd or 3rd day, and thereafter the data were unaffected by the number of days in a condition.

Rat 5 died before completing the 10 versus 20 licks conditions; thus, group data for this pair of sip sizes are from 3 rats. Further, because some rats did not experience conditions with large-sip prices higher than 60 presses, only data from large-sip prices of 10 through 60 were included in the statistical analyses. Differences between the patches in drinking measures were evaluated with two-factor (patch $\times$ large-sip price) repeated measures ANOVAs, with a priori contrasts specified between patches in each condition and $\alpha = .05$. These statistics are reported as in Experiment 1. Group means are presented in the figures for the conditions through the high-sip price of 60 presses; individual-subject data are shown in Appendix A.

Relative measures. In our studies of choice between food patches, we have described the behavior at one patch relative to the other as a function of the profitability of that patch relative to the other (Johnson & Collier, 1987, 1989, 1991). We carried out the same analyses here. For both Experiments 1 and 2, we calculated a single relative measure to describe a rat's behavior (e.g., bout size or daily intake) at both patches in each condition. For the example of bout size, this was the average bout size (milliliters per bout) at one patch divided by the size at the other patch. The numerator was measured from the patch with the more expensive sips (Experiment 1) or the smaller sips (Experiment 2). Similarly, we calculated the relative profitability (i.e., milliliters per bar press or milliliters per minute) in each condition. These relative measures were log transformed to achieve linear scales. We then regressed each log relative behavior measure on each log relative profitability measure to determine the proportion of variance in the behavior that was explained by the differences in profitability.

Fig. 3. Experiment 2. Percentage of opportunities accepted (top panels) and bouts per day (bottom panels) in small- and large-sip patches as a function of the price of the large sips. The sip sizes, in licks, at each patch are shown at the top of each column. The price of the small sips was FR 5 throughout. Values are means ($\pm$ SE) for 4 rats, except in the 10 versus 20 licks conditions, where data are from 3 rats. Asterisks indicate a statistically significant between-patch contrast: * $p < .05$, ** $p < .01$.

RESULTS AND DISCUSSION

The conditions in the first phase of this experiment (sip price of five presses at both patches) were replicated in the second phase. The data from the two phases were similar

and have been combined in the analyses presented here.

The rats accepted nearly all opportunities to drink (Figure 3, top) at both patches until the large-sip price exceeded 40 bar presses; then acceptance of large-sip opportunities fell:

Fig. 4. Experiment 2. Bout size in sips (top panels) and milliliters (bottom panels) in small- and large-sip patches as a function of the price of the large sips. The sip sizes, in licks, at each patch are shown at the top of each column. The price of the large sips was FR 5 throughout. Details as in Figure 3.

Fig. 5. Experiment 2. Daily intake in sips (top panels) and milliliters (bottom panels) in small- and large-sip patches as a function of the price of the large sips. The sip sizes, in licks, at each patch are shown at the top of each column. The price of the small sips was FR 5 throughout. Details as in Figure 3.

patch $\times$ price, 10 versus 40, $F(4, 12) = 5.128$, $p < .05$; 20 versus 40, $F(4, 12) = 4.418$, $p < .05$; 10 versus 20, $F(4, 8) = 3.593$, $p > .05$. Thus, bout frequency (Figure 3, bottom) did not differ between the patches except at the highest large-sip prices: patch $\times$ price, 10 versus 40, $F(4, 12) = 3.073$, $p > .05$; 20 versus 40, $F(4, 12) = 12.710$, $p < .001$; 10 versus 20, $F(4, 8) = 1.763$, $p > .05$. It should be

noted that in Experiment 2 the rats continued to accept high-cost patches over a wider range of prices than in Experiment 1.

The number of sips earned per bout (Figure 4, top) was greater for the small sips, and the difference increased as the large sips became more expensive: patch $\times$ price, 10 versus 40, $F(4, 12) = 11.54$, $p < .001$; 20 versus 40, $F(4, 12) = 7.442$, $p < .01$; 10 versus 20, $F(4, 8) =$

Fig. 6. Experiment 2. Response rate (top panels) and drinking rate (bottom panels) in small- and large-sip patches as a function of the price of the large sips. The sip sizes, in licks, at each patch are shown at the top of each column. The price of the small sips was FR 5 throughout. Details as in Figure 3.

36.102, $p < .001$. The amount of water consumed per bout (Figure 4, bottom) was greater for the large sips when the sip prices were equal (FR 5), although this difference was not statistically significant in the 20 versus 40 condition. But, as the large-sip price increased, bout size decreased at the large-sip patch and increased at the small-sip patch, until more water was consumed in bouts at the small-sip patch: patch $\times$ price, 10 versus 40, $F(4, 12) = 24.084$, $p < .001$; 20 versus 40, $F(4, 12) = 29.703$, $p < .001$; 10 versus 20, $F(4, 8) = 68.5$, $p < .001$. The patterns of daily intake (Figure 5) mirrored those of bout size: patch $\times$ price, 10 versus 40, $F(4, 12) = 17.550$, $p < .001$; 20 versus 40, $F(4, 12) = 20.936$, $p < .001$; 10 versus 20, $F(4, 8) = 24.056$, $p < .001$. Total daily water (43.1 ± 2.1 mL) and food intake (24.2 ± 0.5 g) did not differ in a regular way across conditions.

When the sip prices were equal (five presses) at the patches, the rats pressed the bar faster for small sips, but the drinking rate (milliliters per minute) was higher at the large-sip patch (Figure 6). As the sip price increased for the large sips, the rate of bar pressing for those sips also increased, but not sufficiently to compensate for the increased price, and the drinking rate declined. Rates of bar pressing and drinking were constant at the small-sip patch. The patch $\times$ price interactions were statistically significant for both bar-press rate, 10 versus 40, $F(4, 12) = 9.806$, $p < .001$; 20 versus 40, $F(4, 12) = 13.836$, $p < .001$; 10 versus 20, $F(4, 8) = 28.011$, $p < .001$; and drinking rate, 10 versus 40, $F(4, 12) = 13.377$, $p < .001$; 20 versus 40, $F(4, 12) = 28.496$, $p < .001$; 10 versus 20, $F(4, 8) = 50.244$, $p < .001$. Therefore, as the large-sip price increased, the patch with the greater profitability, in milliliters per bar press or milliliters per minute, shifted from the large-sip to the small-sip patch, as shown in Figure 7: patch $\times$ price (milliliters per bar press), 10 versus 40, $F(4, 12) = 61.376$, $p < .001$; 20 versus 40, $F(4, 12) = 145.0$, $p < .001$; 10 versus 20, $F(4, 8) = 68.500$, $p < .001$; patch $\times$ price (milliliters per minute), 10 versus 40, $F(4, 12) = 24.281$, $p < .001$; 20 versus 40, $F(4, 12) = 63.035$, $p < .001$; 10 versus 20, $F(4, 8) = 69.034$, $p < .001$. The location of the crossover point depends on which currency is used for water cost—time or bar presses. Note that our

profitability calculations were based on the within-patch consumption cost. For simplicity, the costs of searching and procuring, which were constant and small relative to consumption cost, were not included.

For both experiments, we examined the intake patterns at one patch relative to the alternate patch as a function of each profitability measure. Figure 8 shows log-log plots of mean relative acceptance of patches, bout frequency, bout size, and total intake as functions of mean relative profitability, based on the milliliters per bar press data (left column) and the milliliters per minute data (right column) for both experiments. Note that the log value equals zero when the measure (e.g., bout size) is equal at the two patches, is negative when the measure is greater at the patch with the larger sip, and is positive when the measure is greater at the patch with the smaller sip. The proportion of explained variance (r^2) for the regression line fitted to each relationship is given on the graphs, and the proportions for each individual are shown in Table 1. Although both profitability measures were highly correlated with relative intake and bout patterns, in nearly all cases the time-based rate of return explained a greater proportion of the variance. A time-based profitability was also better than one based on effort at predicting feeding patterns in food patches with differing consumption cost (Johnson & Collier 1987, 1989, 1991). Additional support for the relatively greater importance of time, compared to effort, was reported by Bauman (1991), who found that intake was equal on FR and fixed-interval (FI) schedules when the length of the FI was equivalent to the time taken to complete the FR, even though more responses were made during the FR schedule.

GENERAL DISCUSSION

Rats exploit water patches that differ in the cost of consuming water by adjusting both the frequency of exploiting opportunities to drink and the amount consumed per drinking bout at each patch, such that more water is consumed each day from the patch offering less costly water. The greater the cost difference, the greater the intake difference. These results are identical to those of rats choosing among food patches (Johnson & Collier, 1989, 1991).

Fig. 7. Experiment 2. Profitability in milliliters per bar press (top panels) and milliliters per minute (bottom panels) in small- and large-sip patches as a function of the price of the large sips. The sip sizes, in licks, at each patch are shown at the top of each column. The price of the small sips was FR 5 throughout. Details as in Figure 3.

The striking similarity between foraging for food and water suggests that there are general rules for selection among and exploitation of different sources of a commodity that are based on the rates at which the commodity is consumed at each source.

The patterns of patch use are efficient, in that time and energy spent are reduced compared to a random patch exploitation; however, they do not minimize the expenditure of either time or bar presses (cf. Johnson & Collier, 1991). The rats here could have consumed their daily water at lower daily cost by rejecting all high-price patches, because the cost of locating a low-price patch (10 bar presses) was much lower than the cost of drinking more than one sip in a high-price patch. Instead, the rats continued to consume water from the high-cost patch, but with a declining frequency as the difference in costs increased. These suboptimal preferences have been extensively discussed in the literature with no resolution (McNamara & Houston, 1987; Stephens & Krebs, 1986).

For both food and water, the relative rate of intake (profitability) in a patch accounts for a major portion of the variance in acceptance, bout size, and total intake in this foraging paradigm. Deprived rats bar pressing for pellets (or other reinforcers) in short, fixed-length ses-

sions distribute their responses between two sources differing in rate of return (reinforcers per minute) in a way homologous to these foraging results (cf. Johnson & Collier, 1991). That is, they match relative number of responses per session to relative rate of return, a function that has given rise to the matching law (Herrnstein, 1970). It would be interesting to consider the matching law to be a corollary of a general law of choice stating that relative consummatory behavior (choice, number of responses, bout size, total intake, etc.) can be predicted from the relative rates of return from the alternative sources.

Although the patch-choice problem facing the rats in our study may seem analogous to the prey-choice problem in some optimality models (Stephens & Krebs, 1986), this is not the case. Most optimality models were developed in paradigms different from that used here and do not include parameters for all of the activities available to our rats. A major difference is the time frame examined: Our rats were free to initiate and terminate bouts of drinking throughout the day and night. Therefore, within-bout behavior, which is the exclusive subject of many models, is only one aspect of the overall cost-effective behavioral strategy. The pattern of bouts also contributes to cost reduction (Collier & Johnson, 1990),

Fig. 8. Log relative mean acceptance (top row), bout frequency (second row), bout size (third row), and daily intake (bottom row) as functions of log relative mean return on effort (left panels) and log relative mean return on time (right panels) for both experiments. See text for details. The values of r^2 for the regressions are shown.

and in fact, adjusting the amount of water per bout was the primary means by which our rats drank more water from the cheaper patch. Bout size is not a component in prey-choice models. Bout size and frequency are major tools in economizing resource utilization when patches

differ in consumption cost. The determinants of bout size have been the subject of many theories, ranging from the physiological satiety models of Smith and Gibbs (1979) to behavioral models such as the marginal value theorem (Charnov, 1976). It is increasingly clear

Table 1

Values of r^2 from the correlations of log relative acceptance of opportunities, bout frequency, bout size, and daily intake with measures of log relative profitability based on effort and on time for each rat in Experiment 1 and Experiment 2.

Feeding measure	Experiment 1			Experiment 2		
	Rat	Profitability basis		Rat	Profitability basis	
		Effort	Time		Effort	Time
Acceptance of opportunities	1	.68	.73	5	.43	.54
	2	.68	.92	6	.44	.61
	3	.57	.63	7	.33	.20
	4	.51	.74	8	.37	.50
Bout frequency	1	.73	.75	5	.41	.51
	2	.68	.91	6	.42	.60
	3	.58	.65	7	.46	.30
	4	.53	.75	8	.37	.45
Bout size (mL)	1	.94	1.00	5	.86	.87
	2	.81	.97	6	.42	.48
	3	.93	.99	7	.69	.73
	4	.86	.99	8	.75	.84
Daily intake (mL)	1	.94	.99	5	.86	.91
	2	.75	.95	6	.70	.89
	3	.89	.96	7	.70	.69
	4	.74	.92	8	.79	.91

that the sizes of meals or bouts of behavior depend on both economic and physiological consequences. Interestingly, the rate of return is a major parameter of many of the models, although it functions in different ways. The marginal value theorem, for example, deals with environments in which resources deplete with use, and the *changing* rate of return over a bout of patch use is the factor that determines the optimal time to end the bout. In the current study, there was no patch depletion (as is probably true for many natural water sources), and the rate of return was essentially constant across bouts; still, the rate of return appeared to be a critical variable in the rat's decision of when to end a bout.

Finally, this currency (return on time expended) and these rules for economical resource use have been shown to apply to food and water, resources that are consumed. If they truly represent a general law of resource use, they should also apply to other consumable resources, like nesting material. An interesting question is how these rules might transfer, and

what currency would be appropriate, to the choices among sources of commodities that are not explicitly consumed as they are used (e.g., nesting or leking sites, mates, and heat). Furthermore, if we could determine a currency common to multiple commodities or activities (McNamara & Houston, 1986), are there comparable "rules" directing choices among behavioral options? For example, how does an animal decide whether to eat, gather nesting material, or drink at any particular time?

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APPENDIX A

Drinking measures for individual rats in Experiment 2. Blank cells indicate rat did not receive the condition. See text for details.

10- vs. 20-lick sips										
Behavior	Rat	20-lick sip patch, 20-lick sip price						10-lick sip patch, 20-lick sip price		
		5	10	20	40	60	80	5	10	20
% opportunities accepted	5	92.9						92.1		
	6	92.1	93.4	96.3	58.7	32.0		90.0	90.5	97.1
	7	93.8	94.1	97.3	100.0	76.7	42.3	89.1	97.2	98.7
	8	97.5	100.0	100.0	98.1	89.8	73.9	87.2	90.7	100.0
Bouts per day	5	3.9						3.5		
	6	5.8	7.1	7.8	4.4	2.4		5.4	6.7	6.8
	7	6.0	6.4	7.1	6.9	5.6	3.0	5.7	7.0	7.7
	8	3.9	4.4	4.3	5.2	7.9	3.4	3.4	3.9	4.3
Sips per bout	5	67.8						81.7		
	6	45.7	32.8	25.0	10.6	7.0		61.0	60.6	73.0
	7	45.2	35.4	30.1	19.1	17.0	15.6	62.0	52.8	55.9
	8	32.7	25.6	22.2	14.2	8.6	8.8	50.3	43.1	44.1
Milliliters per bout	5	7.8						4.9		
	6	4.8	3.5	2.5	1.2	0.9		3.3	3.3	3.7
	7	5.4	4.6	3.8	2.3	2.0	1.5	3.8	3.4	3.6
	8	4.9	4.4	3.8	2.6	0.8	2.2	3.9	3.8	3.7
Sips per day	5	264.3						286.0		
	6	265.3	232.6	194.8	46.6	16.7		329.5	406.0	496.4
	7	271.4	226.8	213.6	132.1	95.4	46.9	353.2	369.8	430.6
	8	127.7	112.5	95.3	73.8	67.9	29.9	170.9	167.9	189.8
Milliliters per day	5	30.3						17.0		
	6	27.8	25.2	19.8	5.3	2.1		17.9	22.0	25.2
	7	32.3	29.3	26.9	15.9	11.1	4.6	21.9	23.9	27.4
	8	19.2	19.4	16.4	13.7	6.5	7.5	13.1	14.7	16.0
Consumption bar presses per minute	5	28.9						35.5		
	6	36.0	59.1	75.9	80.2	76.9		46.3	48.4	47.8
	7	36.0	57.6	80.6	85.1	91.6	90.0	46.6	48.8	48.1
	8	38.1	64.8	90.0	113.7	100.3	118.0	51.9	53.3	52.2
Sips per minute	5	5.0						6.1		
	6	6.2	4.7	2.8	1.1	0.6		7.6	7.7	7.5
	7	5.5	4.5	3.3	1.6	1.2	1.7	7.2	7.2	7.5
	8	6.7	6.1	3.5	2.3	1.3	1.0	9.4	9.7	9.8
Milliliters per bar press	5	0.023						0.012		
	6	0.022	0.011	0.005	0.003	0.002		0.011	0.011	0.010
	7	0.025	0.013	0.006	0.003	0.002	0.001	0.013	0.013	0.013
	8	0.030	0.017	0.009	0.005	0.002	0.003	0.015	0.018	0.017
Milliliters per minute	5	0.57						0.36		
	6	0.66	0.52	0.29	0.13	0.08		0.43	0.42	0.38
	7	0.67	0.58	0.41	0.19	0.14	0.16	0.45	0.46	0.47
	8	1.01	1.05	0.60	0.43	0.12	0.25	0.73	0.85	0.83

APPENDIX A

(Extended)

10- vs. 20-lick sips			10- vs. 40-lick sips							
10-lick sip patch, 20-lick sip price			40-lick sip patch, 40-lick sip price					10-lick sip patch, 40-lick sip price		
40	60	80	5	10	20	40	60	5	10	20
			85.1	89.3	91.2	81.8	63.6	88.2	85.0	85.5
98.7	97.2		84.5	94.8	90.6	95.8	27.5	85.0	83.6	90.9
95.9	97.1	100.0	96.7	97.2	100.0	100.0	43.4	100.0	97.3	100.0
100.0	96.6	98.1	92.7	94.6	100.0	100.0	100.0	94.7	94.3	85.7
			4.0	5.0	5.2	4.5	4.2	4.5	3.4	5.3
7.4	6.9		4.9	5.5	5.8	6.9	1.9	5.1	4.6	6.0
7.0	6.6	7.1	5.8	7.0	6.5	6.6	3.3	5.6	7.2	6.3
4.4	8.6	5.3	3.8	3.5	4.6	3.4	4.7	3.6	3.3	3.6
			27.5	32.6	12.4	3.2	2.1	54.0	57.1	52.5
93.5	112.8		22.3	19.9	15.3	8.3	3.3	55.0	51.5	54.4
83.3	102.2	122.1	28.8	22.8	11.7	3.5	3.5	57.0	54.1	62.6
51.6	88.2	54.0	19.4	18.5	13.8	10.9	8.3	50.5	49.5	46.3
			6.9	6.5	4.3	1.5	1.0	3.5	3.0	4.2
5.1	6.0		5.8	7.3	5.1	2.7	1.5	3.7	4.3	4.5
5.0	6.1	6.7	5.1	4.5	3.9	1.1	1.0	3.0	2.6	4.3
4.3	5.0	5.0	5.1	5.6	4.6	3.6	2.7	3.6	3.8	3.2
			109.9	162.9	64.7	14.2	8.8	242.8	194.0	278.2
692.1	778.3		109.2	109.5	88.6	57.2	6.3	280.7	237.0	326.2
582.8	674.5	866.8	167.2	159.6	76.0	22.8	11.4	319.3	389.4	394.5
227.0	758.8	286.3	73.7	64.7	63.4	37.0	39.0	181.8	163.2	166.8
			27.6	32.5	22.2	6.9	4.0	15.7	10.2	22.1
37.7	41.5		28.5	39.9	29.6	18.5	2.8	18.9	19.7	26.8
35.1	40.5	47.3	29.4	31.5	25.2	7.1	3.4	16.6	18.9	26.8
19.1	43.0	26.6	19.5	19.5	21.2	12.3	12.6	12.9	12.6	11.6
			21.0	31.4	36.2	39.5	33.3	34.1	33.7	31.9
47.2	46.0		25.5	45.2	62.2	82.6	65.8	47.0	49.3	47.6
51.5	51.9	52.4	22.5	38.2	52.9	71.7	64.1	42.9	44.2	48.1
52.0	50.3	51.1	31.4	47.9	73.9	102.0	110.2	52.9	57.0	53.1
			3.7	2.4	1.4	0.6	0.3	6.0	5.4	5.2
7.7	7.8		4.3	4.1	2.8	1.5	0.6	8.0	9.0	8.4
8.7	9.0	8.2	3.4	2.8	1.6	0.9	1.1	5.8	5.7	8.2
9.2	8.6	9.5	5.1	4.5	3.4	2.0	1.6	8.9	10.8	9.0
			0.052	0.021	0.017	0.012	0.007	0.013	0.011	0.016
0.011	0.011		0.053	0.035	0.017	0.008	0.005	0.014	0.018	0.016
0.012	0.012	0.011	0.036	0.020	0.017	0.008	0.005	0.010	0.010	0.013
0.017	0.013	0.019	0.053	0.031	0.017	0.009	0.005	0.014	0.016	0.014
			0.97	0.48	0.46	0.24	0.15	0.39	0.29	0.41
0.42	0.42		1.15	1.37	0.95	0.50	0.20	0.54	0.77	0.66
0.52	0.54	0.46	0.60	0.56	0.53	0.29	0.34	0.29	0.28	0.55
0.79	0.54	0.88	1.34	1.40	1.15	0.67	0.51	0.64	0.84	0.62

APPENDIX A

(Continued)

Behavior	Rat	10- vs. 40-lick sips		20- vs. 40-lick sips				
		10-lick sip patch, 40-lick sip price		40-lick sip patch, 40-lick sip price				
		40	60	5	10	20	40	60
% opportunities accepted	5	90.5	81.3	85.7	84.9	87.0	86.0	28.3
	6	94.1	92.0	84.7	85.1	93.0	90.0	43.5
	7	100.0	100.0	98.1	95.6	98.2	95.3	82.0
	8	96.2	95.9	92.1	100.0	100.0	100.0	97.3
Bouts per day	5	5.7	5.2	4.2	4.5	6.0	4.9	1.5
	6	6.4	6.9	5.0	5.7	6.6	6.3	3.0
	7	7.0	6.0	5.3	6.5	5.4	6.1	5.0
	8	5.0	4.7	3.5	4.2	3.8	3.6	3.6
Sips per bout	5	81.2	75.5	22.1	14.3	5.9	2.3	2.5
	6	61.4	76.2	20.8	16.6	15.1	10.4	7.3
	7	74.3	93.9	20.2	22.7	15.9	12.7	7.1
	8	49.5	52.9	19.0	17.6	15.0	10.9	8.1
Milliliters per bout	5	6.1	6.3	5.2	3.2	1.3	0.7	1.1
	6	4.8	5.7	5.1	3.9	3.0	2.1	1.3
	7	5.4	6.9	6.1	4.5	3.2	3.2	1.9
	8	4.2	4.2	5.0	4.8	4.0	3.4	2.7
Sips per day	5	462.7	392.8	92.9	64.2	35.6	11.1	3.7
	6	393.2	526.0	104.0	94.7	99.9	65.3	22.0
	7	520.2	563.1	107.0	147.3	86.1	77.7	35.3
	8	247.6	248.6	66.6	73.8	57.0	39.4	29.0
Milliliters per day	5	34.6	32.6	21.8	14.6	7.6	3.4	1.6
	6	30.7	39.5	25.6	22.0	20.1	13.3	4.0
	7	38.1	41.4	32.3	29.2	17.4	19.8	9.4
	8	20.9	19.8	17.5	20.1	15.2	12.2	9.6
Consumption bar presses per minute	5	30.3	30.5	20.3	28.9	36.5	44.4	38.7
	6	50.0	49.6	24.6	41.6	59.5	79.0	81.5
	7	48.0	48.6	22.1	39.8	56.3	72.8	76.4
	8	53.8	54.0	25.1	44.6	72.6	103.3	111.8
Sips per minute	5	4.9	5.1	3.2	1.5	1.1	0.7	0.4
	6	9.4	8.9	4.4	3.7	2.4	1.6	0.9
	7	8.1	7.6	3.3	2.5	1.8	1.2	0.8
	8	10.0	10.0	4.4	4.0	3.4	2.6	2.2
Milliliters per bar press	5	0.015	0.017	0.048	0.021	0.010	0.008	0.005
	6	0.016	0.015	0.049	0.024	0.010	0.005	0.003
	7	0.015	0.015	0.060	0.027	0.010	0.006	0.004
	8	0.017	0.016	0.053	0.029	0.013	0.008	0.006
Milliliters per minute	5	0.37	0.43	0.78	0.31	0.21	0.21	0.10
	6	0.74	0.67	1.09	0.91	0.50	0.32	0.17
	7	0.59	0.56	1.01	0.66	0.37	0.32	0.22
	8	0.84	0.80	1.18	1.21	0.92	0.82	0.73

APPENDIX A

(Extended, Continued)

20- vs. 40-lick sips										
40-lick sip patch, 40-lick sip price			20-lick sip patch, 40-lick sip price							
80	100	120	5	10	20	40	60	80	100	120
			90.0	93.8	90.6	93.4	79.1			
9.4			86.4	84.1	83.8	88.9	89.4	96.7		
65.2			98.1	81.3	93.7	96.7	97.2	98.6		
80.9	73.9	41.9	97.4	100.0	100.0	100.0	100.0	95.7	100.0	96.0
			4.5	4.5	5.8	5.7	5.3			
0.6			5.1	5.3	5.7	6.4	5.9	5.9		
4.5			5.2	6.5	5.9	5.9	6.9	7.0		
3.8	3.4	1.8	3.8	3.6	3.4	3.8	4.7	4.4	4.3	4.8
			40.5	37.9	47.0	39.4	49.9			
23.3			36.2	33.6	39.5	49.0	65.0	71.3		
4.0			35.1	36.5	64.7	45.2	44.2	49.0		
6.8	7.0	6.6	30.9	30.1	33.8	32.2	29.5	32.8	33.7	32.5
			5.1	4.0	4.5	5.9	7.0			
16.7			4.5	4.0	3.9	4.9	6.1	6.9		
1.1			5.0	3.7	5.9	5.8	5.9	6.6		
2.3	2.4	2.7	4.0	4.5	4.5	5.1	4.9	5.3	5.5	5.5
			182.3	170.5	272.4	224.6	264.7			
14.0			184.5	177.9	224.9	313.9	383.4	420.6		
17.9			182.5	237.5	382.0	266.8	305.3	342.9		
26.0	23.9	11.8	117.6	108.2	114.9	122.4	138.6	144.1	144.9	155.8
			22.8	18.1	26.2	33.8	37.0			
10.0			23.2	21.2	22.3	31.2	35.8	40.8		
4.9			26.0	24.2	35.0	34.5	40.9	46.4		
8.8	8.0	4.8	15.3	16.1	15.3	19.2	23.1	23.5	23.5	26.2
			26.9	24.7	27.0	27.6	27.6			
78.1			36.0	35.3	34.0	41.4	34.7	35.2		
73.0			34.7	34.0	37.1	36.4	37.8	37.7		
106.0	126.2	116.3	38.3	38.7	40.3	40.2	40.3	49.0	39.9	39.9
			4.2	4.0	4.6	4.7	5.0			
0.6			6.3	6.2	6.1	6.4	5.3	5.7		
0.5			5.1	5.5	5.9	5.4	6.0	5.9		
1.1	0.8	0.7	6.9	7.0	7.1	7.1	6.5	7.3	6.5	7.2
			0.025	0.021	0.021	0.030	0.029			
0.003			0.025	0.024	0.020	0.020	0.019	0.020		
0.003			0.028	0.028	0.020	0.026	0.027	0.027		
0.004	0.003	0.003	0.026	0.030	0.026	0.031	0.033	0.033	0.032	0.033
			0.52	0.42	0.48	0.72	0.71			
0.13			0.80	0.75	0.62	0.64	0.53	0.57		
0.14			0.72	0.76	0.59	0.69	0.80	0.81		
0.37	0.28	0.25	0.91	1.06	0.94	1.10	1.09	1.20	1.05	1.20

APPENDIX B

Drinking measures for individual rats in Experiment 1. See text for details.

Behavior	Rat	Sip price at each patch									
		5	5	5	10	5	20	5	40	5	80
% opportunities accepted	1	79.7	80.3	64.7	67.7	78.6	71.4	83.4	55.6	82.1	11.8
	2	90.1	88.9	92.8	93.8	85.8	81.3	87.6	32.1	92.5	2.1
	3	97.9	93.8	98.5	91.4	95.8	93.9	100.0	82.6	100.0	15.6
	4	95.0	95.6	100.4	90.9	95.3	97.7	93.3	93.0	98.6	22.9
Bouts per day	1	2.2	2.5	2.4	2.3	3.6	3.0	3.7	2.5	3.4	0.5
	2	4.8	5.0	5.2	5.6	5.7	5.2	5.2	2.1	5.7	0.1
	3	4.4	4.3	4.7	4.6	5.6	5.6	4.9	4.0	4.6	0.7
	4	3.6	4.1	4.1	3.8	4.1	4.2	3.8	4.1	4.8	1.2
Sips per bout	1	77.2	87.0	107.0	85.4	108.6	28.2	145.2	3.3	138.4	1.4
	2	40.4	42.5	52.4	34.2	60.7	23.3	78.3	12.9	76.2	0.6
	3	52.0	50.0	77.1	67.9	74.1	20.7	97.1	3.8	110.1	1.3
	4	43.0	38.3	42.4	40.0	49.1	28.9	51.5	21.3	52.4	6.8
Sips per day	1	172.7	219.6	252.1	193.9	389.5	83.6	530.0	8.1	465.6	0.7
	2	192.2	210.7	273.2	192.9	343.1	121.8	408.1	26.6	433.9	0.1
	3	230.1	216.9	365.3	310.9	411.5	116.1	470.9	15.1	510.4	0.9
	4	155.7	158.8	173.3	153.3	199.0	121.5	194.8	86.9	254.0	8.0
Milliliters per day	1	14.9	18.9	19.1	14.7	33.1	7.1	34.5	0.5	38.6	0.1
	2	18.4	20.2	20.7	14.6	24.5	8.7	36.4	2.4	35.6	0.0
	3	23.6	22.2	24.3	20.7	32.9	9.3	38.7	1.2	38.3	0.1
	4	14.9	15.2	15.5	13.7	19.3	11.8	17.5	7.8	24.9	0.8
Consumption bar presses per minute	1	26.6	26.7	30.8	45.7	29.4	52.4	26.0	34.9	27.2	36.2
	2	34.7	34.9	34.6	52.5	34.8	70.3	34.7	68.9	35.6	59.4
	3	34.2	34.3	45.5	45.3	36.2	63.7	36.7	63.1	35.2	60.4
	4	35.0	34.3	34.1	54.9	34.1	80.0	34.5	98.5	33.1	86.6
Sips per minute	1	4.6	4.7	5.1	3.6	4.6	1.7	4.2	0.4	4.3	0.2
	2	6.0	5.8	5.6	3.9	5.5	2.4	5.4	0.8	5.6	0.2
	3	5.4	5.2	5.1	5.3	6.1	2.1	5.8	0.7	5.5	0.3
	4	5.6	5.7	5.4	4.8	5.8	3.1	6.0	1.7	5.6	0.5
Milliliters per bar press	1	0.017	0.017	0.015	0.008	0.017	0.004	0.013	0.002	0.017	0.001
	2	0.019	0.019	0.015	0.008	0.014	0.004	0.018	0.002	0.016	0.001
	3	0.020	0.020	0.013	0.007	0.016	0.004	0.016	0.002	0.015	0.001
	4	0.019	0.019	0.018	0.009	0.019	0.005	0.018	0.002	0.020	0.001
Milliliters per minute	1	0.39	0.40	0.38	0.28	0.39	0.15	0.27	0.03	0.35	0.02
	2	0.57	0.55	0.42	0.29	0.39	0.17	0.48	0.07	0.46	0.01
	3	0.55	0.53	0.34	0.35	0.49	0.17	0.47	0.06	0.41	0.02
	4	0.54	0.55	0.48	0.42	0.56	0.30	0.54	0.15	0.55	0.04