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PATCH CHOICE AS A FUNCTION OF PROCUREMENT COST AND ENCOUNTER RATE

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The effects of patch encounter rate on patch choice and meal patterns were studied in rats foraging in a laboratory environment offering two patch types that were encountered sequentially and randomly. The cost of procuring access to one patch was greater than the other. Patches were either encountered equally often or the high-cost patch was encountered more frequently. As expected, rats exploited the low-cost patch on almost 100% of encounters and exploited the high-cost patch on a percentage of encounters that was inversely proportional to its cost. Meal size was the same at both patches. Surprisingly, when low-cost patches were rare, the rats did not increase their use of high-cost patches. This resulted in spending more time and energy searching for patches and a higher average cost per meal. The rats responded to this increased cost by reducing the frequency and increasing the size of meals at both patches and thereby limited total daily foraging cost and conserved total intake.

Key words: foraging, patch choice, bar press, procurement cost, meal patterns, food intake, rat

Choice has been one focus of interest in the literature on operant behavior, witnessed, for example, by the extensive literature generated by the matching law (Herrnstein, 1970) and the delay-reduction models (Fantino, 1985). These studies have used concurrent choice paradigms in open economies. In contrast, foraging theorists have presented models of successive choice (Schoener, 1971). Because food sources are usually clumped and distributed discontinuously, or patchily, an animal must forage to come into contact with food. As it forages, it may sequentially encounter food patches (or individual prey items within a patch), and it can either exploit an encountered patch or reject it and continue to search. This choice should be governed by two considerations: using time and effort efficiently and meeting intake requirements (Houston, Clark, McNamara, & Mangel, 1988; Schoener, 1971).

The problem of optimal choice was first elucidated by MacArthur and Pianka (1966) who considered two problems, *patch choice* or choosing which patches to exploit, and *item choice* or choosing among items of food within a single patch. Emlen (1966) developed a stochastic solution to the item choice problem. According to MacArthur, the optimal exploitation of items within a patch would be for the animal "to pursue an item if and only if, during the time the pursuit would take, it could not expect both to locate and to catch a better item" (MacArthur, 1972, p. 62). This solution was stated formally in the contingency model by a number of authors in terms of net energy gain per time spent in a bout of foraging (for reviews see Schoener, 1971, 1987) and was expanded formally to include patch choice (Schoener, 1974).

As with tests of the matching law and delay reduction, most empirical tests of the MacArthur and Pianka (1966) model have been done in open laboratory economies, that is, with deprived animals choosing among items of different value in experimenter-initiated short test sessions (Cassini, Kacelnik, & Segura, 1990; Fantino, 1985; Hanson, 1987; Krebs, Erichsen, Webber, & Charnov, 1977; Redhead & Tyler, 1988; see Krebs, Stephens, & Sutherland, 1983; Schoener, 1987; and Stephens & Krebs, 1986, for reviews). The economy in the session paradigm is open in the sense that the supply of the commodity is unrelated to the consumer's demand. No behavioral strategy of the animal can meet its requirements (Collier & Johnson, in press).

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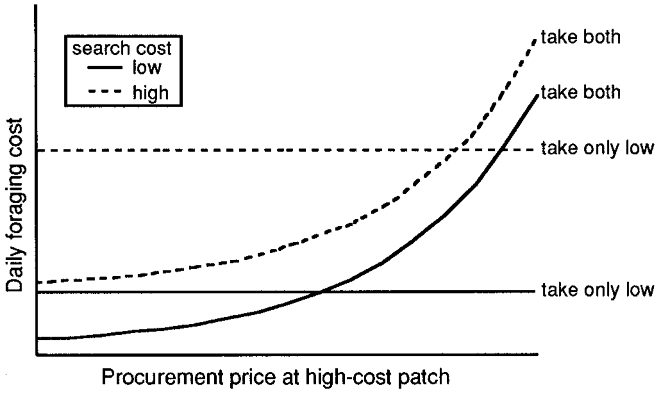

Fig. 1. Theoretical daily foraging costs at a low and a high search cost for a strategy of exploiting all encountered patches (take all) and for a strategy of exploiting only low-cost patches (take only low) as the procurement price at the high-cost patch increases (the low-cost price is fixed).

In contrast, we have tested this model in a closed economy in which the animal lives continuously, initiating and terminating feeding in any pattern to consume its daily intake. The supply of the commodity is equal to the consumer's demand and the animal can regulate (Collier & Johnson, in press). Briefly, there are two feeders (analogous to patches), each providing food at a fixed cost, and the animal presses a bar to search for a patch, to procure access to an encountered patch, and to consume items of food (e.g., 45-mg pellets) within a patch. Cost at each step (i.e., search cost, procurement cost, and consumption cost) is manipulated independently by the fixed-ratio (FR) requirement to complete that step. Each completion of the search FR produces an encounter with one of two food patches, chosen randomly, that differ only in procurement cost. The animal can procure access to the encountered patch by completing the procurement FR and then can exploit the patch (i.e., eat a meal) by repeated completions of the consumption FR, each of which causes a food pellet to be delivered. Alternatively, the animal can reject an encountered patch and search further (Collier, 1982; Collier & Johnson, 1990; Kaufman, 1979). Thus the animal searches for a random sequence of high- and low-cost food patches, and chooses which of those patches to exploit. As has been reported for freely feeding rats (Richter, 1927), in our paradigm daily food intake is divided into multiple meals that vary in size and intermeal interval, and foraging is primarily nocturnal, with about 70% of intake occurring in the dark.

In addition to the feeding economy, the current experiment differs from many others in these additional respects: Each search was initiated by the animal and search cost was constant, the patches contained the same food and were encountered either equally often (some conditions) or unequally often (other conditions), and the animal controlled the frequency of foraging and the size of meals. Only the costs of access to the two patches varied. The animal's decision was whether to pay the price to procure access to a patch it had encountered or to search further. These conditions satisfy the assumptions of the patch-choice model (Schoener, 1987).

The cost-minimizing pattern of patch use in our paradigm can be modeled by assuming a constant daily intake and considering the daily cost of feeding (i.e., the total number of instrumental responses necessary to provide the daily food requirement) as a function of the difference in the costs of access to the two patches. Because the cost of pellets is the same at both patches, daily pellet cost is unaffected by patch choice and can be ignored for this analysis. The foraging cost for each meal is the sum of the cost of the preceding search and the cost of procuring access to the accepted patch. Rejection of an encountered patch results in additional search responses. The daily cost is the cumulative cost of the meals taken. Figure 1 shows the hypothetical daily costs of feeding for two possible choice strategies, *take only low,* rejecting all high-cost patches and performing the extra searches necessary to exploit only low-cost patches, and *take both,* searching just once for each meal and exploiting whichever patch is encountered. As the cost difference between patches increases, the cost-minimizing strategy shifts from take both to take only low. The intersection shifts to the right if search cost increases.

Three predictions of this model are analogous to those of the item-choice model (Stephens & Krebs, 1986): (a) the low-cost patch should always be exploited; (b) the high-cost patch should either always or never be exploited, that is, the acceptance function should be a discontinuous step function of the cost difference between patches; and (c) the switch from acceptance to rejection of the high-cost patch should depend on the abundance of the low-cost, but not the high-cost, patch. This is because less abundant patches cost more to locate—they require more searches—and when low-cost patches are rare, a larger procurement cost difference between patches is required before it is cost effective to reject opportunities to eat in the high-cost patch. Two other predictions arise from the fact that the animal in our paradigm controls not only patch choice but also the frequency of patch exploitation (i.e., meal frequency) and the amount consumed on each occasion (meal size), and these decisions affect the daily cost. Therefore, as the average cost of meals increases, either because the access cost for one or both patches increases or because the search cost increases, animals should eat fewer meals because this will save foraging costs. And, because freely feeding animals tend to maintain a constant daily intake, the size of meals should increase compensatorily (Collier & Johnson, 1990).

We have found (Collier, 1982) that, as expected, animals exploit low-cost patches nearly 100% of the time they are encountered. In agreement with other tests of the model, however, we have not found support for the prediction of a discontinuous acceptance function for high-cost patches. Rather, the acceptance of the high-cost patches is a monotonic, decreasing function of their cost. Various accounts of these *partial preferences* have been given (Houston et al., 1988; Schoener, 1987; Stephens & Krebs, 1986), but none account for the regular decline in acceptance as a function of cost. We did confirm the prediction that the transition from acceptance to rejection of the high-cost patch should be a function of the abundance of the low-cost patch. Increasing the search cost in our paradigm (simulating an equal decrease in the abundance of both patches) did increase acceptance of high-cost patches (Collier & Rovee-Collier, 1981; Kaufman, 1979).

One of the variables that affected foraging cost in our simulations, but not in traditionally modeled prey-choice paradigms, is meal size. Once an animal decides to eat in a particular patch, it also must decide how much to eat on that occasion. This amount may vary as a function of the cost of access (Collier & Johnson, 1990) and, if the patch depletes, as a function of the rate of depletion (Charnov, 1976; Johnson, Triblehorn, & Collier, 1995). This decision can have a dramatic effect on the overall foraging cost and on the cost-minimizing strategy of patch choice. For example, meals could be proportionally larger in the patch with the higher procurement cost so that the benefit:cost ratio would be equal in low- and high-cost patches. In that case, accepting all opportunities to eat in both patches would be the best strategy. However, rats do not use this option; rather, they eat meals of the same size at both the high- and low-cost patches (Collier & Johnson, 1990). Meal size is not fixed, however, but varies with the average procurement cost of the two patches. Thus, meals at both patches are larger (and less frequent) when the average cost is high. These results support our additional predictions, stated above, about meal frequency and size.

In the current experiment we further examined the effects of patch abundance on the meal patterns of laboratory rats choosing between two available patches that differed in procurement cost. The patches were either equally abundant or the low-cost patch was less abundant than the high-cost patch (cf. Hanson & Green, 1989). We expected that acceptance of opportunities to eat in the high-cost patch would (a) decrease gradually as the access cost difference increased and (b) be greater when low-cost patches were rare. We further determined how the meal frequency and meal sizes exhibited by the rats contributed to a cost-effective feeding strategy.

METHOD

Subjects

Six naive 50-day-old male Sprague-Dawley derived rats, obtained from Camm Research, were used. They were marked with black ink at the base of the tail for identification.

Apparatus

The experimental chambers were located in a room that was maintained at 22 ± 2 °C with lights on from 8:00 a.m. to 8:00 p.m. Each stainless steel cage measured 43 cm by 25 cm by 17.5 cm and was equipped with two T-shaped response bars and four 1.3-cm cuelights. Both bars extended 3 cm into the cage, and a response required 0.35 N applied through a throw of 1 cm. One bar (the search bar), 3.5 cm above the floor, and light (the search light), 4 cm above the bar, were located in the center of one end wall of the cage. At the opposite end of the cage, the food bar was located in the same position. One light (the meal light) was mounted 4 cm above the bar, and two other lights (the patch lights) were mounted 6 cm to each side of the bar. A pellet dispenser (BCS) delivered 45-mg pellets (rodent chow formula, BioServ) to a cup on the floor under the bar. Water was freely available from a drinking tube mounted on the side of the cage. Each cage was equipped with a running wheel (Wahmann) and a black acrylic nest box.

Procedure

The rats were housed continuously in the experimental apparatus except for a maintenance period of about 1 hr each day. During this time the rats were weighed and placed together in a holding cage, the data were recorded, the food and water were replenished, the apparatus was cleaned and tested, and any changes in the contingencies (costs) were made. If foraging was in progress at the beginning of maintenance, the rat received credit for those responses when it was returned to its cage.

The cages operated as follows: The search light was on during intermeal intervals, and the rat could initiate a search at any time by completing five bar presses on the search bar. This caused the search light to go out and one of the patch lights at the other end of the cage to come on, indicating which of two food patches had been encountered. The rat could accept or reject this meal opportunity. The rat accepted an opportunity by completing a fixed number of responses, the procurement price, on the food bar. This caused the meal light to come on, indicating that further responses on the food bar would earn pellets; each pellet cost 10 bar presses. The meal continued until 10 consecutive minutes passed without a response on the food bar. At that time the patch and meal lights were extinguished and the apparatus reverted to the search mode. Alternatively, a meal opportunity was rejected if the rat made no response on the food bar for 1 min after completing search (passive rejection) or, having made at least one response on the food bar but not completing the procurement price, pressed the search bar three times (active rejection). After a rejection, the patch light went out and the search mode was resumed. There was no time limit on the completion of a search or procurement FR; that is, once the rat made one search or procurement response, it could pause for any length of time between responses. This resulted in search and procurement times that varied from less than a minute to (occasionally) hours.

Initial training. We adapted the rats to their cages and the response contingencies over a period of about 3 weeks. During this training phase, we changed the contingencies only when the rat had gained weight from the previous day. First, during magazine training, both bars were removed and a surfeit of pellets was delivered automatically over the day and night. Then the food bar was installed, the meal light was continuously illuminated, and each response delivered a pellet. The pellet price was increased to two, five, and 10 bar presses. Then the procurement contingency was added: At the end of each meal, the meal light went out and one of the patch lights, chosen randomly, was turned on. When the rat completed the procurement price, the meal light also came on and pellets could be earned. The procurement price (equal at the right and left patches) was initially five, and then it was increased to 10. The search bar was then installed with a search cost of one response; the rejection options were not available. The search cost was increased to two and then to five, and then the rejection options were added. No shaping for any of these contingencies was required.

Experimental conditions. During the experiment, the procurement price at one patch, the low-cost patch, was always 10 bar presses. The price at the other, high-cost, patch was 10, 40, 80, 160, or 320 bar presses. The high prices were presented first in increasing order and then in a random order. Each price was in effect for 10 days (or sometimes more due to occasional equipment failures). The right-left location of the low- and high-cost patches was alternated with each new price condition.

For 3 rats the probability of encountering a low-cost and a high-cost patch was equal at .5. This was called the 50/50 encounter condition. For the other 3 rats, low-cost patches were rarer: The probability of encountering a low-cost patch was .2, and the probability of encountering a high-cost patch was .8. This was called the 20/80 encounter condition. In each case, the patch that became available after a search was chosen randomly, with the provision that these probabilities were satisfied over each 10-meal frame. After receiving all price conditions with these encounter conditions, each rat was switched to the other encounter condition and the price conditions were repeated. Thus, all rats received all conditions.

Data analysis. Data from the last 7 days of each condition were analyzed. For each rat in each condition, we calculated the mean body weight, the daily food intake, the encounter and meal frequencies at each patch, and the meal size at each patch. There were no statistically significant differences in the data from the two exposures (ascending and random) to the high prices, and they were combined in the analysis presented here. Effects of patch type (low cost, high cost), encounter probability (50/50, 20/80) and high-cost patch price (10, 40, 80, 160, 320) were analyzed with repeated measures analyses of variance with alpha = 0.05. In general, data are shown as means in the figures, and the individual rats' data are presented in the Appendix.

RESULTS

The rats accepted nearly 100% of meal opportunities at the low-cost patch in all conditions (Figure 2). Acceptance of high-cost opportunities decreased as a function of the price in both the 50/50 and the 20/80 encounter conditions, $F(5, 25) = 41.36$, $p < .01$. Although some rats did shift abruptly from accepting nearly all to accepting almost no high-cost opportunities in either the 50/50 (4 rats) or 20/80 (1 rat) conditions, there was no consistency to this result, and no rat showed a step function in both conditions. There was no effect of encounter probability on the acceptance of high-cost opportunities, $F(1, 5) = 0.06$, $p > .05$.

Because the high-cost patch was encountered more often in the 20/80 conditions, the actual number of rejections (Figure 3) was greater in the 20/80 conditions than in the 50/50 conditions, $F(1, 5) = 8.89$, $p < .05$. The type of rejection, passive or active, varied among individuals: All rats used both the passive and active rejection options, but active rejections predominated (60% to 80% of rejections) for 3 rats, passive rejections predominated (70% to 75% of rejections) for 1 rat, and 2 rats showed equal proportions of passive and active rejections. The frequency of searching was related to the number of rejections: The rats searched more often as the price of the high-cost patch increased, $F(5, 25) = 10.36$, $p < .01$, and slightly, but not significantly, more often in the 20/80 conditions than in the 50/50 conditions, $F(1, 5) = 2.56$, $p > .05$ (Figure 4).

Meal frequency at each patch is shown in Figure 5. The rejection of opportunities at the high-cost patch as its price increased resulted in a decrease in the number of meals eaten (i.e., number of accepted opportunities) at that patch. Concurrently, the number of meals at the low-cost patch increased: Patch × Price interaction, $F(5, 25) = 22.13$, $p < .01$. These changes were not compensatory, however, and the total number of meals per day decreased as the high price increased, $F(5, 25) = 19.61$, $p < .01$. Meal frequency was also a function of the relative encounter rate: The rats ate fewer meals in the 20/80 conditions than in the 50/50 conditions, $F(1, 5) = 28.52$, $p < .01$. Within each condition, meals were the same size at the

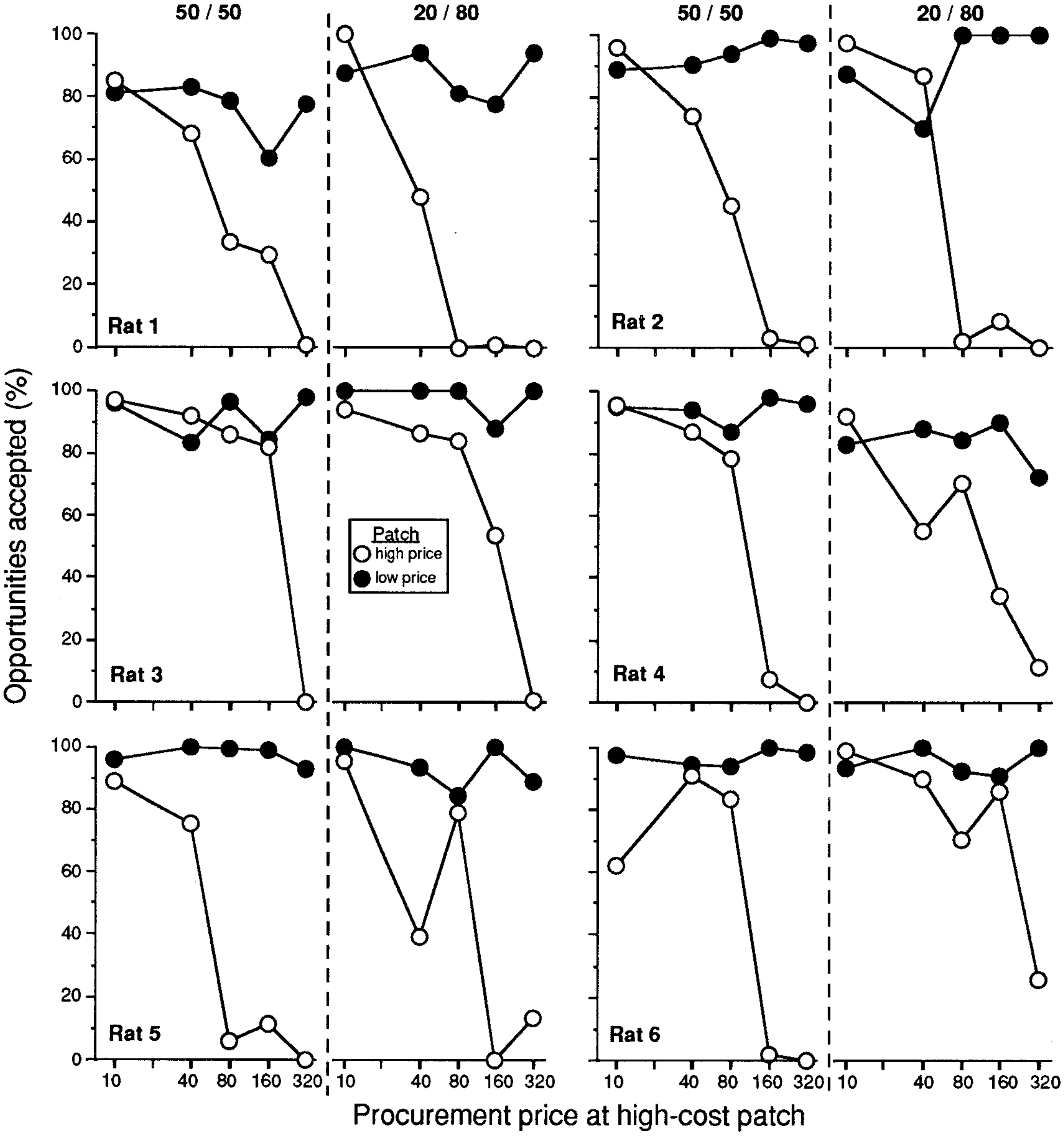

Fig. 2. Percentage of meal opportunities accepted at the low-cost (procurement price = 10) and high-cost patches as a function of the procurement price at the high-cost patch when the patches were encountered equally often (50/50, left) and when the low-cost patch was encountered only 20% of the time (20/80, right).

low- and high-cost patches (Figure 6), and as meal frequency declined with high price, meal size increased at both patches, $F(5, 25) = 7.06$, $p < .01$. Meals were larger in the 20/80 conditions than in the 50/50 conditions, $F(1, 5) = 46.85$, $p < .01$.

These meal patterns resulted in a differential intake from the two patches (Figure 7). In both encounter conditions, intake decreased at the high-cost patch and increased at the low-cost patch as the high price increased: Patch × High-Price interaction, $F(5, 25) = 15.24$, $p < .01$. In the 50/50 encounter conditions, more food was eaten at the low-cost patch, and the difference increased with increasing high price. In contrast, in the 20/80 encounter conditions, more food was eaten initially at the more frequently encountered high-cost patch; but then, with increasing high price, intake decreased at the high-

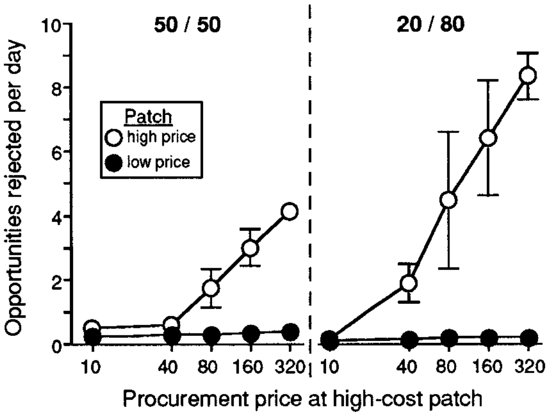

Fig. 3. Mean (±*SE*) number of meal opportunities rejected at the low-cost (procurement price = 10) and high-cost patches as a function of the procurement price at the high-cost patch when the patches were encountered equally often (50/50, left) and when the low-cost patch was encountered only 20% of the time (20/80, right).

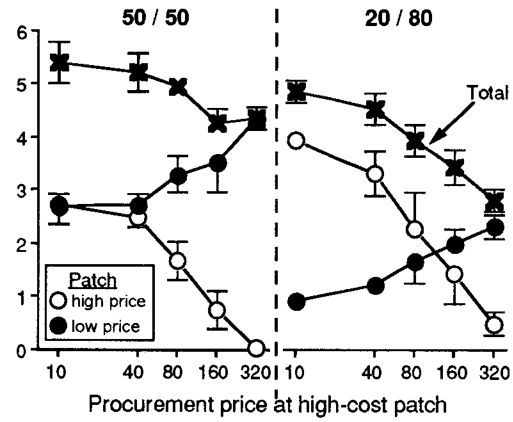

Fig. 5. Mean (±*SE*) daily meal frequency at the low-cost (procurement price = 10) and high-cost patches as a function of the procurement price at the high-cost patch when the patches were encountered equally often (50/50, left) and when the low-cost patch was encountered only 20% of the time (20/80, right).

cost patch and increased at the low-cost patch until more was consumed at the low-cost patch: Patch × Encounter Rate interaction, $F(1, 5) = 10.56$, $p < .01$. Overall, the total daily food intake was unaffected by condition, and the rats maintained a constant or increasing body weight throughout the experiment.

DISCUSSION

In this simplified laboratory paradigm, three foraging decisions were made by the rat: how often to search, whether to accept or reject an encountered patch, and how much to consume in each meal. The rats' behavior was orderly, but conformed to the optimal choice model of MacArthur and Pianka (1966) in only some respects. The rats exploited nearly 100% of opportunities to consume meals in the low-cost patch. Rather than following the optimal strategy for exploiting the high-cost patch, however, they often accepted high-cost patch opportunities in de-

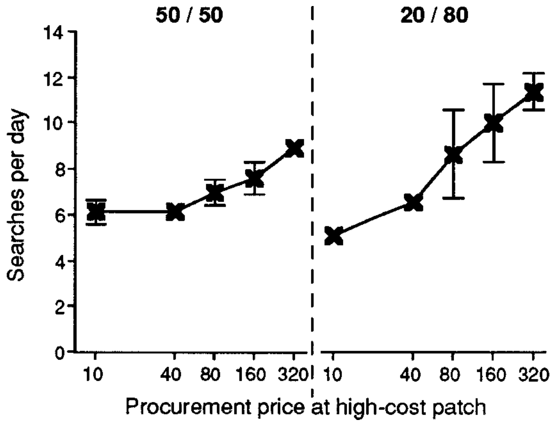

Fig. 4. Mean (±*SE*) daily search frequency as a function of the procurement price at the high-cost patch when the patches were encountered equally often (50/50, left) and when the low-cost patch was encountered only 20% of the time (20/80, right).

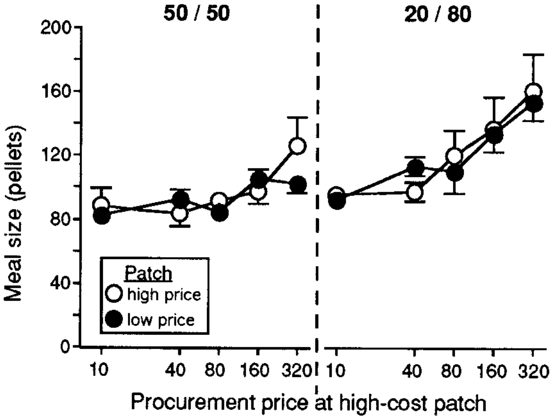

Fig. 6. Mean (±*SE*) meal size at the low-cost (procurement price = 10) and high-cost patches as a function of the procurement price at the high-cost patch when the patches were encountered equally often (50/50, left) and when the low-cost patch was encountered only 20% of the time (20/80, right).

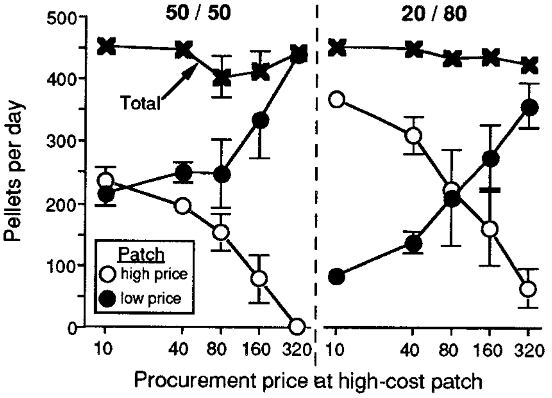

Fig. 7. Mean (±*SE*) daily intake at the low-cost (procurement price = 10) and high-cost patches as a function of the procurement price at the high-cost patch when the patches were encountered equally often (50/50, left) and when the low-cost patch was encountered only 20% of the time (20/80, right).

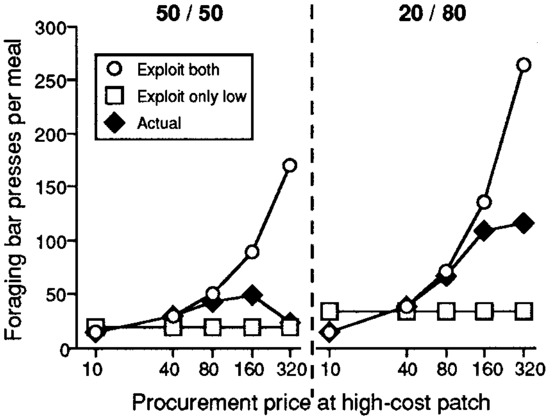

Fig. 8. Foraging cost per meal for two theoretical patch-choice strategies—exploit all patches or reject all high-cost patches—and for the actual strategy used by the rats.

creasing proportion to their price, although the individual functions were variable and sometimes approached the theoretically optimal discontinuous functions. Surprisingly, the relative encounter rate did not affect this decision. When the relative abundance of the low-cost patches was reduced, the animals did not increase their exploitation of high-cost patches, even though this meant that they rejected a greater number of high-cost patch opportunities. This result challenges a simple version of the delay-reduction hypothesis (Fantino, 1985) in that the rejections generally increased the time to reinforcement. We did not directly test the predictions of a delay-of-reinforcement model (Mazur & Vaughan, 1987) because the times taken to search, reject, and procure were too variable within rats in our laboratory foraging simulation.

The rats were efficient in that their total cost was lower than if they had foraged randomly, but they failed to minimize daily food cost. Because meal size was the same at both available patches, the cost-minimizing pattern of patch use is described by optimality models (MacArthur & Pianka, 1966; Schoener, 1987) that compare the costs of two strategies: take both patch types versus take only low-cost patches. We have calculated the number of foraging (search and procurement) bar presses required per meal by each of these strategies in each condition in this study (Figure 8). A cost-minimizing rat would have switched from the take-both to the take-only-low strategy when the high cost was 40 in the 50/50 conditions and when the high cost was 80 in the 20/80 conditions. Instead, the rats here reduced acceptance of the high-cost patch as its price increased, and their actual foraging costs were intermediate between the costs of the theoretical strategies.

We would note that the ratio of acceptance at the two patches in this study was related to the ratio of patch-access costs in a manner that is reminiscent of the matching law (Herrnstein, 1970). If the rate of reinforcement differs at two levers, the ratio of the response rates on the levers during an experimental session is a linear function of the ratio of reinforcement rates. Why this relationship should also appear in the very different patch-choice situation is not obvious. We do not wish to argue the relative merits of matching and optimizing because they have been discussed elsewhere (Herrnstein & Loveland, 1975; Houston, 1983), and we believe matching describes, rather than explains, these data. However, it is important to realize that a matching-type relation may suggest a fundamentally different choice process or mechanism than one that would produce a cost-minimizing result.

The failure of the abundance of low-cost patches to influence the acceptance of high-cost patches was surprising. Most tests of this prediction of the item-choice model have at least qualitatively confirmed the model (Stephens & Krebs, 1986). The current results may differ from these for at least two reasons. The difference in search costs between encounter conditions may not have been large enough to produce a detectable difference in acceptance. Note that the optimal point to switch from accepting to rejecting high-cost patches does not move far to the right in the 20/80 conditions compared to the 50/50 conditions (Figure 8). That is, for both encounter conditions, it is not until the high price of 80 that the difference in cost is solidly in favor of rejecting high-cost opportunities. A second hypothesis is that a search bar press may not be equivalent to a procurement bar press in the rat's evaluation of costs. This could markedly alter the cost comparison between expending procurement responses to procure access to a high-cost patch and expending search responses to find a low-cost patch.

The gradual, rather than discontinuous, decrease in acceptance of patches or items as price increases, commonly called partial preferences, has been found in a number of studies, and has been interpreted in various ways (reviewed in Stephens & Krebs, 1986). We have reported a similar decrease in meal frequency by animals foraging in an environment that offers only a single patch: The frequency of initiating meals declines monotonically as the log procurement price increases (see Collier & Johnson, 1990, for a review). This suggests again that search responses and procurement responses may be unequal in the rat's cost metric, and that in our patch-choice situation the rat does not weight the search cost resulting from rejecting a patch as highly as the cost of procuring access to an encountered patch.

The rats did reduce daily foraging cost by employing a third tactic: decreasing meal frequency and increasing meal size as the overall cost of foraging increased, either with the price of the high-cost patches or with the decreased abundance of low-cost patches. Meal frequency declined as the procurement cost increased at the high-cost patch, and at all patch costs the rats ate fewer meals in the 20/80 conditions than in the 50/50 conditions. The effectiveness of this change can be seen in Figure 9, which shows the rats' actual daily foraging bar presses compared to those that would have been expended if they had made choices as they did but had eaten a constant 5.5 meals per day (the meal frequency shown in the 50/50 conditions at a high procurement price of 10). Adjustments in meal frequency and meal size thus can be important elements in an animal's overall foraging strategy; these variables are not included in most optimality models (see Collier & Johnson, 1990).

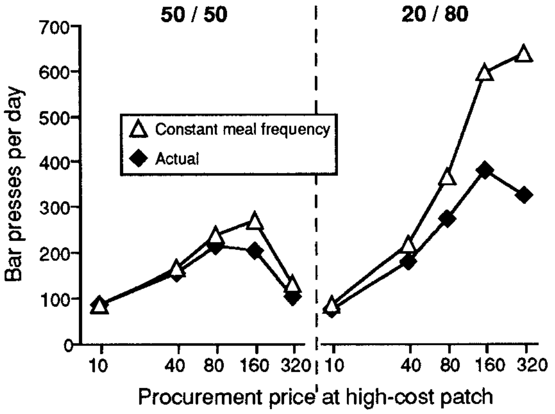

Fig. 9. Foraging cost per day for the patch-choice strategy used by the rats to eat 5.5 meals per day (constant meal frequency) or to eat the number of meals the rats actually ate.

Finally, it should be noted that rats' patch-choice decisions and meal patterns when patches differ in procurement cost, as in the present study, are not the same as those when patches differ instead in consumption cost (e.g., the price of pellets within a meal). Although rats do eat more meals in patches in which consumption cost is relatively low, they also eat larger meals in those patches, and in fact, meal size is the primary factor producing a greater daily intake in lower-consumption-cost patches (Collier, Johnson, Borin, & Mathis, 1994; Johnson & Collier, 1987, 1989, 1991). The reason for these differences is not immediately apparent, but they are another indication that costs that arise in different portions of the chain of behavior that leads to ingestion have differential and independent effects on the pattern of intake.

A striking feature of these data is that under all combinations of prices and encounter rates, the rats maintained a constant daily food intake. Although the initiation and termination of meals are functions in part of patch encounter rates and costs, the particular combination of meal frequency and size chosen by an animal also provides a particular amount of food. This long-range outcome appears to be relatively invariant with respect to alterations in foraging costs, at least in our laboratory simulations.

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APPENDIX

Behavioral measures for the individual rats in each condition.

			Encounter probability (low-cost patch/high-cost patch)									
			50/50					20/80				
			Price at high-cost patch									
		Rat	10	40	80	160	320	10	40	80	160	320
Searches per day		1	5.8	6.1	7.8	7.8	9.7	4.3	6.4	16.8	16.7	14.5
		2	6.4	7.3	7.6	7.6	9.3	4.8	6.3	12.0	11.9	10.6
		3	5.4	4.8	5.4	4.7	6.9	5.1	5.5	4.9	6.5	11.9
		4	4.2	6.4	5.9	8.3	8.8	5.6	7.9	6.2	9.4	11.5
		5	7.3	5.5	9.1	7.2	9.1	5.0	7.4	5.1	10.3	8.5
		6	7.7	6.7	6.2	10.0	9.6	5.9	6.0	6.8	5.6	11.3
Rejects per day	High-cost patch	1	0.6	1.2	2.6	2.8	4.7	0.0	2.5	13.1	13.0	11.1
		2	0.2	1.0	2.4	3.5	4.5	0.1	0.7	8.9	8.7	8.2
		3	0.1	0.2	0.4	0.5	2.9	0.3	0.6	0.7	2.8	9.4
		4	0.1	0.3	0.6	3.8	4.2	0.4	3.5	1.7	5.6	8.0
		5	0.6	0.6	4.0	2.8	4.2	0.2	3.6	0.8	7.8	5.8
		6	1.4	0.3	0.5	4.6	4.4	0.1	0.6	1.9	0.7	7.6
Rejects per day	Low-cost patch	1	0.6	0.6	0.8	1.5	1.3	0.1	0.1	0.7	0.8	0.2
		2	0.3	0.4	0.2	0.1	0.2	0.1	0.3	0.0	0.0	0.0
		3	0.1	0.4	0.1	0.3	0.1	0.0	0.0	0.0	0.2	0.0
		4	0.1	0.3	0.4	0.1	0.2	0.2	0.3	0.2	0.2	0.9
		5	0.2	0.0	0.1	0.1	0.5	0.0	0.1	0.2	0.0	0.2
		6	0.1	0.2	0.2	0.0	0.1	0.1	0.0	0.1	0.1	0.0
Meals per day	High-cost patch	1	2.6	2.0	1.3	1.3	0.1	3.5	2.3	0.0	0.1	0.0
		2	3.3	2.6	1.4	0.1	0.1	3.9	4.6	0.2	0.8	0.0
		3	3.0	2.2	2.4	2.3	0.0	3.9	3.6	3.4	2.4	0.1
		4	2.1	3.1	2.2	0.3	0.0	4.0	2.7	3.4	1.8	0.7
		5	3.1	2.1	0.3	0.5	0.0	3.9	2.3	3.0	0.0	0.9
		6	2.3	3.0	2.5	0.1	0.0	4.5	4.5	3.6	3.6	1.3
Meals per day	Low-cost patch	1	2.1	2.4	3.2	2.3	3.7	0.7	1.5	3.0	2.8	3.2
		2	2.7	3.3	3.6	3.9	4.6	0.7	0.7	2.9	2.4	2.4
		3	2.2	2.0	2.5	1.6	3.9	1.0	1.3	0.9	1.2	2.5
		4	1.9	2.7	2.7	4.1	4.4	1.0	1.5	0.9	1.9	1.9
		5	3.5	2.8	4.8	3.9	4.5	0.9	1.4	1.1	2.5	1.6
		6	3.9	3.2	3.0	5.3	5.1	1.3	1.0	1.3	1.2	2.4
Meals per day	Total	1	4.6	4.4	4.5	3.6	3.7	4.2	3.8	3.0	2.9	3.2
		2	5.9	5.9	5.0	4.0	4.7	4.6	5.3	3.1	3.2	2.4
		3	5.2	4.2	4.9	3.9	3.9	4.9	4.9	4.3	3.6	2.5
		4	4.0	5.8	4.9	4.4	4.4	5.0	4.2	4.3	3.7	2.6
		5	6.5	4.9	5.1	4.4	4.5	4.8	3.7	4.1	2.5	2.5
		6	6.2	6.2	5.5	5.4	5.1	5.8	5.4	4.9	4.8	3.7
Pellets per meal	High-cost patch	1	111.5	108.4	86.7	129.0	211.0	110.0	118.5		235.0	
	patch	2	81.6	67.9	97.1	95.0	87.0	95.3	85.5	182.5	130.5	
		3	88.0	94.7	93.3	105.9		93.1	90.3	97.7	138.7	111.0
		4	125.7	72.9	95.5	82.3		88.9	90.7	103.2	112.5	144.8
		5	67.1	92.1	95.4	94.7		104.9	107.7	100.8		161.1
		6	60.0	62.7	81.4	76.0		78.0	89.9	91.6	97.4	131.4
Pellets per meal	Low-cost patch	1	100.9	109.5	99.5	131.2	113.6	97.4	118.6	148.4	129.9	141.6
		2	81.9	86.3	84.5	110.4	97.0	84.3	127.4	157.6	133.4	166.9
		3	70.3	105.5	88.0	102.4	128.3	107.5	106.9	88.0	137.3	187.9
		4	93.4	72.4	88.4	96.6	91.5	89.7	105.8	108.0	116.3	155.0
		5	73.0	100.7	86.3	102.3	99.7	91.6	127.8	78.5	183.4	160.6
		6	78.3	80.6	63.8	92.8	86.6	82.3	94.1	83.8	105.5	110.4
Pellets per day	High-cost patch	1	284.6	198.7	133.9	138.3	10.6	384.9	272.5	0.0	23.5	0.0
	patch	2	262.5	175.7	131.1	9.5	4.4	371.8	393.3	36.5	104.4	0.0
		3	264.0	208.4	223.9	243.6	0.0	350.9	323.5	328.4	310.5	5.6
		4	264.0	226.0	210.2	24.7	0.0	347.0	229.9	340.7	174.7	79.7
		5	204.3	186.6	23.9	48.8	0.0	409.0	247.8	302.3	0.0	145.0
		6	138.0	188.2	203.6	7.6	0.0	344.7	400.1	329.6	350.7	164.3

APPENDIX

(*Continued*)

			Encounter probability (low-cost patch/high-cost patch)									
			50/50					20/80				
			Price at high-cost patch									
		Rat	10	40	80	160	320	10	40	80	160	320
Pellets per day	Low-cost patch	1	204.7	275.7	318.0	131.4	413.9	68.2	177.9	445.1	363.6	453.1
		2	211.8	284.8	313.2	430.6	442.2	59.0	89.2	457.0	320.1	400.6
		3	154.6	211.0	22.0	163.9	500.4	106.8	137.1	78.6	160.0	459.8
		4	177.5	195.4	238.6	396.2	402.4	89.4	169.3	97.2	234.5	302.5
		5	250.1	277.8	413.7	397.5	440.5	82.4	178.9	86.3	458.5	256.9
		6	305.3	257.8	191.5	491.7	441.8	106.9	87.3	103.6	127.3	283.4
Pellets per day	Total	1	489.3	474.4	451.9	269.7	424.5	453.1	450.4	445.1	387.1	453.1
		2	474.3	460.5	444.2	440.1	446.5	430.8	482.5	493.5	424.5	400.6
		3	418.6	419.4	245.9	407.5	500.4	457.6	460.6	407.0	470.5	465.3
		4	441.5	421.4	448.8	420.9	402.4	436.4	399.2	437.8	409.1	382.1
		5	454.4	464.4	437.6	446.3	440.5	491.4	426.7	388.6	458.5	401.9
		6	443.3	446.0	395.1	499.3	441.8	451.6	487.4	433.2	478.0	447.6