Evaluating the Value of Cage Enrichments using a Foraging Model

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Abstract

I investigated if a foraging model used in ecology could be employed in evaluating rat preferences for features believed to enrich their housing. The foraging model used in the following experiments was Brown's modified version of Charnov's Marginal Value Theorem: harvest rate (H) = predation (P) + metabolic cost (C) + missed opportunity cost (MOC). Several ecologists have used this equation to show that animals will leave foraging patches at different Hs depending on the values of P and C. The following experiments attempted to employ this approach by using H to evaluate cage features shown by previous experiments to provide benefits to rats. The rats were provided with two foraging patches – one being their home cage with standard food and the other being a highly attractive food patch. Home cages were enriched, with either conspecifics or shelter, or not enriched using a cross-over design. It was expected that the H values for the enriched and not enriched conditions would give a relative valuation of the enrichment items. In contrast to what was predicted, neither enrichments of social contact nor a very sheltered environment produced H values that suggested they were of more value to the animal than the control. I conclude that the method, as employed in this experiment, is not a suitable measure of rat preference for environmental enrichment.

Introduction

Marian Dawkins (1990) suggested that understanding animals' preferences is an important component of understanding animal welfare. According to Dawkins (1990), these preferences give observers the initial indication of how an animal views its world. Preference testing – allowing animals to choose between different options or environments – has been used in welfare experiments since Hughes and Black (1973) offered chickens choices between different flooring materials to evaluate the recommendations of the Brambell Committee. Preference testing has since been used to indicate the value of many different housing features presented to animals. Options have included access to increased space (Dawkins 1977; Baumans et al., 1987; Patterson-Kane, 2002), availability of nesting materials or shelters (Buhot-Aversang, 1981; Manser et al., 1998ab), social companionship (Matthews and Ladewig, 1994; Sherwin and Nicol, 1996) and avoidance of unpleasant techniques of restraint (Rushen, 1986).

On common method of testing preference is via choice tests, such as dwelling-time measures and T-maze tests. Manser et al. (1998a), for example, used dwelling time to determine the preferences of rats for nest-boxes and nesting materials and Bradshaw and Poling (1991) used t-mazes to assess rat preferences for cages enriched with pipes, platforms, wood chips and paper towels.

The main limitations of these tests are that dwelling time procedures may require large numbers of animals to achieve statistical significance depending on the variability of the results (Blom et al., 1993) and T-maze experiments may require a large number of pair-wise comparisons to rank the relative preferences of a number of items. As well, choice tests are only a relative measure and, therefore, may not differentiate between strong and weak preferences (Manser et al., 1998b). Furthermore, because these tests are relative, they cannot determine whether the animal perceives the given options as aversive or appetitive (Jensen and Sandoe, 1997).

In order to address these difficulties, two alternate approaches were developed: economic demand and gold standard experiments. Economic demand experiments measure the amount of effort, for example, the amount of weight on a weighted door the animal is willing to lift in order to reach what is on the other side of the door. Gold standard experiments measure the amount an animal will "pay" in terms of a standard commodity, such as food, in order to gain access to a particular item or environment.

In economic demand experiments the subjective value of an item or the environment is quantified as the maximum amount of work the animal will perform to gain access to or avoid it. This provides data that is ratio level; because the data is numerical, such as amount of weight lifted, the value of one item can be compared to the value of another on a ratio scale. Manser et al. (1998b) employed this type of experiment to re-evaluate their earlier findings that suggested rats preferred nest-boxes and nesting materials over empty cages. They found that rats would lift 327.5 g to reach an alternate cage with a nest-box and 290 g to reach an alternate cage with nestpaper, whereas they would only lift 150 g to reach another empty cage. These values give an indication of the relative value of these two enrichment items compared to an empty cage, whereas the previous choice tests only suggest that animals would choose each commodity over an empty cage.

Despite the fact that demand experiments can provide a ranking system for various commodities, this ranking is not absolute because of the difficulty in differentiating what portion of an animal's response is due to demand and what is due to confounds. For example, the method of reward delivery can directly influence demand. Using number of lever presses as a measure of preference, Sorenson (2001), found that rats did not have a preference for social contact when the companion was held behind a wire mesh. In contrast, Patterson-Kane et al. (2002) found a substantial preference for social contact when rats were allowed five minutes of direct contact as a reward. Similarly, critics suggest that Matthews' and Ladewig's (1994) findings that pigs prefer social contact just slightly more than lever pressing are questionable due to the short period of social contact provided as a reward (Mason et al. 1998). The suitability of the type of response performed to the commodity obtained can also affect the results. It has been shown that hens have a higher demand for extra space when they have to walk on a treadmill than when they have to peck a lever (Dawkins and Beardsly, 1996). Dawkins and Beardsly (1996) suggest this is because the hens associate walking and space more closely than pecking and space.   Sorenson (2001) also points out that these tests, like the choice tests, do not show whether both the standard condition and the alternative are aversive or whether the animal would suffer if it did not have access to the reinforcer that it works hardest for.   Because of these limitations, some researchers have developed alternative experimental methods.

One such alternative is the gold standard experiment, which requires that the animal give up access to a 'standard' commodity in order to gain access to alternative commodities. For example, Dawkins verified her chicken preference experiments by making the chicken choose between a battery cage containing food and an outside run without food (1977). Because these types of experiments demand that animals give up one thing in order to obtain another, they suggest that the animals' choice is not whimsical.

The current experiment attempted to further the 'gold standard' approach by comparing the point at which a rat will give up on a foraging patch if its home cage is enriched compared to when it is not. In this experiment, an enriched environment is considered to be one that includes items that improves the quality of life for rats by allowing natural behaviours (for example a place to hide). Research in ecology has indicated that animals base decisions on how long to stay in a foraging patch upon other factors such as shelter, predation risk and the value of alternative feeding patches (Krebs and Davies, 1984; Lima and Dill, 1990). Models have been designed to describe how factors like predation influence the use of foraging patches, therefore, these models may also be useful for evaluating the value of enrichment items by monitoring how these items affect foraging behaviour.

Many researchers have shown that animals change their behaviour in response to predation risk and the quality of a resource patch. Nonacs and Dill (1990; 1991) found that ants ate more from a riskier patch when the relative quality of that patch increased compared to a safer patch, and that the amount of food taken from each patch was equal only when the mortality risks were approximately offset by increased colony growth. Backswimmers, fish and deer mice have also been shown to adjust their behaviour in response to predation level and patch quality (Sih, 1980; Abrahams and Dill, 1989; Holtcamp et al, 1997). In tests with rodents, Kotler and Blaustein (1995) determined that food in open patches had to be 4-8 times richer than food in bush patches for gerbils to use them equally.

Charnov (1976) derived a model, Charnov's Marginal Value Theorem, to determine when animals should give up on a feeding patch with diminishing returns or resource depression. He defined a patch to be a distinctive place where animals fed. A patch that has diminishing returns results in a decreased rate of acquisition over time, so the graphical representation of this patch is an asymptotic curve, also known as the gain curve. Charnov suggests that the point at which an animal should leave, T optimal, is the point at which the tangent to the gain curve intersects the x-axis at the negative value for travel time between that patch and an alternative patch and has the steepest slope:

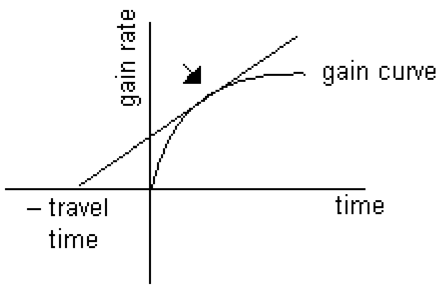


Figure 1: Charnov's Marginal Value Theorem

In the case of multiple patches, Charnov suggests animals should leave a patch when the gain rate within the patch falls to the average gain rate in the environment.

The limitation of this model is that it is dependent on many assumptions. These include the animal recognising the patch instantaneously, the travel time being known or measurable by the experimenter, equal energetic cost of travel time and searching and a smooth gain curve that is continuous and decelerating over time.

Despite its limitations, Charnov's model has held in some experiments. Cowie (1977) found that great tits forage patches of mealworms in a manner that follows Charnov's model. Cook and Cockrell (1978) and Giraldeau and Kramer (1982) found that waterboatmen and wasps, respectively, both leave forage patches at "T optimal" as well.

However, the above experiments were all done under ideal conditions where there was no risk of predation. In order to account for risk of predation, Brown (1988) developed a modified model to explain foraging behaviour in a patch with diminishing returns. His model is:

$H = P + C + MOC$

where H is the harvest rate when the animal leaves the patch, P the predation risk, C the metabolic cost and MOC the missed opportunity cost, which is the resources an animal has to give up to forage in a specific patch. An animal should leave the patch when the benefits of foraging (H) match the costs. Several ecological studies have utilised this model in determining the value of different habitats for different species of foragers. Holtcamp (1997) employed this model to show how predators affect the foraging behaviour of deer mice. He found that deer mice were more willing to take risks - forage with a predator nearby - when foraging in a high quality patch than when foraging in a low quality patch. Kotler (1997) used this model to show that gerbils value a covered feeding patch approximately the same as an uncovered patch with food of four times the quality of that in the covered patch. Abramsky et al. (2002) also employed this model in showing that gerbils valued a stabilised dune habitat over a non-stabilised sand habitat.

The aim of this experiment was to employ Brown's foraging model in order to assess the value of an enriched cage environment for laboratory rats, assuming that missed opportunity cost would give a measure of the value of enrichment. This was done by keeping the actual predation risk fixed and the metabolic cost constant so that the value of H at which the animals left an attractive food patch would be proportional to the missed opportunity cost of foraging in that patch as opposed to foraging in a patch with standard food. By using different enrichments to manipulate the overall quality of the standard patch, it was expected that the missed opportunity cost would change and, therefore, the harvest rate at which the animals would leave would also change. By comparing the leaving harvest rates one should be able to determine what value laboratory rats place on each of the enrichments.

Materials and Methods

Rat Housing

In both studies rats were housed in 21x 40.5 x 50.5 cm Macrolon cages containing aspen-chip bedding (Nepco, Warrensburg, NY, USA) and covered by a wire mesh top (Lab Products Inc, Seaford, Delaware, USA). The cages were in a colony room with an artificial 12 hour light/dark cycle with lights on at 21:00 for the first study and 20:00 for the second study, at a temperature of 22 degrees Celsius. Except for a daily withdrawal period, subjects had access to tap water and food pellets (lab diet 5001, PMI nutrition international, Inc., Brentwood, MO, USA) ad libitum.

Study 1

Subjects

The subjects were 4 female, pair housed, Wistar rats used in prior t-maze experiments.

Procedure

In order to choose food for the attractive foraging patch, split peas, sesame seeds, sunflower seeds, raisins and dried apricots were provided in a preliminary trial to determine the rats' preference. Split peas were selected for this study as they were of medial preference and because they were an ideal colour (green) and size for detection both when the rats were consuming them and when they were later separated from the substrate. To ensure that the number of peas provided in this trial would not satiate the rats, they were given access to a bowl of 100 peas. All 4 rats ate all the peas in under 11 minutes with a maximum pause in eating of less than 2 minutes.

The testing apparatus consisted of the home cage connected lengthwise to another cage of the same size via a 65 cm long, 10 cm diameter PVC tunnel (Figure 2). Both cages contained bedding to a depth of 4.5 cm. The rats had regular access to water and rat pellets in their home cage. The second cage served as the foraging cage and contained peas during the training and testing periods. Although training and testing took place during the dark period of the light schedule, animals were trained and tested under florescent lighting to facilitate feeding observations.

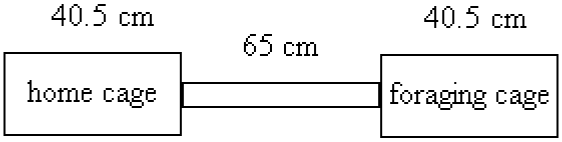


Figure 2: Cage set-up for study 1

On training and testing days, food was removed from the cage just prior to the beginning of the dark period. Testing took place approximately 2 hours later, between 11 and 12. Food was returned to the home cage 5 minutes before testing. This was done to ensure the rats knew that there was some food in their home cage since the theoretical basis of the experiment is dependent upon the rats choosing between different qualities of foraging patches.

Immediately prior to training or testing, the rats were transferred in the home cage to a separate testing room. At this time the foraging cage, which had been pre-arranged with peas, was attached to the home cage. Initially, the rats were trained to traverse the tunnel from the home cage to the foraging cage. During this stage of training, the peas were not buried and the rats were allowed several visits to the cage. As the rats progressed with the task - ate 10 or more peas per visit on 3 consecutive daily trials, which took 3 days - 50 peas were pushed into the substrate in a specific pattern (Figure 3) and access to the foraging cage was limited to one visit per day. The rats' behaviour was considered stable when the total number of peas eaten per bout did not vary by more than 5 peas for 3 days in a row. It took 7 days before all rats reached this point.

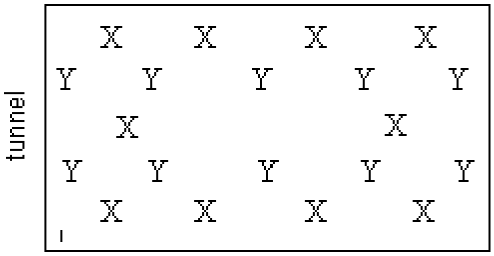


Figure 3: Arrangement of peas in Trial 1. X and Y represent alternating layers: X represents peas pushed down to depths that were 1, ½ and 0 times the depth of the substrate (4.5, 2.25 and 0 cm) and Y down to ¾ and ¼ (3.375 and 1.125 cm).

When all 4 rats were exhibiting stable foraging behaviour, each rat pair was assigned to either a *social* or *isolated* condition. The *social* pair had a divider (½"wire mesh) placed in their cage 5 minutes prior to testing to divide the test rat from its companion. The *isolated* pair had the same divider placed in the cage 5 minutes prior to testing, but the companion rat was removed at the same time. Each rat was trained using these conditions for 4 days prior to testing in order to habituate them to the procedure. An individual rat's training session ended when she returned to her home cage from the foraging cage. She was then given a five minute period in her home cage during which she could forage or interact with her companion without interruption. After these five minutes the second rat of the pair was tested or the next pair was tested until all four rats had gone through the procedure. The order of testing was rotated daily.

The rats were then tested for 4 consecutive days using the same procedures employed during the final stage of training. After the 4 days of testing with the first condition, the conditions were reversed and the rats were again given 4 days of training to habituate to their new condition. This was then followed by 4 more days of testing with the new condition.

During testing, a stopwatch was used to record the times at which each pea was taken. The observer was 1 m away from the testing apparatus as these rats were habituated to observers from previous experiments.

Study 2

Subjects:

The subjects were 4 female, individually housed, Wistar rats. They were different rats than those used in Study 1 and had previously been used for breeding.

Procedure:

These rats showed a poor response to peas, eating only 0-5 peas within 3 days of the peas initially being placed in their home cages. Therefore, these rats were tested with miniature chocolate chips (Chipits, Hershey). All 20 pieces initially offered were consumed within 2 days and another 20 offered thereafter were consumed the following night. Rats have been shown to eat 60 or more chocolate chips within 10 minutes (Patterson-Kane and Drissler, in press), so satiety was not expected to significantly affect consumption during this study as only 20 were offered during each daily trial.

The testing apparatus in this study consisted of home cage connected to a foraging cage via a small connector tube with a length of 7.5 cm and a diameter of 7.8 cm (Figure 4) . The small connector tube was used instead of the tunnel as the tunnel provided an attractive hiding place and I didn't want to measure the desire to return to this hiding place. In this study all training and testing took place under red light to maintain dark conditions while allowing for video monitoring and recording of foraging behaviour.

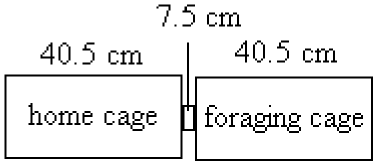


Figure 4: Cage set-up for study 2

On alternate days, food was removed from the home cage 3 hours before training and testing, just prior to the start of the dark period. On the other days rats had continuous access to food in their home cage. This was done to determine the effect of food removal on the procedure. Training and testing was done between 10:45 and 11:45. On the days of food withdrawal, food was returned to the home cage 1 minute prior to testing because the rats were observed to interact with the food, touching it with their noses, almost immediately after it was returned.

During the training period, 3 different types of enrichment items were added to the home cage for 5 days to introduce the rats to them. The items included red tunnels (Bio-Serve; 15.3 cm long, 7.7 cm), crawl balls (Bio Serve, circumference 34.5 cm) and nest-boxes (shelter enclosed on 3 sides, constructed out of 0.5 cm thick plastic). Various researchers have found nest-boxes to be preferred by laboratory rats (review by

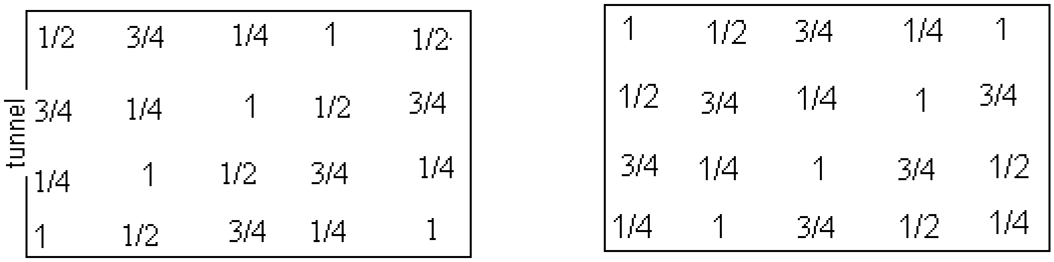
Patterson-Kane, 1999; Manser et al., 1998ab) and tunnels and crawl balls are marketed to improve the housing of laboratory rats (Bioserv).

During this study, the rats had continuous access to the foraging cage in order to lessen any neophobic response to that cage. Immediately prior to training or testing, the foraging cage was removed for a short period of time to insert chocolate chips in a set pattern. Just prior to each individual training or test period the foraging cage was reconnected. Initially, the chocolate chips were placed in the top of the bedding and the rats were allowed to visit the foraging cage several times before any leftover chips were removed. As the rats progressed with the task - ate 5 or more chips per visit on 3 consecutive daily trials, which took 5 days – 20 chips were pushed into the substrate in a specific pattern (variations of Figure 5) and the rats were only allowed one daily visit before the foraging cage was temporarily disconnected to remove leftover chips. The rats' behaviour was considered stable when the total number of chips eaten per bout did not vary by more than 3 chips for 3 days in a row. It took 10 days before all rats reached this point.

Once all 4 rats were exhibiting stable foraging behaviour they were assigned to either an *enriched* or *control* condition. All three enrichment items were placed in the home cages of the *2* rats in the *enriched* condition and the shelving above that cage was moved to 1 cm above the top of the home cage. Moving the shelf was done in order to create an enclosed environment, which, according to Blom (1992), is preferred by rats to an open environment. It was expected all these items together would produce pronounced results. The home cages of the 2 rats in the *control* condition had none of those items and the shelving was kept at 25 cm above the top of the home cage. Each rat was trained under these conditions for 4 days prior to testing, in order to habituate them to the procedure. A training session was considered over as soon as the rat left the foraging cage. At this time the observer, who was in the adjacent room monitoring the test, would enter the test room and disconnect the cages. The video equipment was adjusted for the next rat and then food was reintroduced in that rat's home cage and the cages were reconnected. This was done until all rats had been tested. The order of testing rotated daily.

The rats were then tested for 6 consecutive days using the same procedures employed during the final stage of training. The chocolate chips were placed in the foraging cage in the pattern depicted in Figure 5a. After the 6 days of testing the conditions were reversed and the rats were given another 4 days to habituate to their new condition. Then they were tested for another 6 days with chips placed in the pattern depicted in Figure 5b. This was done to account for the fact that the rats may have learned where to find the food within the cage.

All testing was recorded using a Panasonic WV-BP330 camera and a Panasonic WJ-FS216 video recorder. The testing procedure was monitored from an adjacent room using a 10" Pelco PMM1201 monitor connected to the recording equipment.



1/2	3/4	1/4	1	1/2
3/4	1/4	1	1/2	3/4
1/4	1	1/2	3/4	1/4
1	1/2	3/4	1/4	1

(a)

1	1/2	3/4	1/4	1
1/2	3/4	1/4	1	3/4
3/4	1/4	1	3/4	1/2
1/4	1	3/4	1/2	1/4

(b)

Figure 5: Arrangement of chocolate chips in Trial 2 in week one (a) and week 2 (b). The numbers represent the relative depth to which the chocolate chips were pushed compared to the depth of the substrate (1= 4.5 cm, ¾ = 3.375 cm, ½ = 2.25 cm, ¼ = 1.125 cm).

Data analysis:

For both of the studies the number of the food item taken was plotted against the average time that piece was taken to allow for visual comparisons of the harvest rate at which animals were leaving during each condition. The harvest rate at the leaving time was also estimated by averaging the amount of time taken to find the last food item. This gives the approximate slope of the gain curve at the leaving point. Because of the small sample size, the variability of the data, and the overlap of standard deviations between conditions no statistical analyses were performed.

Results

Study 1

The rats were expected to forage in a way that would produce an asymptotic curve like that predicted by Charnov's model for foraging with diminishing returns (Figure 1). Figure 6 shows that only the behaviour of Rat 1 approximated such a curve whereas the other rats showed more of a linear relationship between time and number of peas consumed. The slope of the curve of Rat 1, however, changed between the two conditions.

All four rats left at a lower harvest rate, the slope of the gain curve at the leaving point, in the social condition than in the control condition (Figure 6, Table 1) . For all rats the average harvest rate at the leaving point for each condition fall within one standard deviation of each other.

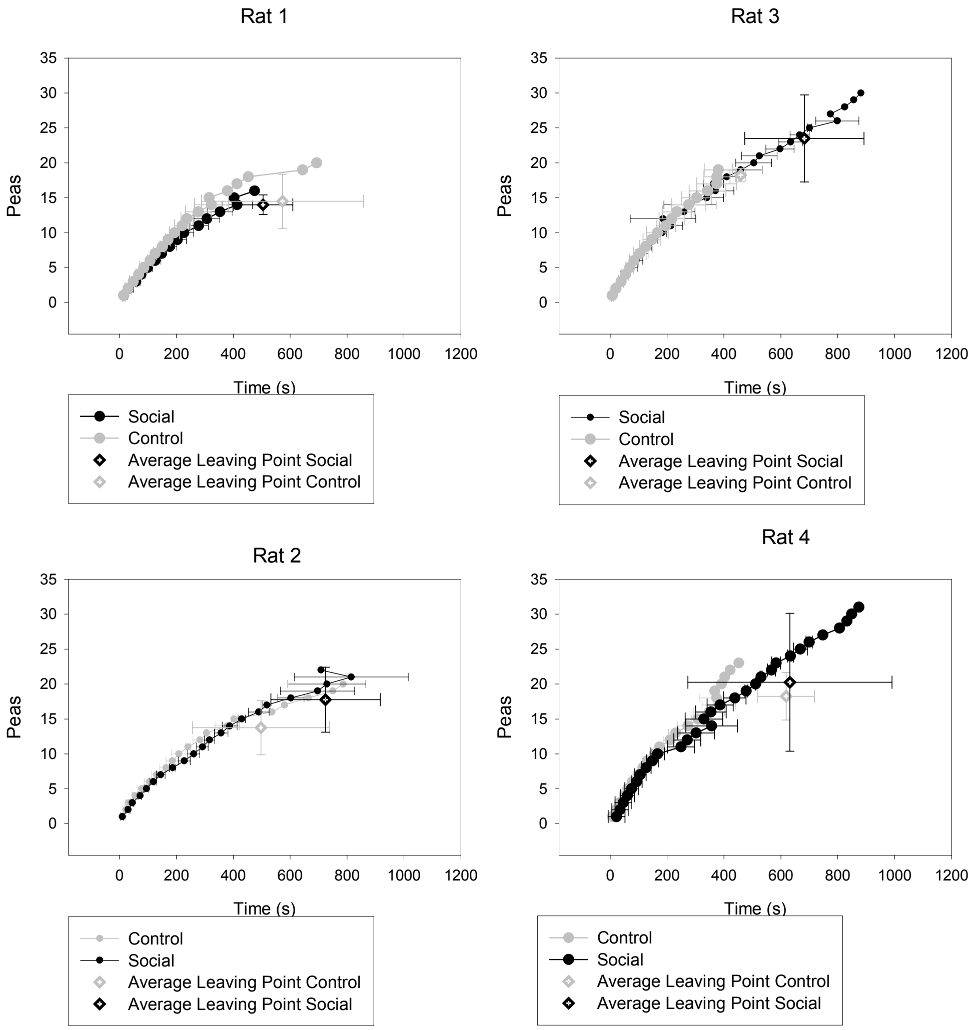


Figure 6: Relationship between time and pea taken for rats in the social and control conditions, with a food withdrawal period of 2 hours. Data points are an average of 4 trials and are given with standard deviations.

Table 1: Harvest rates (peas per second) at which the rats chose to leave in the control and social conditions, with a food withdrawal period of 2 hours. Harvest rates are an average of 4 trials and are given with standard deviations.

	Control (peas/s)	Social (peas/s)
Rat 1	.0334 ± .0173	.0196 ± .0048
Rat 2	.0264 ± .0190	.0248 ± .0208
Rat 3	.0486 ± .0254	.0293 ± .0156
Rat 4	.0420 ± .0130	.0368 ± .069

Study 2

Although the graphs appeared to approximate an asymptotic curve more than in the first study, the relationship between the time and number of chocolate chips eaten is still quite linear, especially for Rat 2 (Figures 7 and 8). There are also notable differences in slopes between the enriched and control conditions for Rats 2, 3 and 4 when there was food withdrawal (Figure 7), and Rats 3 and 4 when there was no withdrawal (Figure 8). As well, there was substantial disparity in the number of chocolate chips consumed by Rat 1 between the two conditions.

When there was a 3 hour period of food withdrawal Rats 1, 2 and 3 left at a higher harvest rate in the enriched condition than the control (Table 2). Rat 4 left at a lower harvest rate in the enriched condition than the control.

When there was no period of food condition, Rats 1 and 2 and left at a higher harvest rate in the enriched condition than the control (Table 3). Rats 3 and 4 left at a lower harvest rate in the enriched condition than the control.

For all rats the average harvest rate at the leaving point for each condition fall within one standard deviation of each other.

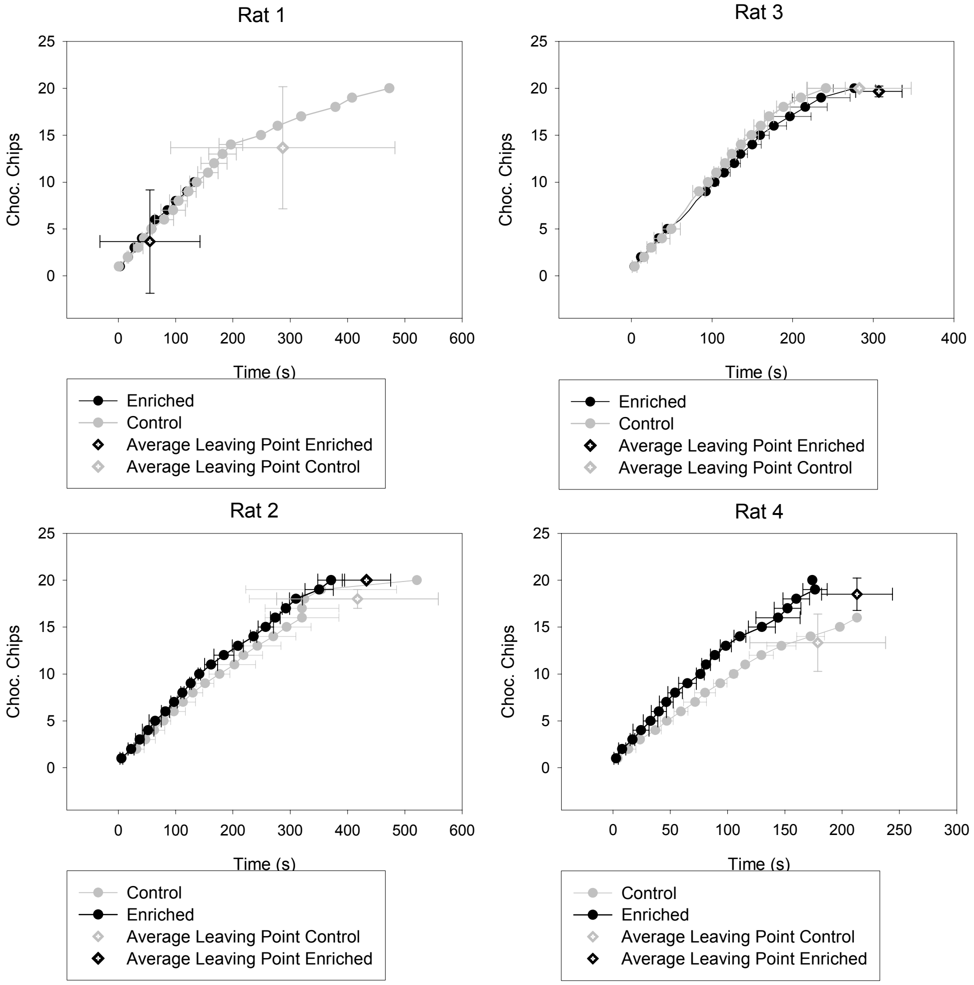


Figure 7: Relationship between time and chocolate chip taken for rats in the control and enriched conditions, with a food withdrawal period of 3 hours. Data points are an average of 3 trials and are given with standard deviations.

Table 2: Harvest rates (chocolate chips per second) at which the rats chose to leave in the control and enriched conditions, with a food withdrawal period of 3 hours. Harvest rates are an average of 3 trials and are given with standard deviations.

	Control (chips/s)	Enriched (chipss/s)
Rat 1	.0520 ± .0091	.0764 ± .0303
Rat 2	.0378 ± .0158	.0470 ± .0121
Rat 3	.0369 ± .0117	.0459 ± .0127
Rat 4	.1145 ± .0793	.0679 ±.0155

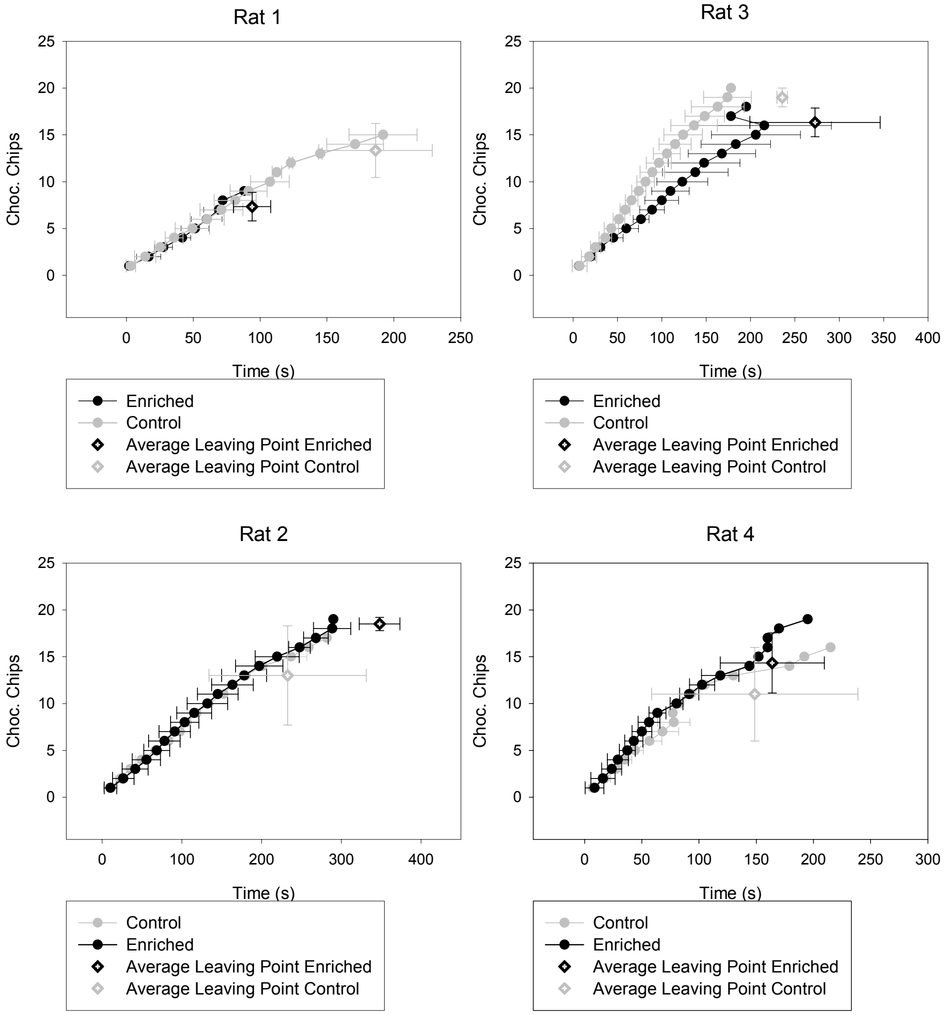


Figure 8: Relationship between time and chocolate chip taken for rats in the control and enriched conditions, with no period of food withdrawal. Data points are an average of 3 trials and are given with standard deviations.

Table 3: Harvest rates (chocolate chips per second) at which the rats chose to leave for the control and enriched conditions, with no period of food withdrawal. Harvest rates are an average of 3 trials and are given with standard deviations.

	Control (chips/s)	Enriched (chips/s)
Rat 1	.0399 ± .0222	.2083 ± .1768
Rat 2	.0251 ± .0103	.0429 ± .0086
Rat 3	.0852 ± .1104	.0265 ± .0092
Rat 4	.0972 ± .0293	.0684 ± .0315

Discussion:

Studies done by Kotler (1997) and Abramsky et al. (2002) have shown that rodents will leave a good quality foraging patch at different harvest rates (H) depending on the other variables of Brown's equation $H = MOC + P + C$ (missed opportunity cost, predation and metabolic cost, respectively). In this thesis, the experiments held actual predation (P) and metabolic cost (C) constant in order to assess whether measurements of H would depict anticipated differences in missed opportunity costs when home cages were enriched or bare. Missed opportunity costs might include benefits like security (perceived protection), alternative benefits of companionship besides security, such as grooming, or interactions with the enrichments, such as climbing.

For each of the studies, it was expected that the missed opportunity cost would by higher in the social or enriched condition relative to their respective controls. Using Brown's equation, the harvest rate – slope of the gain curve - at which the animal left would be higher when the missed opportunity cost was higher. Therefore, I expected the harvest rates at the leaving points would be higher in the enriched and social conditions in comparison to the respective controls (Figure 9).

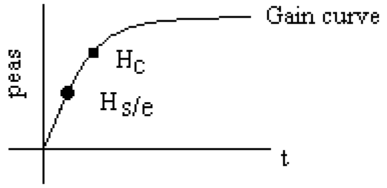


Figure 9: Visual depiction of expected results; the circle and square represent different instantaneous harvest rates (H) at which the rats would choose to leave (as the slope of the gain curve decreases the rate of gain also decreases, so H_c is lower than $H_{s/e}$). The difference in H values is proportional to the missed opportunity cost when a rat is foraging in the high quality patch.

Study 1

Dewisbury (1992) suggests that the reinforcing value of intraspecific social interactions is very high for rats. Morgan and Einon (1975) found that social housing is beneficial to rat temperament and health and Patterson Kane et al. (1999, 2002) found that rats prefer social housing over isolated housing. Therefore, it was anticipated that the rats in this experiment would value returning to a social companion more than returning to a cage without one. As a result, the harvest rate at which the rats left should have been higher in the social condition.

In contrast to what was expected, the rats showed a trend towards leaving at a lower rate of gain in the social condition. However, despite this trend, there was quite a bit of daily variation in the results. There was a change in the slope of the graphs of one Rat 1 between the conditions which suggests she may have been still learning the task during the experiment. Therefore it is difficult to conclude whether this trend is the true response of rats to the difference in the two cage conditions. If it is true, there are a few explanations that may suggest why the rats did not behave as expected. Dewisbury (1992) suggests that rats who have companionship are less nervous. In this experiment the rats in the social condition may have been able to communicate via auditory, olfactory or visual cues as the two cages were parallel in height and clear plastic, and the tops were open. Because of social contact, perhaps the rats felt safer, resulting in increased exploration of a new environment. Similarly, the rats that were in the isolated condition may have been more anxious and less eager to explore. This anxiety may have been a product not only of isolation but also of the removal of a companion just prior to the experiment. This may have signalled some kind of danger to the rats, thereby decreasing the length of time they felt comfortable foraging for.

Another possible explanation for the trend is that rats may not find short periods of separation from social companions aversive as social companions can be sources of aggression and competition as well as protection (Lawlor, 2002). Because this experiment was based on foraging the rats may have perceived their companion as a threat to resources. As a result the rats with companions may have stayed longer in the foraging cage to ensure they got a sizeable proportion of the resources before the other rat could come and harvest this attractive patch.

Study 2

According to various experiments, rats show a significant preference for enclosed shelters and other items in which they can hide. Specifically, Manser et al. (1998) showed that rats would lift over twice as much weight to gain access to a cage with a nest-box than they would to gain access to a control cage and Blom (1992) showed that rats prefer low ceilings. These two elements were combined with products marketed for rat enrichment, a crawl ball and a tunnel, to create the *enriched* environment. It was assumed that the rats would experience a higher missed opportunity cost when their home cage had a series of enrichment items then when it did not. According to this assumption, it was expected that rats would leave at a higher harvest rate in the enriched condition than in the control.

The results of this study were even more variable than the first. When the period of food withdrawal was maintained, three of four rats left at a higher harvest rate in the enriched condition, but when there was no period of food removal, only two out of four rats left at a higher harvest rate in enriched condition. This difference occurred despite the fact that the experiment alternated daily between the food withdrawal/no withdrawal conditions. Because the experiment alternated daily it was expected that the results would be the same if the food withdrawal did not change motivation, or that results would show less variability if it did. The large standard deviations that are present in the food withdrawal data suggest to me that the withdrawal period did not affect motivation, which makes it questionable as to why one rat would change her behaviour between the conditions, unless the results were random.

If the data from the food withdrawal condition are considered alone, there is a trend towards leaving at a higher harvest rate in the enriched condition. If this trend depicts what the rats experienced, the results are consistent with what was expected. However, the rats only showed a very minor difference in behaviour between enriched and control conditions and only 2 of the rats left at higher rates of gain in the enriched condition when food was withdrawn. Therefore, it appears more likely that there was no true effect of treatment on the rats' response.

Possible reasons for indefinite results

As the sample sizes used in these studies are small, it may be that the trend seen in the data is simply coincidental and that there is no difference between the conditions. In both studies the results do not give a clear indication that harvest rate at the leaving point can be used to assess the value of enrichments for rats. Possible reasons for this include: a lack of diminishing returns, the length of trials, novelty and motivation to explore, a lack of distinctive food patches, and food deprivation.

The relatively linear gain curves seen in both Studies 1 and 2 suggest that the rats did not experience distinct diminishing returns. This is crucial because the theory depends on the rats choosing to leave the attractive foraging patches in response to increased difficulty in finding the food items. The reason behind the near linear gain functions may have been the ease of finding the food items for the rats. Finding food may have been easy because the rats have an acute sense of smell and could quite easily dig through the substrate.

Another possible reason for the inconclusive findings is that the time frame of the experiment may not have been long enough to really affect the choices of the rats. In both studies the rats only had a few minutes of access to the attractive food items whereas other researchers gave subjects a much greater time frame to access resources by testing them overnight (Kotler, 1997; Abramsky et al., 2002). In Study 1, the rats spent, on average, 10 minutes in the foraging cage. In Study 2, because of the ease of finding and consuming chocolate chips, this was further reduced to 4.5 minutes. The cost of leaving the resources in their home cages may not have been very significant for this short period of time. In Study 1, for example, short periods of separation from companions may be natural to rats and therefore not cause any concern for the isolated rats. As well, a portion of this short period of time may have been devoted towards exploration.

The effects of exploration and novelty are particularly pertinent in Study 1 because the only time the rats had access to the foraging cage in this study was during the training and testing periods. The possible excitement or uneasiness in response to the relative novelty of the foraging cage may have had a greater influence on the behaviour of the rats than the benefits offered by the home cage. The importance of this factor is questionable though, as Patterson-Kane et al (2002) did show that rats would choose, via a t-maze cage, environments with social companions over those without, even when they only had a short time period of access. However, prior to testing these rats were given two forced choices of 5 minutes each in which they could explore both options.

The change in methodology in Study 2 should have also addressed concerns about novelty and exploration by providing continual access to the foraging cage and testing the animals in their holding room. However, there may have still been some motivation to explore when the cages were reattached after a short removal to insert the chocolate chips.

One of the other methodological adjustments in Study 2, removing the tunnel, may have also influenced the results. This adjustment may have caused the rats to view the foraging cage as an extension of their home environment. In Kotler's research (1997) the distance between cover and the unprotected foraging patch was 1-2 metres and Holtcamp et al. (1997) comment in their methods that to successfully employ Brown's model it is vital that the animals perceive the foraging patches as distinct. If the rats did not distinguish the home cage from the foraging cage the experiment may have simply been measuring the desire to forage for treats, which would be expected to be similar for all rats.

The period of food deprivation may have also influenced the motivation of the animals to perform the foraging task. Although short, this period may have made the rats highly motivated to forage. If a rat is highly motivated by food it may not matter whether or not there is a companion nearby and thus, there would be no difference between the conditions. However, when food was left in the cages during Study 2 there was neither a trend nor less variability in the results, suggesting that the period of food deprivation did not actually affect the results, assuming the trends are coincidental, or improved them, if the trends were true.

Although Study 2 was expected to provide more clear results than Study 1, the results of Study 2 did not really show a trend in any direction. The experimental procedure in Study 2 was adjusted to minimise any effects of novelty, motivation to explore and food withdrawal but unfortunately the adjustments shortened the time frame of the experiment and may have made the patches indistinguishable to the rats. However, it may be that none of these concerns were very important, rather the lack of distinguishable results may have been a product of not being able to provide distinct diminishing returns.

Suggestions for further research

Concerning choice of attractive food items for this type of test, chocolate does not seem like an appropriate option. Although it was used in Study 2 because of the relative ease of habituating rats to it, it shortened the test period substantially. The peas required more handling time by the rats, prolonging the experimental period, and were slightly more difficult to find, but unfortunately did not provide suitable gain curves. It may be appropriate to use peas, however, the spatial distribution of the food items needs to be adjusted in order to get a good diminishing returns rate. A larger patch for the attractive food items or a substrate that is more difficult to forage in would have to be provided to get this ideal rate of diminishing returns. A larger patch would allow for the food items to be spread out, which would make them harder to detect via smell and therefore, require more search time as the number of food items decrease. A substrate that is more difficult to foraging in would make foraging for deeply buried food items much more challenging than foraging for ones near the surface.

For a successful approach, the apparatus must create two distinctive foraging patches. Either a larger distance between patches or a distinctive barrier should be set up around foraging patches to ensure that they are recognised as two separate environments. This may be challenging in the conventional lab setting due to the size of commercial cages (our cages were the largest available for small laboratory animals). Self-constructed cages connected by a central cage devoid of alternate material may be appropriate. This would create a distinctive space that is different from each of the foraging patches but not ideal for the rats to stay in because it is open and void of other commodities (Blom, 1992). Another idea may be to use a dog run or some other type of large animal caging for the experiment. This would allow for the home cage to be put on one side and the foraging patch at a distance from that cage, similar to an aviary used in Kotler's research (1997).

The time frame of the experiment, both the length of access to the patch and the length of access to the resources, should be manipulated to assess if they effect behaviour. As the length of access to the patch and resources increases, novelty and exploratory responses would likely become negligible and the experiment would measure the motivation to forage more accurately.

Conclusion

This experiment was not successful in using Brown's foraging model to assess the value of different enrichments. Its lack of success may have been due to a number of influencing factors such as lack of distinctive foraging patches or diminishing returns, the short time frame of the experimental procedures or the novelty of the foraging cage. If this experimental approach is to succeed, these problems will need to be addressed.

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