"Risk-Sensitivity" in a Rat Population Under Interval Schedules of Reinforcement: Open and Closed Economies

by

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Abstract

A group consisting of eight male Hooded rats was tested for risk-sensitive foraging preferences in an eight station operant arena, under conditions of open and closed economies. The group could choose to forage at either four fixed interval stations or four variable interval stations of the same mean interval value. The visual, tactile, and spatial discriminative stimuli associated with the fixed and variable stations was enhanced to assist in discriminating between the variances of the schedules associated with the stations. The following four interval values were tested, with each in effect for five consecutive days: 15, 30, 90, and 180 seconds. The open economy was defined by a 30 minute session conducted twice a day followed by a supplemental feeding at the end of each day. The closed economy consisted of continuous 24 hour access to the stations, with no supplemental feeding. Results revealed differential effects upon foraging choices by the two different economies. In the open economy, the group of rats were risk-indifferent in their foraging preferences, while in the closed economy the rats foraged in a manner that was contrary to risk-sensitive theory. During the closed economy the rats were risk-prone when net energetic gain was high and became less risk-prone as net energetic deficits occurred. Discussion is given on the possible influence of competition and discriminatory cues

upon a rat populations foraging preferences.

For a decade and a half now, behavioural ecologists and operant psychologists have been investigating a theory known as risk-sensitive foraging. The theory was first proposed by Thomas Caraco (1980), and has its roots in optimal foraging theory. The major premise of optimal foraging theory is that the fitness level of a foraging animal is a function of the animal's ability to maximize net energetic gain per unit foraging time (Pyke, Pulliam, Charnov, 1977). To achieve this maximization the animal must be sensitive to the mean amount of available food in a given patch. Optimal foraging theory assumes that an animal will switch to another patch when the time and effort spent obtaining food in the current patch falls to a level below that of the environment as a whole. Charnov (1976) has referred to this as the marginal value theorem, which predicts that optimal foragers will leave a patch once the mean level of available resources within that patch falls to the relative overall level of the environment.

Risk-sensitive foraging theory has forced a re-evaluation of optimal foraging theory because optimal foraging theory had assumed that mean reward was enough to predict foraging preferences (see Stephens & Krebs, 1986). Caraco et al. (1980) point out that resources in the environment have a range of variability associated with them in terms of how much food is in a given food patch, and when this food becomes available. They assume that natural selection has acted on the preference behaviour of those animals faced with environmental variation, and suggest that the choice of where to forage will reflect not only the mean reward, but also the variances in foraging benefits (Caraco, Martindale, & Whittam, 1980). Caraco's (1980) risk-sensitivity model asserts that when the expected mean reward is high enough to provide a positive net energetic gain, the animal will choose a patch in which variability of reward is low. This is referred to as being risk-averse. However, when the expected mean reward falls to a level resulting in a negative net energetic gain, the animal will display risk-prone behaviour; that is, the animal will gamble foraging in a patch of high variability, thus exposing it to the risk of obtaining an even lower amount of food. But this risk also entails the chance of obtaining the positive side of the distribution. In short, Caraco's (1980) risk-sensitivity theory assumes that animals are generally risk-averse and are driven towards risk-prone behaviour by a need to fulfil energy requirements necessary for survival.

Since Caraco et al's. (1980) initial demonstration of risk-sensitive foraging preferences with yellow-eyed juncos, several supportive studies have been conducted with a wide variety of subjects that have included bumble bees (Cartar, 1991), Black-capped Chickadees (Barkin, 1990), and pigeons

(Hamm & Shettleworth, 1987) (see also Stephens & Krebs, 1986). The common feature of these studies and with other experiments by Caraco (e.g., Caraco, 1981, 1982, 1983; Caraco, Blanckenhorn, Gregory, Newman, Recer, & Zwicker, 1990; Caraco & Lima, 1985), is that the subject is always offered a choice between a fixed reward or a variable reward with equal means.

However not everyone has found support for the risk-sensitivity theory postulated by Caraco. Experiments using rats in operant chambers have found constant risk-aversion for both positive and negative levels of net energetic gain (Battalio, Kagel, & MacDonald, 1985; Kagel, Battalio, White, MacDonald, & Green, 1986), while Mazur (1988) has found constant risk-prone behaviour. These inconsistencies may be a result of a difference in what is being varied. McNamara and Houston (1992) describe how variability in amount tends to lead to risk-aversion, whereas variability in delay to reinforcement tends to lead to risk-prone behaviour. In any event this raises questions as to the importance of net energetic gain as the sole relevant factor influencing an animals foraging decisions.

Goldstein's experiments in the operant arena, in which eight rats can competitively forage simultaneously at any of eight stations, has demonstrated schedule control of dispersion and density patterns (Goldstein, 1981; Goldstein, Johnson, & Ward, 1989; Goldstein, & Mazurski, 1982). Goldstein et al. (1989) found that variable schedules exerted a differential influence on these foraging patterns relative to their fixed counterparts. This evidence has led to the hypothesis that risk-sensitivity is governed by schedules of reinforcement, rather than net energetic gain. In fact, it is believed that animals will prefer to forage in a patch offering a variable presentation of food as opposed to a fixed presentation.

A common problem with most tests of risk-sensitivity is their use of a fixed schedule. Such a schedule in the wild is extremely rare, and is at best artificial when it does occur. A more realistic study would use a choice between two variable food patches. Such research has been conducted using grey jays as subjects (Ha, 1991; Ha, Lehner, & Farley, 1990). The jays were offered the choice between two variable ratio schedules with identical means but different variances around the mean. Foraging in the low variance patch indicates risk-aversion, while foraging in the higher variance patch indicates risk-prone behaviour. Ha and colleagues found that contrary to Caraco's risk-sensitivity theory, all subjects foraged in the higher variance patch for all levels of net energetic gain, indicative of constant risk-prone behaviour.

Goldstein's operant arena provides an excellent opportunity to compare low variance schedules with high variance schedules. Due to the presence of conspecifics in the operant arena, a subject foraging at a fixed schedule station will not always get the reinforcer. Therefore there exists a small amount of variance at these fixed stations. When the difference in variance between the fixed and variable stations is high enough to be detected (ie. more discriminable) by the foraging animal, it should shift to spending more time foraging at the higher variance stations.

In the first test of risk-sensitivity using Goldstein's operant arena, results indicated an overwhelming preference for risk-aversion (Berklund, 1988). However, there was a gradual decrease in the magnitude of the preference for risk-aversion as schedule value increased. It is possible that the increased variance created by conspecifics at the fixed-schedule stations reduced the discrimination between fixed and variable foraging sites. However, as the means increased, the variance at the variable stations would gradually get larger than the variance created by conspecifics at the fixed stations. This then resulted in a corresponding increase in the ease of discriminating the fixed and variable stations. This would account for the decrease in risk-averse behaviour of the rats reported in Berklund's (1988) experiment.

If the discrimination between the fixed and variable schedules were increased, outside of changing the mean levels of reinforcement, it is theorised that risk-prone behaviour will be exhibited at all levels of mean reward rate. This then greatly reduces the control of the animal's behaviour by an internal drive state (amount of food deprivation), in favour of an external control. This external mechanism is the schedule of reinforcement.

Morse (1966) states that it has been found repeatedly that the effects of deprivation depends on the controlling schedule and that it has different effects with different schedules. Deprivation is most important during the early stages of conditioning when strong conditioned behaviour is not yet developed. A prolonged history of intermittent reinforcement attenuates the effects of deprivation so that it becomes less important for the maintenance of schedule - controlled behaviour.

It is hypothesized that the theory of risk-sensitivity could be explained without an internal drive mechanism (food deprivation) acting upon foraging choices. The theory may be better explained through the controlling effects imposed by the schedules of reinforcement. If the discriminatory cues associated with the concurrent fixed and variable equal mean station groups in the operant arena are increased, this should assist in a preponderance of risk-prone behaviour over risk-averse behaviour, at any level of net energetic gain (ie., negative or positive). This would be exhibited by a higher number of rats observed foraging at the variable interval stations, with a corresponding higher number of responses and reinforcements at these same stations. This would then be evidence for schedule control of risk-sensitive foraging behaviour.

In a previous experiment reported by Gregory (1993), a significant preference, as measured by number of rats foraging at the stations, for the variable interval scheduled bars over the fixed interval bars was found. However this occurred only when the interval value was at the highest level used in the experiment. The shorter interval values did not produce a preference for either the variable schedule or the fixed schedule. This indifference was also reported by Barnard and Brown (1985), who found that foraging shrews were risk-indifferent in the presence of an apparent resource competitor and risk-averse in its absence. It should be noted that competitors in their experiment were separated from the test subject at all times by a clear plexiglas partition and was therefore not a true test of conspecific competitiveness. Barnard and Brown reason that shrews take into account possible factors likely to influence the predictability of food in the future.

Gregory (1993) suggested that the findings obtained in his experiment may have resulted from constraints imposed by the experimental design. In his experiment, the subjects were tested in what Hursh (1980, 1984) has termed an open economy. An economy is open when "the total daily consumption of food [is] not the result of the subjects' interaction with the environment during the sessions, but [is] arbitrarily controlled by the experimenter" (Hursh, 1980, p. 221) This refers to the giving of supplemental or 'free' food after the experimental sessions, as was the case in Gregory's (1993) experiment. Hursh also defines a second economy, known as the closed economy, which occurs when the "total daily food consumption [is] determined solely by the subjects' interaction with the schedules of reinforcement, either across a 24 hour day . . . or during a timed session . . . [during which] no extra food [is] provided' (Hursh, 1980, p. 222).

It is suggested that the temporal constraint of access to the bars in the open economy reduced the opportunity for all eight rats to forage entirely on the variable side of the arena. This temporal constraint is a direct result of all eight rats having to forage at the same time. If the same experiment were conducted under a closed economy, where the rats had 24 hour access to the bars, a single rat would not be compelled to forage at the same time as its conspecifics. This would allow the group of rats to choose between the fixed and variable stations when constraining factors are minimized. In addition, the use of a closed economy would be more generalizable to the natural environment since the two share critical common features (Hursh, 1984). The use of the operant arena increases this generalization since it addresses a criticism directed at the use of closed economies for foraging studies (Houston & McNamara, 1989). Houston and McNamara state that in natural environments subjects can interact with other animals and be disturbed by predators, a situation not present in typical closed economy studies. This would be the case in single subject experiments, but not in the operant arena since the eight rats are in an interactive state with each other throughout the experiment.

The purpose of this thesis was first to study the preference of the rat population for concurrent equal mean fixed-interval/variable-interval bars, under conditions in which the discriminative cues associated with these differing variance intervals were enhanced. The second purpose of this thesis was to investigate for possible differing effects of an open versus a closed economy.

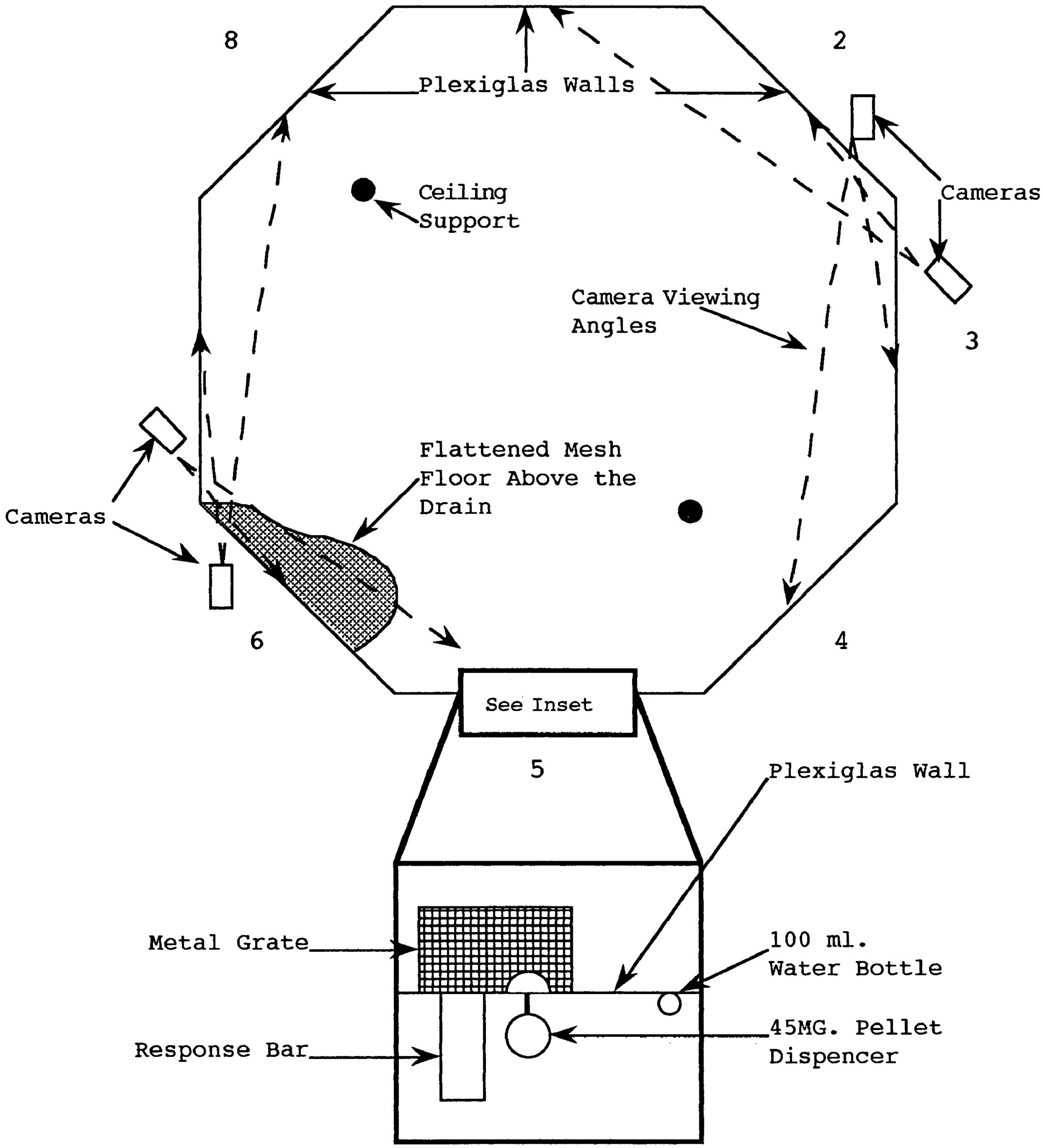
Method

Subjects:

Eight male Hooded rats (*Rattus norvegicus*) that had been trained on various schedules of reinforcement in the operant arena, were used in the experiment.

Apparatus:

The rats were maintained throughout the experiment in a 4.50 m. wide octagon arena, with 1.25 m. high Plexiglas walls enclosed at the top by wire mesh (see Figure 1). Each station consisted of an automatically insertable and retractable response bar (Gerbrands Model G312), a 45-mg pellet dispenser (Gerbrands Model D-1), a food cup, and a 100 ml graduated water bottle. The floor of the arena was a white flattened mesh that allowed urine and feces to pass through to a Plexiglas sub-floor. This sub-floor funnelled down to a drain centred below the arena, and water was discharged through perforated copper pipes to rinse away the debris four times a day. Four video cameras (Hitachi Model HV-720C) positioned around the arena, recorded each session onto 8mm video cassette via a digital video recorder (Sony Model EVT-801). Each camera's field of view encompassed two feeding stations, for example the camera behind station 2 recorded stations 3 and 4 simultaneously (see Figure 1). Illumination for the arena was provided by fluorescent lights mounted on the ceiling of the lab in which the arena was housed. Lighting was set on a 16:8 light/dark cycle. During the dark phase of the light/dark cycle, low level illumination was used to allow for continued video monitoring. This resulted in more of a light/dusk cycle rather than light/dark. A large exhaust fan mounted in the ceiling above the arena ventilated the area.



<u>Figure 1</u>. Overhead view of the eight station operant arena. The inset displays an example of the arrangement of equipment at each station (Note: Only stations 3 through 6 contain a metal grate).

A Pet Model 4032 Commadore computer was programmed to provide station-by-station control of reinforcement schedules, data collection and data analysis (Goldstein, Blekkenhorst, & Mayes, 1982).

Procedure:

Three types of modality cues were used to increase discrimination between the fixed and variable stations. These cues were of a spatial, visual, and tactile nature. The spatial cue was established by randomly selecting four stations on one side of the arena for fixed interval schedules, and the four stations opposite for the variable interval schedules. Stations 1, 2, 7, and 8 were independently programmed to payoff on the fixed interval schedules, and stations 3, 4, 5, and 6 were programmed to payoff on the variable interval schedules.

The visual discriminatory cue was created by placing a 55.5 cm by 39 cm sheet of black construction paper, on the back of the Plexiglas wall, centred around feeding stations 3, 4, 5, and 6. A similar sized sheet of white construction paper was placed in the same manner at stations 1, 2, 7, and 8.

The tactile cue involved placement of 44.5 cm by 25.5 cm black metal grates on top of the white flattened mesh floor, centred beneath the bar and foodcup at stations 3, 4, 5, and 6. The black metal grate was of a different texture than the flattened mesh floor.

Phase #1:

The eight rats were exposed to concurrent fixed interval and variable interval 30, 90, and 180 sec. schedules in a sequentially ascending order.

The entire phase of this part of the experiment was conducted over a 15 day period, with each interval value in effect for 5 consecutive days. The rats were given access to the bars for two 30 minute sessions, at 10:00 a.m. and 4:30 p.m. each day. This resulted in 10 sessions for each interval value. The bars were simultaneously and automatically inserted into the arena at the beginning of each session and retracted simultaneously at the end of each session. The Pet 4032 computer recorded the number of bar press responses and the number of reinforcements that occurred at each station during each of the sessions.

At 1 minute intervals during each session, the number of rats at each station was recorded onto a tally sheet, to provide a measure of preference for either the fixed or variable stations. The observed count could be verified by reviewing the video recordings taken during each session. The identity of the rats was not taken into consideration.

To ensure the rats remained healthy and did not starve during the open economy, a food supplement (Purina Rat Chow 5012) was supplied a half hour after the end of the PM session each day.

Phase #2:

The eight rats were given continuous or 24 hours access to the bars at each of the eight stations. The interval schedules were 30, 90, and 180 sec. with each interval in effect for five consecutive days. The whole phase of this part of the experiment took 15 days. Responses and reinforcements were again recorded by the Pet 4032 computer. Video recordings of the experiment were analyzed to obtain a measure of preference for either the fixed or variable stations. This was achieved by counting the number of rats at either the fixed or variable stations, using a 10 minute sampling interval, for each 24 hour period of video recorded data (Goldstein, Gregory, & Fry, 1995).

The rats produced their entire daily food requirement from bar pressing during this phase. No supplemental feeding was provided. Careful monitoring of the daily reinforcements produced by the rats was maintained to ensure food requirements were being met.

Phase #3:

Observations of the reinforcements produced during phase #2 suggested that a shorter interval value might produce a significant difference between the fixed and variable scheduled stations. This phase of the experiment involved 24 hour exposure to the stations on a 15 sec. interval for five consecutive days. Similar procedures as those used in phase #2 were followed in this phase.

Phase #4:

For symmetry of results, this phase was conducted utilizing a 15 sec. interval and following the same procedures used in phase #1 for the open economy. This phase of the experiment was conducted over five consecutive days.

Results

Four measures of preference for the fixed or variable stations were analyzed. These included the number of rat observations at either station type, number of reinforcements produced, number of responses, and the mean number of responses per reinforcement. These measures are presented in the above order under each of the following three sections, Open Economy, Closed Economy, and Comparisons of the Open and Closed Economies.

Open Economy:

Number of rat observations at either the fixed interval (FI) or the variable interval (VI) stations

The total number of rat observations at either the fixed or variable interval stations, is a measure of risk - sensitivity. When a significantly greater number of rats was observed at the fixed interval stations as opposed to the variable stations, the animals were said to be risk-averse. When the variable stations were observed to have a significantly greater number of rats than the fixed stations, the animals were said to be risk-prone.

The number of rats observed at the four fixed stations were added together to get the total number of rat observations on the fixed side of the arena. This was likewise done for the four variable stations.

T-tests were first performed to compare the AM sessions with the PM sessions. Results indicated that for fixed interval 15, significantly more rats were observed during the AM sessions (n = 599) than during the PM sessions (n = 550; $t(8) = 2.57$, $p < .05$). No significant difference was found between the AM and PM sessions for any of the other interval values (see Appendix 1).

A 2(fixed, variable) x 4(15, 30, 90, and 180 sec. interval) ANOVA found no significant overall difference between the fixed and variable stations for number of rat observations, nor was there a significant difference between the interval values. The interaction between the stations variance and interval values was also non-significant. Due to the observed reduction in number of rats at the 180 sec. interval for the fixed stations (see Figure 2) it was felt that oneway ANOVAs should be conducted between the four interval values for both the fixed and variable stations. As expected a significant difference was found for the fixed stations ($F(3, 16) = 3.69$, $p < .05$), but not the variable

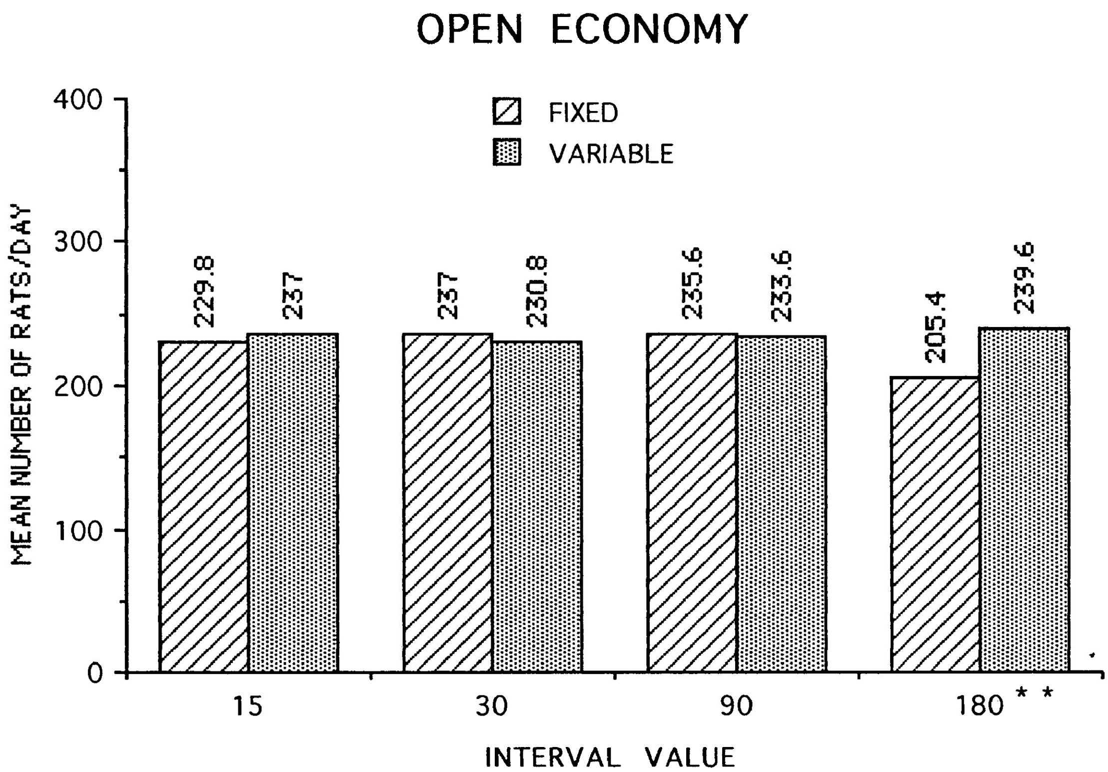


Figure 2. Preference, as measured by the mean number of rats/day observed between the fixed and variable stations for each of the four interval schedules in the open economy (** = significant at $p < .01$).

stations. Using a significance level of $p < .05$, the Tukey post hoc test of significance revealed that FI30 differed from FI180. No other differences were found.

Chi-squares were performed to individually compare the fixed interval stations with the variable interval stations for each of the four interval values. Due to the fact that all eight rats were not always observed to be at one of the stations during a count, the combined total number of all rats observed foraging at the fixed and variable stations during like interval sessions, was divided in half to obtain the expected number of foraging rats when no difference existed between the fixed and variable stations. Table 1 displays the five day totals of the number of rats observed at the fixed and variable stations, as well as the expected number when no difference would be present. The only significant difference was found at the 180 sec. interval (χ^2 (1, N = 2226) = 13.29, $p < .01$). At this interval value, significantly more rats were observed at the variable stations (n = 1198) than at the fixed stations (n = 1027).

Figure 2 displays the mean number of rats/day observed between the fixed and variable stations during each of the four interval schedules in the open economy. The figure shows that when possible net energetic gain was at its lowest, during interval 180 sec., significantly less rats were observed at the fixed stations.

Table 1. Five day totals of the minute-to-minute sampling of the number of rats observed at the fixed and variable stations, as well as the expected number when no significant difference would exist, for each of the four interval schedules in the open economy (** = significant at $p < .01$).

Interval Schedule	Fixed	Variable	Total	Expected
15	1149	1185	2334	1167
30	1185	1154	2339	1169.5
90	1178	1168	2347	1173.5
180**	1027	1198	2226	1113

<u>Number of reinforcements between the FI and the VI stations</u>

T-Tests comparing the AM and PM sessions for the fixed and variable sides separately were found not to differ significantly from each other (see Appendix 2).

The 2 x 4 ANOVA found no significant overall difference between the fixed and variable stations for number of reinforcements produced, but did reveal a significant difference between interval values ($F(3, 32) = 2161.32$, $p < .01$. No interaction effect was present. Both oneway ANOVAs conducted on the interval values were significant (Fixed, $F(3, 16) = 1454.24$, $p < .01$; Variable, $F(3, 16) = 864.77$, $p < .01$). The Tukey post hoc test revealed that for both the fixed and variable stations each interval value was significantly different from the other three interval values in terms of reinforcements produced.

T-Tests individually comparing the fixed side with the variable side, indicated no significant differences at any of the four interval schedule values (see Appendix 2).

Figure 3 illustrates the mean number of reinforcements produced per day at the fixed and variable stations, during each of the four interval schedules in the open economy. The figure shows that the number of reinforcements produced between the fixed and variable stations remained relatively equal during each of the four interval values.

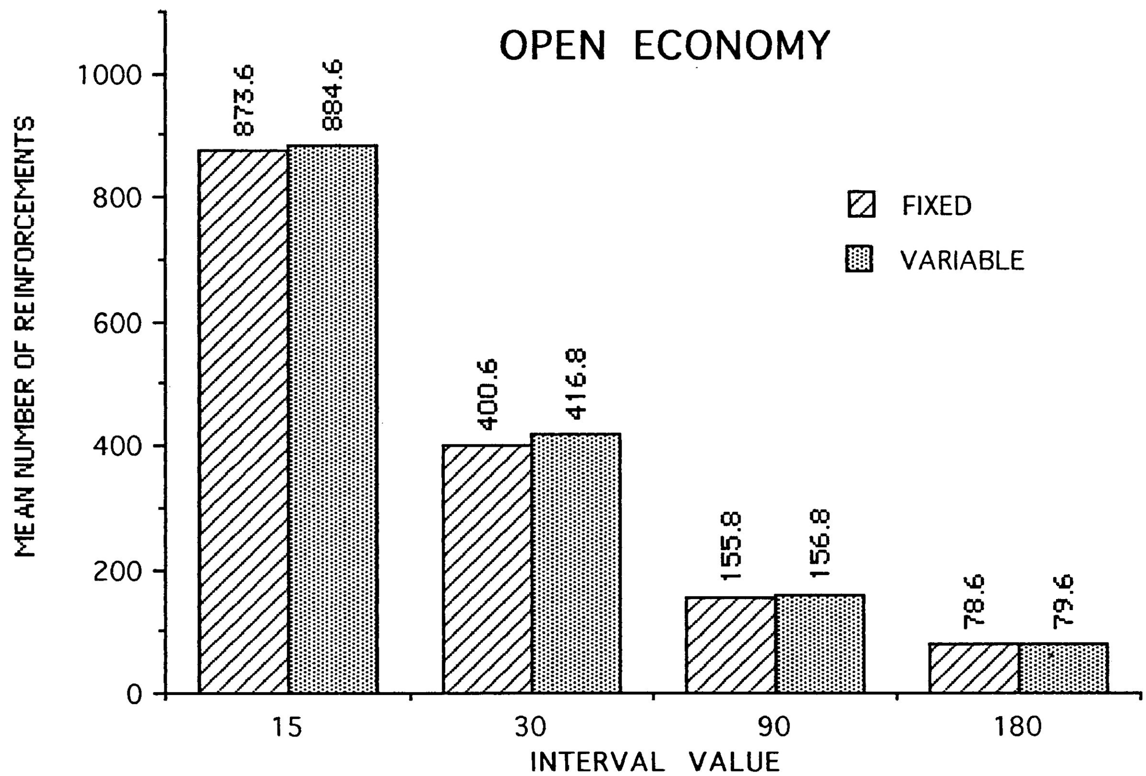


Figure 3. Mean number of total reinforcements produced per day at the fixed and variable stations, during each of the four interval schedules in the open economy.

<u>Number of responses between the FI and the VI stations</u>

T-Tests comparing the responses made between the AM and PM sessions on the fixed and variable sides during each of the four interval schedule values were not found to be significantly different (see Appendix 3).

A 2 x 4 ANOVA found a significant overall difference between the fixed (overall x = 12395.8) and variable (overall x = 16112.85) stations for number of responses ($F(1, 32) = 18.9$, $p < .01$), and a significant difference between intervals ($F(3, 32) = 124.57$, $p < .01$), but no interaction effect. Both oneway ANOVAs conducted for the intervals were found to be significant (Fixed, $F(3, 16) = 88.62$, $p < .01$; Variable, $F(3, 16) = 48.39$, $p < .01$). The Tukey post hoc test revealed that for the fixed stations, only FI15 was significantly different from each of the other three interval values. For the variable stations, VI15 was also different from each of the other three interval values, and VI90 was different from VI180. No other differences were found.

T-Tests individually comparing the fixed side with the variable side during each of the four interval schedule values, indicated that there was a significant difference at interval 30 ($t(8) = 3.76$, $p < .01$), and interval 90 ($t(8) = 5.00$, $p < .01$). In both cases significantly more responses were made per day on the variable side (VI30, x = 12702.2; VI90, x = 13885.8) as opposed to the fixed side (FI30, x =

7182.6; FI90, x = 7892.6).

Figure 4 illustrates the difference in mean responses per day between the fixed and variable stations during each of the four interval schedule values in the open economy. The figure shows that significantly more responses occurred at the variable stations when interval length was 30 and 90 sec., but the difference disappeared when it increased to 180 sec. See Appendix 3 for a display of the stability of responding over the five day period for each of the four interval schedule values.

Mean number of responses per reinforcement between the FI and the VI stations

The mean number of responses/reinforcements was obtained by dividing the number of responses by reinforcements produced, and is a measure of the cost of a pellet (COP).

The 2 x 4 ANOVA found a significant overall difference between the fixed (overall x = 48.45) and variable (overall x = 63.76) stations for the COP ($F(1, 32) = 24.02$, $p < .01$), as well as a difference in interval values ($F(3, 32) = 121.63$, $p < .01$) and an interaction between the stations variance and interval value ($F(3, 32) = 6.23$, $p < .01$). Both oneway ANOVAs were found to be significant (Fixed, $F(3, 16) = 65.16$, $p < .01$; Variable, $F(3, 16) = 62.98$, $p < .01$). The Tukey post hoc test revealed that for the fixed stations, both FI90 and FI180 were each significantly different from each of the

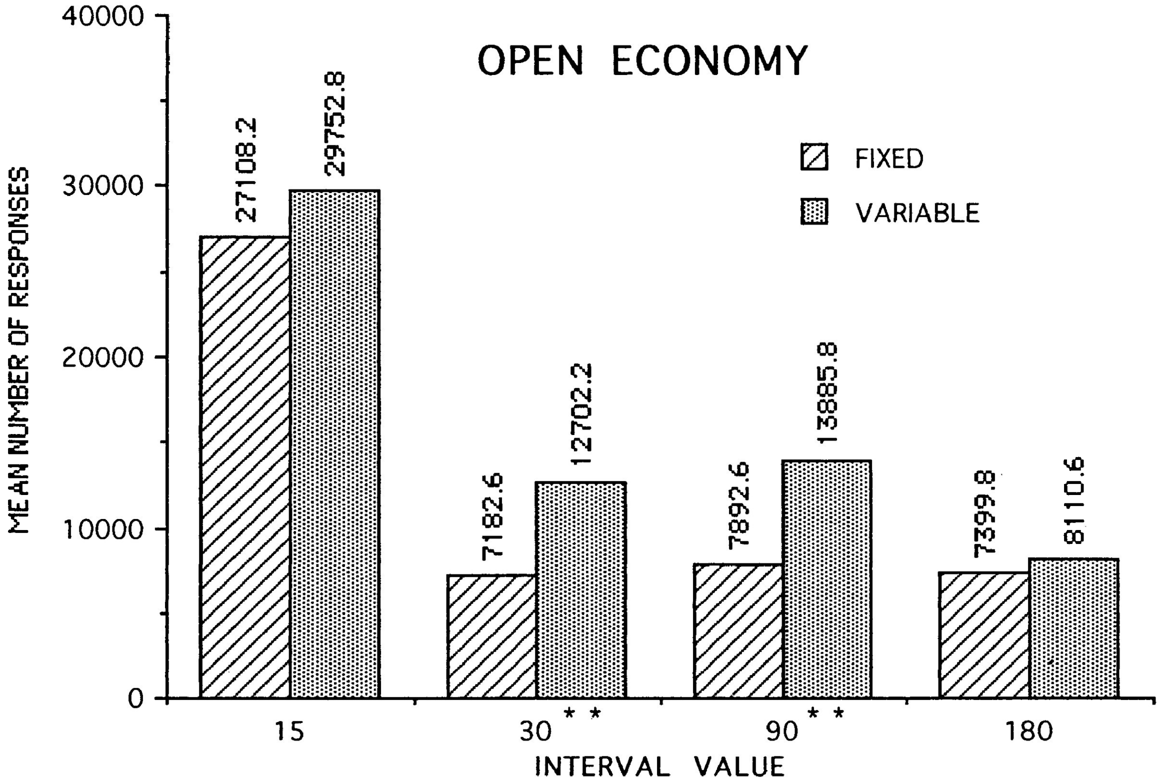


Figure 4. Mean number of total responses per day at the fixed and variable stations, during each of the four interval schedules in the open economy (** = significant at $p < .01$).

other three interval values, with no other differences present. For the variable stations, VI90 and VI180 were different from both VI15 and VI30 but not each other. No other differences were found.

T-Tests individually comparing the fixed stations with the variable stations found a significant difference at only interval 30 sec. ($t(8) = 4.49$, $p < .01$) and interval 90 sec. ($t(8) = 4.82$, $p < .01$). For both interval values the mean COP was higher at the variable stations (VI30 = 30.24; VI90 = 88.65) than at the fixed stations (FI30 = 18.05; FI90 = 50.75) (see Appendix 4).

Figure 5 displays the mean COP per day at the fixed and variable stations, during each of the four interval schedules in the open economy. The figure shows that relative to the fixed stations, COP was higher at the variable stations, reaching significance at intervals 30 and 90 sec. Overall, the COP became much greater as the interval length increased.

Closed Economy:

<u>Number of rat observations at either the FI or the VI stations</u>

To verify the accuracy of the 10 minute interval sampling used for the closed economy, one day for each of the interval values was randomly selected, and the minute-to-minute count of the number of rat observations between the fixed and variable stations was obtained for comparison with

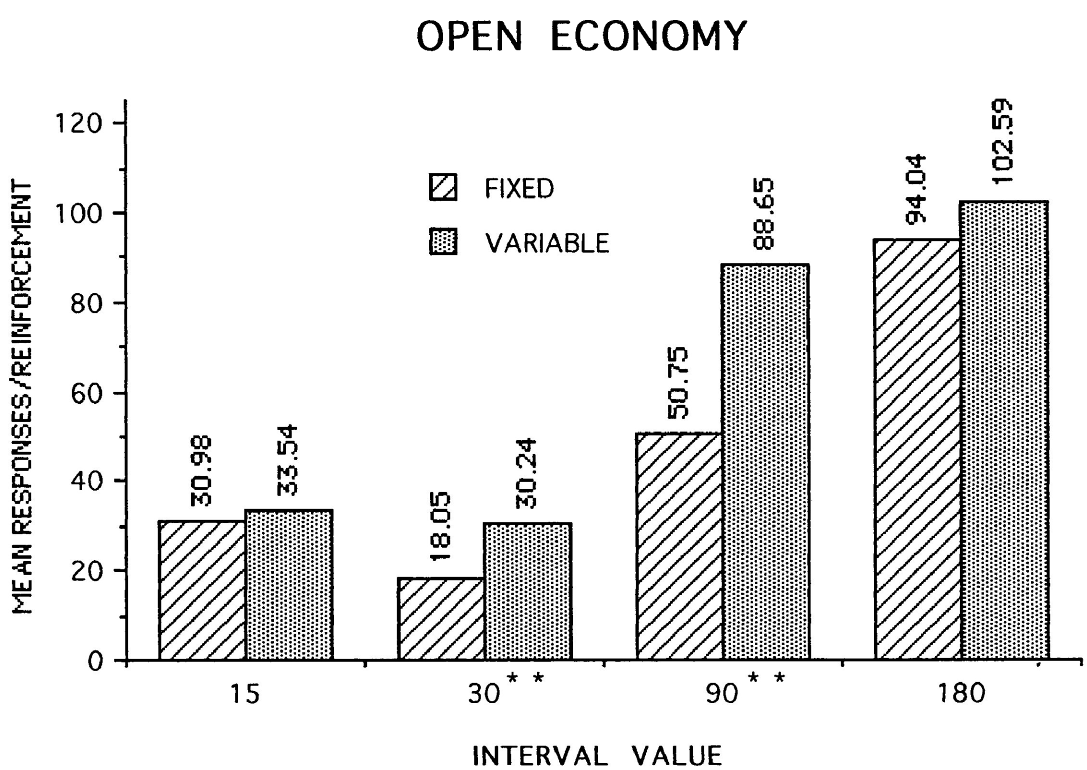


Figure 5. Mean cost of a pellet per day at the fixed and variable stations, during each of the four interval values in the open economy (** = significant at $p < .01$).

the 10 minute sampling. Table 2 displays the comparison of the number of rat observations for the minute-to-minute interval sample, with the 10, 30, and 60 minute samplings. The average percentage of error over the four days sampled for the 10 minute sampling interval was 1.75%. A 2% error was used to test for possible changes in the chi-squares obtained between the four interval schedules. Although this error could be in a direction that favoured significance, a conservative stance was taken where the error calculations were in the direction that did not favour significance.

Table 3 displays the five day totals of the 10 minute interval sampling of the number of rat observations at the fixed and variable stations, as well as the expected number when no difference would be present.

A 2 x 4 ANOVA indicated a significant overall difference between the fixed (overall x = 64.75) and variable (overall x = 112.4) stations ($F(1, 32) = 48.48$, $p < .01$), as well as a difference in intervals ($F(3, 32) = 13.31$, $p < .01$) and an interaction between the stations variance and interval value ($F(3, 32) = 4.86$, $p < .01$). Both oneway ANOVAs conducted on the interval values were significant (Fixed, $F(3, 16) = 11.46$, $p < .01$; Variable, $F(3, 16) = 6.95$, $p < .01$). The Tukey post hoc test revealed that for the fixed stations, the only difference was for FI180, which was significantly different from each of the other three interval values. For

Table 2. 1, 10, 30, and 60 minute samplings of the number (percentage) of rat observations at either the fixed or variable stations for a randomly selected day during each of the four interval schedules of the closed economy (F = Fixed, V = Variable).

Interval	Sampling Interval in Minutes							
	1		10		30		60	
Value	F	V	F	V	F	V	F	V
15	207 (15)	1162 (85)	23 (17)	112 (83)	5 (12)	36 (88)	3 (11)	24 (89)
30	398 (28)	1012 (72)	40 (29)	97 (71)	14 (30)	32 (70)	10 (36)	18 (64)
90	724 (49)	756 (51)	68 (46)	79 (54)	25 (46)	29 (54)	12 (43)	16 (57)
180	1166 (44)	1496 (56)	119 (43)	158 (57)	36 (39)	57 (61)	22 (44)	28 (56)

Table 3. Five day totals of the 10 minute sampling interval of the number of rat observations at the fixed and variable stations for each of the four interval schedules, as well as the expected number when no significant difference would exist between the fixed and variable stations, for the closed economy (** = significance level of $p < .01$).

Interval Schedule	Fixed	Variable	Total	Expected
15**	140	581	721	360.5
30**	322	571	893	446.5
90**	304	389	693	346.5
180**	529	707	1236	618

the variable stations, the only difference found was between VI90 and VI180.

Individual Chi-squares for all four interval levels, revealed that significantly more rats were observed to forage at the variable stations over the fixed stations (15 sec., χ^2 (1, N = 721) = 269.74, $p < .01$; 30 sec., χ^2 (1, N = 893) = 69.43, $p < .01$; 90 sec., χ^2 (1, N = 693) = 10.43, $p < .01$; 180 sec., χ^2 (1, N = 1236) = 25.63, $p < .01$) (Note: refer to Table 3 for the number of rat observations at the variable and fixed stations respectively). When the 2% error is taken into account, all except the 90 sec. interval remained at the same significance level of $p < .01$ (see Appendix 5). However the 90 sec. interval did remain significant (χ^2 = (1, N = 693) = 4.73, $p < .05$).

Figure 6 displays the comparison of the mean number of rats/day observed between the fixed and variable stations during each of the four interval schedules in the closed economy. The figure shows that at all interval values, significantly more rats were observed to forage at the variable stations, indicating a preference for the variable stations.

<u>Number of reinforcements between the FI and the VI stations</u>

A 2 x 4 ANOVA indicated a significant overall difference between the fixed (overall x = 1772.75) and variable (overall

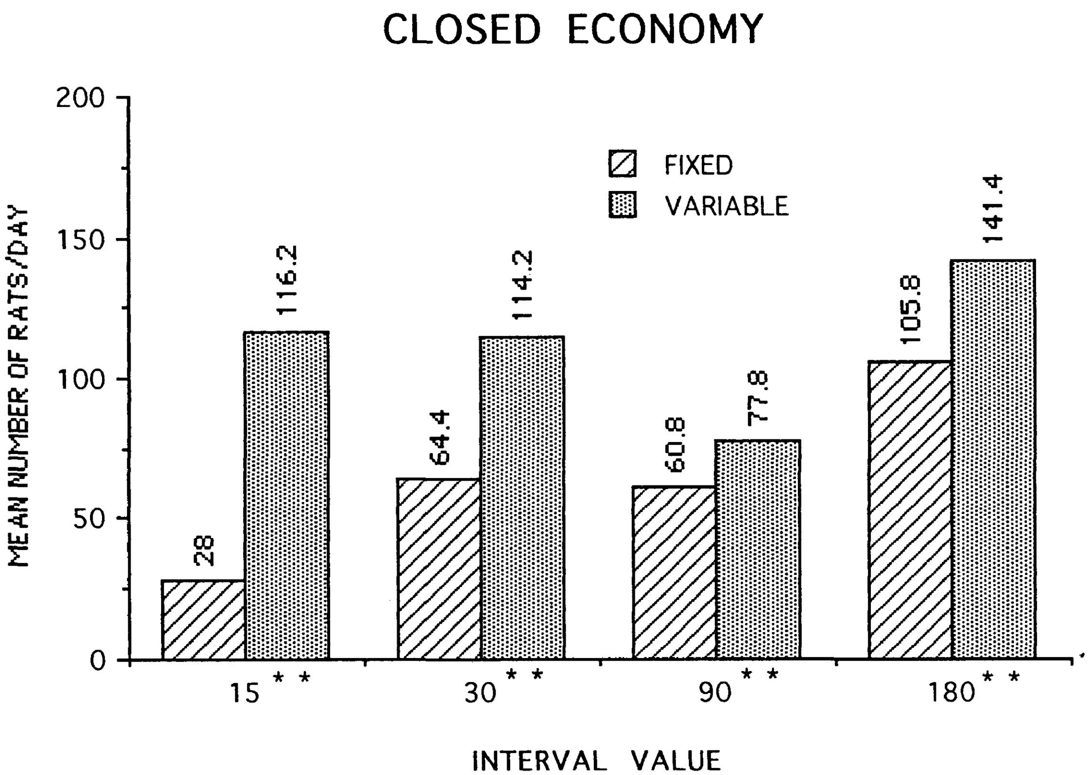


Figure 6. Preference, as measured by the mean number of rats/day observed between the fixed and variable stations for each of the four interval schedules in the closed economy (** = significant at $p < .01$).

x = 2569.6) stations ($F(1, 32) = 20.22$, $p < .01$), as well as a difference between intervals ($F(3, 32) = 15.9$, $p < .01$) and an interaction between the stations variance and interval value ($F(3, 32) = 15.36$, $p < .01$). Oneway ANOVAs conducted on the interval values, indicated a significant difference for the variable stations ($F(3, 16) = 69.56$, $p < .01$) but not the fixed stations. The Tukey post hoc test conducted on the variable interval stations indicated that both VI15 and VI30 were each significantly different from all three other interval values. No other differences were observed.

T-Tests comparing the fixed side to the variable side for each of the four interval schedule values, indicated that the only significant difference was at interval 15 sec. ($t(8) = 5.60$, $p < .01$), where significantly more reinforcements were produced on the variable side (x = 4326.6) than on the fixed side (x = 1474.4) (see Appendix 6).

Figure 7 illustrates the mean number of total reinforcements produced per day at the fixed and variable stations, during each of the four interval values in the closed economy. The figure shows that when net energetic gain was potentially at its highest, at interval 15 sec., significantly more reinforcements were produced at the variable stations, but this difference disappeared when the interval value was increased in length.

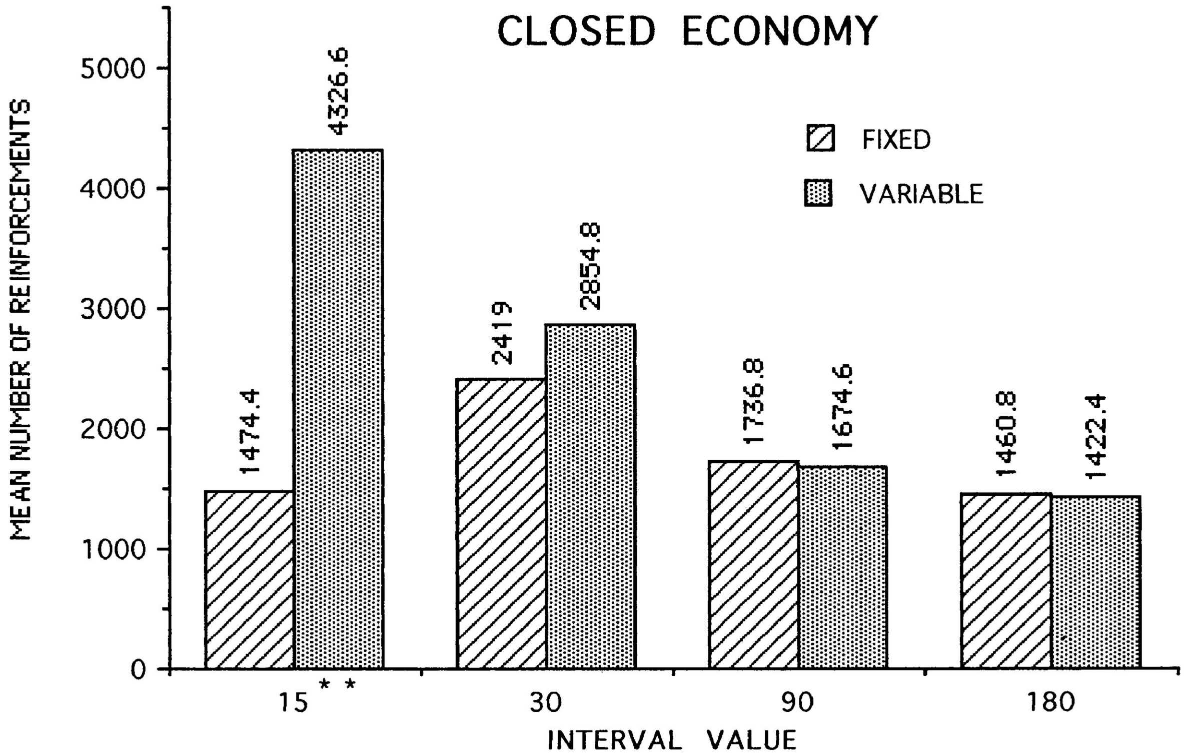


Figure 7. Mean number of total reinforcements produced per day at the fixed and variable stations, during each of the four interval schedules in the closed economy (** = significant at $p < .01$).

Number of responses between the FI and the VI stations

A 2 x 4 ANOVA indicated no overall difference between the fixed and variable stations, but a difference did exist between interval value ($F(3, 32) = 3.02$, $p < .05$) and an interaction effect was present between the stations variance and interval value ($F(3, 32) = 10.37$, $p < .01$). Oneway ANOVAs conducted on the interval values, indicated a significant difference for the variable stations ($F(3, 16) = 20.83$, $p < .01$) but not the fixed stations. The Tukey post hoc test conducted on the variable interval stations indicated that VI15 was significantly different from each of the other three interval values, and that VI30 was different from VI90. No other differences were found.

T-Tests individually comparing responses between the fixed and variable stations, indicated that at interval 15 sec., significantly ($t(8) = 4.45$, $p < .01$) more responses were made on the variable side (x = 51556) than on the fixed side (x = 13602.8). However this reversed for interval 90 ($t(8) = 3.81$, $p < .01$), and interval 180 ($t(8) = 4.03$, $p < .01$) which each had significantly more responses to the fixed stations (FI90, x = 21769.2; FI180, x = 33417.6) over the variable stations (VI90, x = 14016; VI180, x = 21592). No significant difference was found for interval 30 (see Appendix 7).

Figure 8 illustrates the difference in mean responses

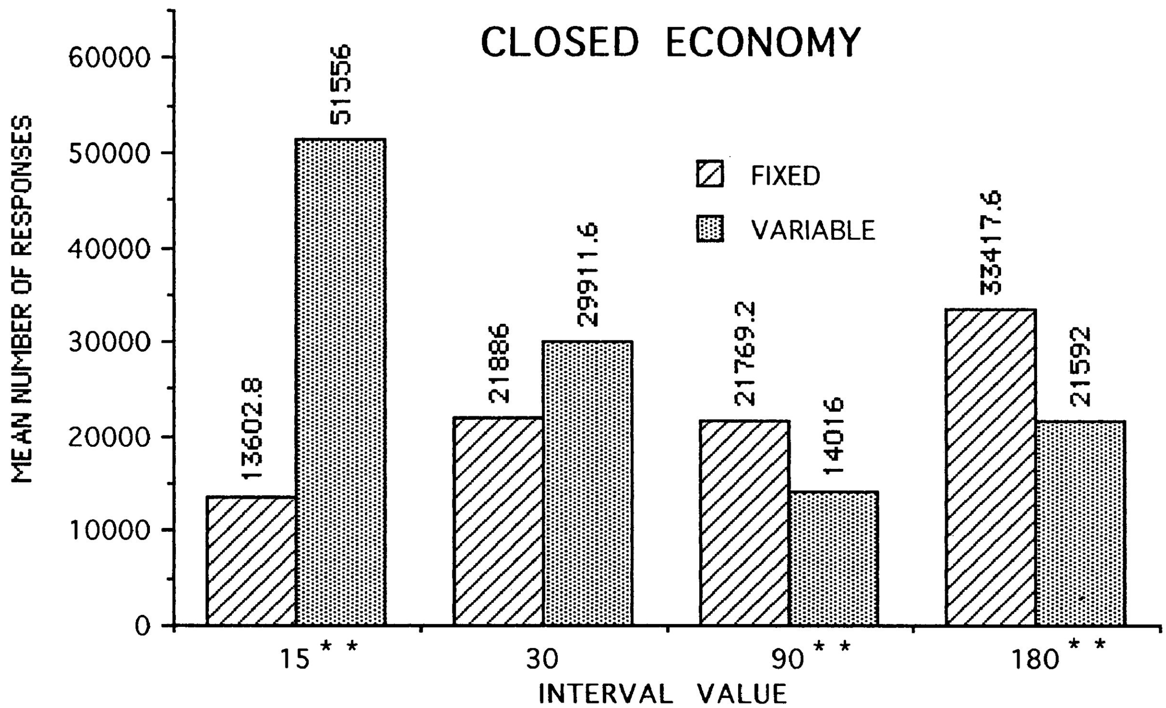


Figure 8. Mean number of total responses per day at the fixed and variable stations, during each of the four interval schedules in the closed economy (** = significant at $p < .01$).

per day between the fixed and variable stations during each of the four interval schedule values in the closed economy. The figure shows that at the shorter interval values, more responses were made at the variable stations, but this difference reversed when the interval durations became longer. See Appendix 7 for a display of the stability of responding over the five day period for each of the four interval schedule values.

Mean number of responses per reinforcement between the FI and the VI stations

The 2 x 4 ANOVA found no significant overall difference between the fixed and variable stations for the COP, but did reveal a difference between interval values ($F(3, 32)$ = 221.03, $p < .01$) and an interaction effect between the stations variance and interval value ($F(3, 32) = 10.62$, $p < .01$). Both oneway ANOVAs were found to be significant (Fixed, $F(3, 16) = 27.89$, $p < .01$; Variable, $F(3, 16) = 6.35$, $p < .01$). The Tukey post hoc test revealed that for the fixed stations, FI180 was significantly different from each of the other three interval values, with no other differences present. For the variable stations, VI90 and VI180 were different from each other. No other differences were found.

T-Tests individually comparing the fixed stations with the variable stations found a significant difference at interval 15 sec. ($t(8) = 2.8$, $p < .05$), interval 90 sec.

($t(8) = 2.92$, $p < .05$) and interval 180 sec. ($t(8) = 4.61$, $p < .01$). For interval 15 the mean COP was higher at the variable stations (VI15 = 11.92) over the fixed stations (FI15 = 7.01), where as at intervals 90 and 180 sec.,the COP was higher at the fixed stations (FI90 = 12.59; FI180 = 22.86) over the variable stations (VI90 = 8.46; VI180 = 15.09; see Appendix 8).

Figure 9 displays the mean COP per day at the fixed and variable stations, during each of the four interval schedules in the closed economy. The graph shows that at the shorter interval lengths the COP was higher at the variable stations, but as the interval length increased, the COP at the fixed stations increased at a greater rate to eventually become significantly more than the variable stations.

Comparisons of the Open and Closed Economies

To compare the differing effects of the two economies upon the measure of number of rat observations between the fixed and variable stations, the data was converted to proportions between the fixed and variable stations for each interval value within each economy (see Table 4). This was necessary due to the differing sampling intervals utilized between the open and closed economies. Utilizing the relative proportion of rats at the variable stations, a 2(open, closed) x 4(15, 30, 90, and 180 sec. interval) ANOVA indicated an overall difference between the open (x = .510)

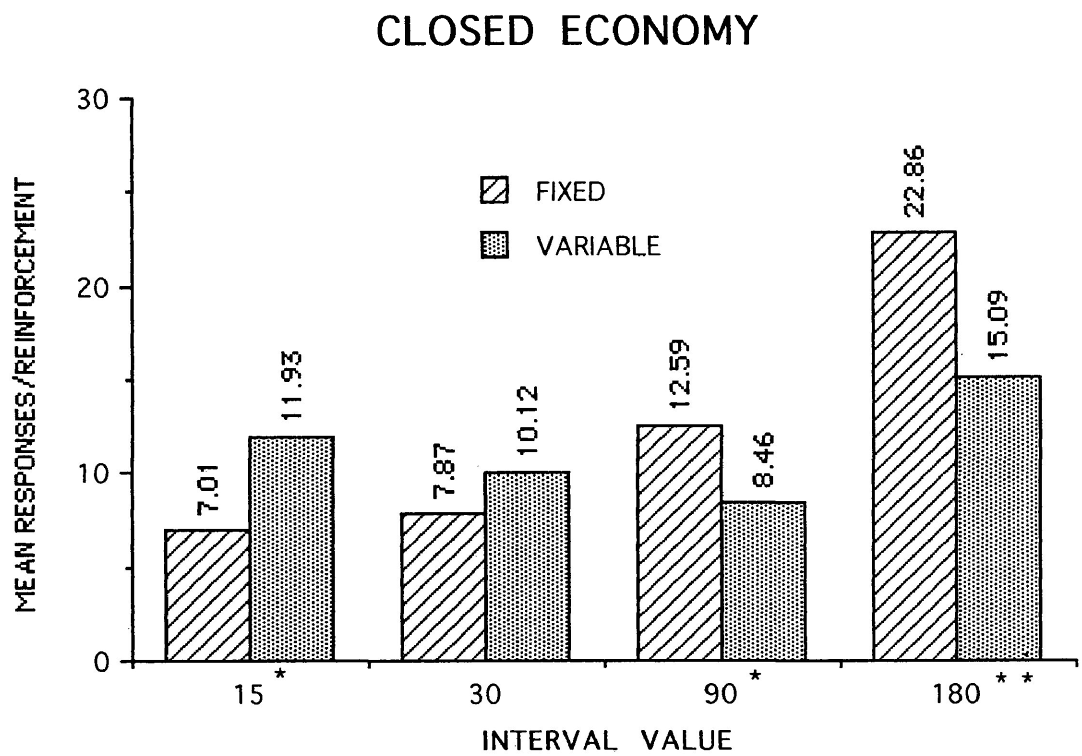


Figure 9. Mean cost of a pellet per day at the fixed and variable stations, during each of the four interval values in the closed economy (* = significant at $p < .05$; ** = significant at $p < .01$).

Table 4. The relative proportions of the mean number of rats observed foraging at the fixed and variable stations for each of the four interval values during the open and closed economies.

	Open Economy		Closed Economy	
Interval Schedule	Fixed	Variable	Fixed	Variable
15	.492	.508	.178	.822
30	.507	.493	.349	.651
90	.500	.500	.437	.563
180	.462	.538	.433	.567

and closed (x = .651) economies ($F(1, 32) = 18.9$, $p < .01$).

Figure 10 displays the proportion of the number of rats foraging at the variable stations in the open and closed economies. The dotted line indicates equal proportions between the fixed and variable stations, while points falling above the dotted line indicates a greater proportion of rats at the variable stations. Conversely, a point that falls below the dotted line indicates a greater proportion of rats at the fixed stations. Figure 10 shows that in the open economy the relative proportion remains near equal between the fixed and variable stations until the 180 sec. interval when relatively more rats are observed at the variable stations. This difference was revealed above as a decline in rats foraging at the fixed stations, and not an increase in rats at the variable stations. In the closed economy, significantly more rats were observed at the variable stations during all four interval values, with the greatest difference occurring during the shortest interval. This relative difference became progressively less as the interval value increased in length.

Figure 11 provides the comparison of the open and closed economies with the actual sampled mean number of rat observations per day at either the fixed or variable stations. Note that the different sampling intervals used between the fixed and variable stations accounts for some of

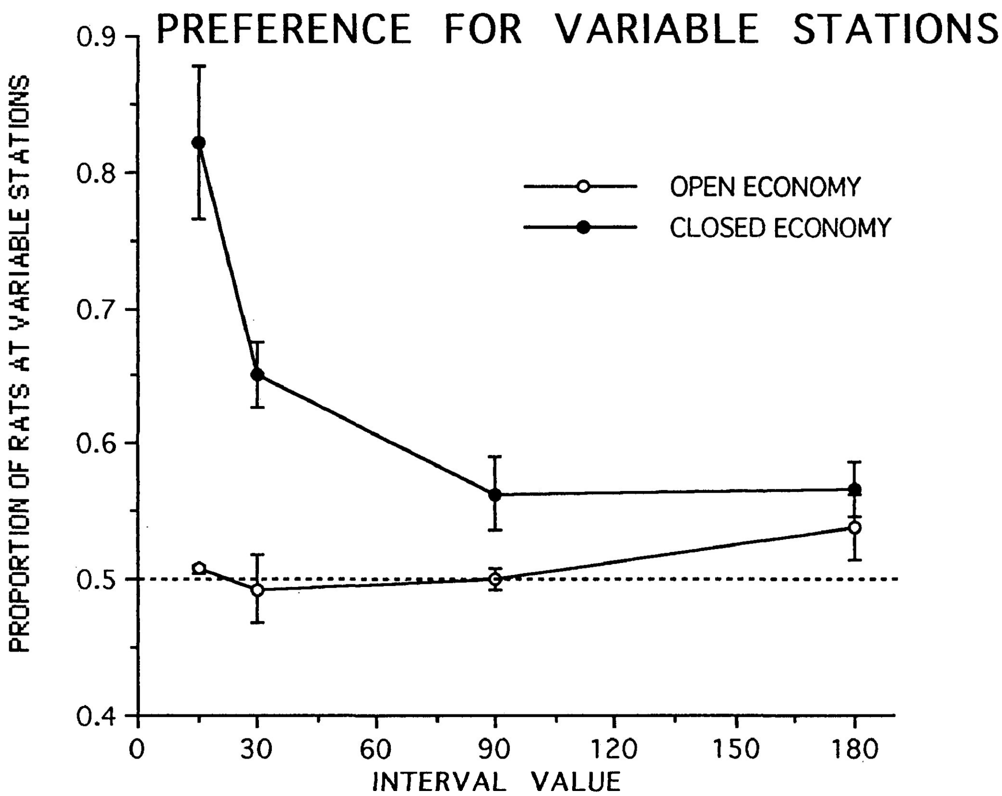


Figure 10. Displays the relative proportion (± SEM) of rats observed at the variable stations in both the open and closed economies during each of the four interval values.

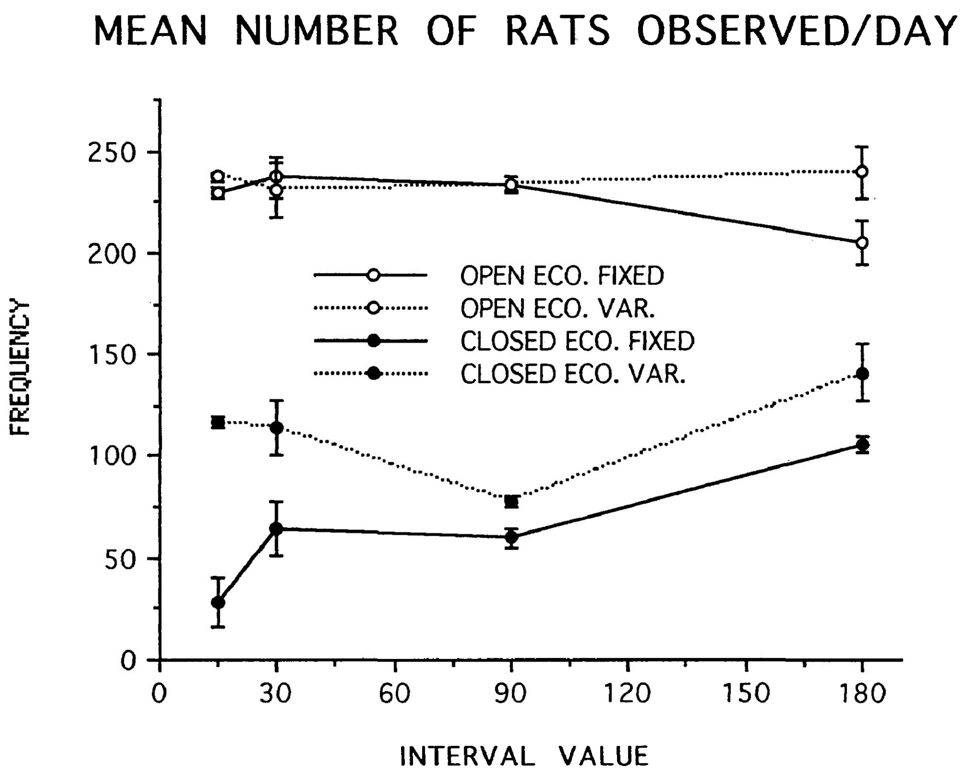


Figure 11. Mean number of rats/day (± SEM) observed between the fixed and variable stations in both the open and closed economies (Note: Different sampling intervals were used between the two economies. Refer to the Method section for an explanation).

the difference observed in the graph between the two economies. Figure 11 more readily displays the reduction in rats at the fixed stations during interval 180 sec. of the open economy. The figure also shows that during the closed economy, the number of rats at the variable stations was consistently higher than at the fixed stations indicating a clear preference for variability along this measure.

The main effect of the 2(economy) x 2(variance) x 4(interval value) ANOVA for mean reinforcements per day indicated an overall difference between the open (x = 380.8) and closed (x = 2171.18) economies ($F(1, 64) = 18.59$, $p < .01$). Figure 12 displays the comparison of mean reinforcements per day between the open and closed economies. As can be seen from the graph, in the open economy the mean number of reinforcements was virtually identical for both the fixed and variable stations, where as in the closed economy significantly more reinforcements were produced at the variable stations during the 15 sec. interval but as the interval length increased the difference became progressively more negligible. Aside from interval 15 sec. the graphs follow similar patterns.

The main effect of the 2 x 2 x 4 ANOVA for mean responses per day indicated an overall difference between the open (x = 14254.4) and closed (x = 25968.9) economies ($F(1, 64) = 39.32$, $p < .01$). Figure 13 displays the comparison of

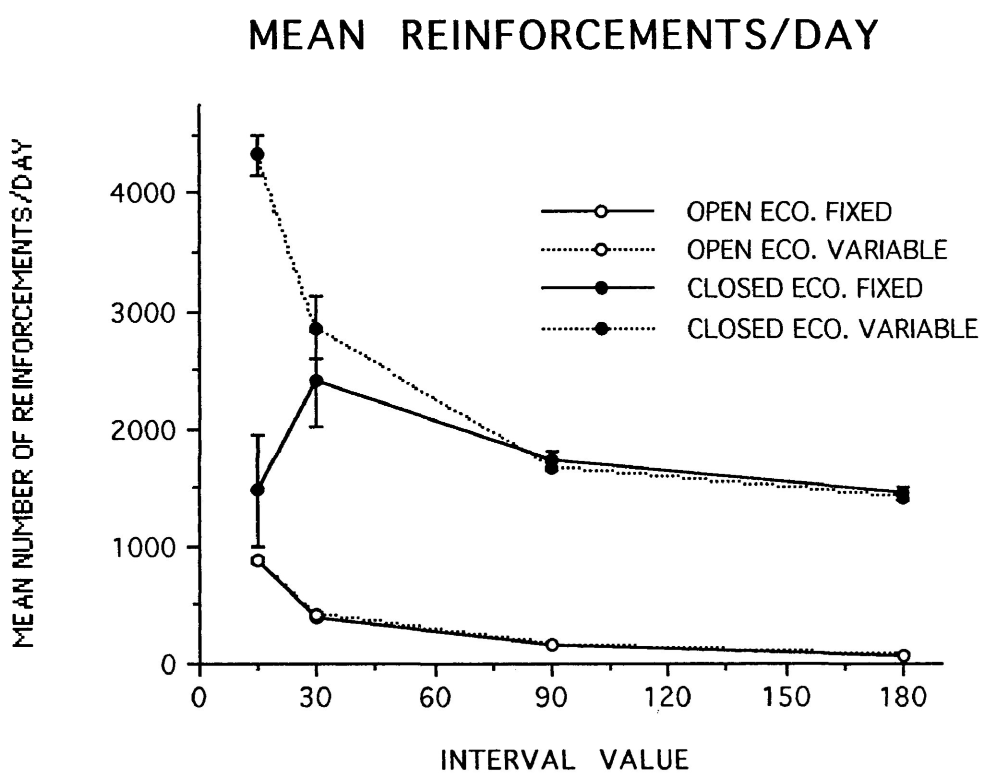


Figure 12. Mean number of reinforcements/day (± SEM) for the fixed and variable stations in both the open and closed economies.

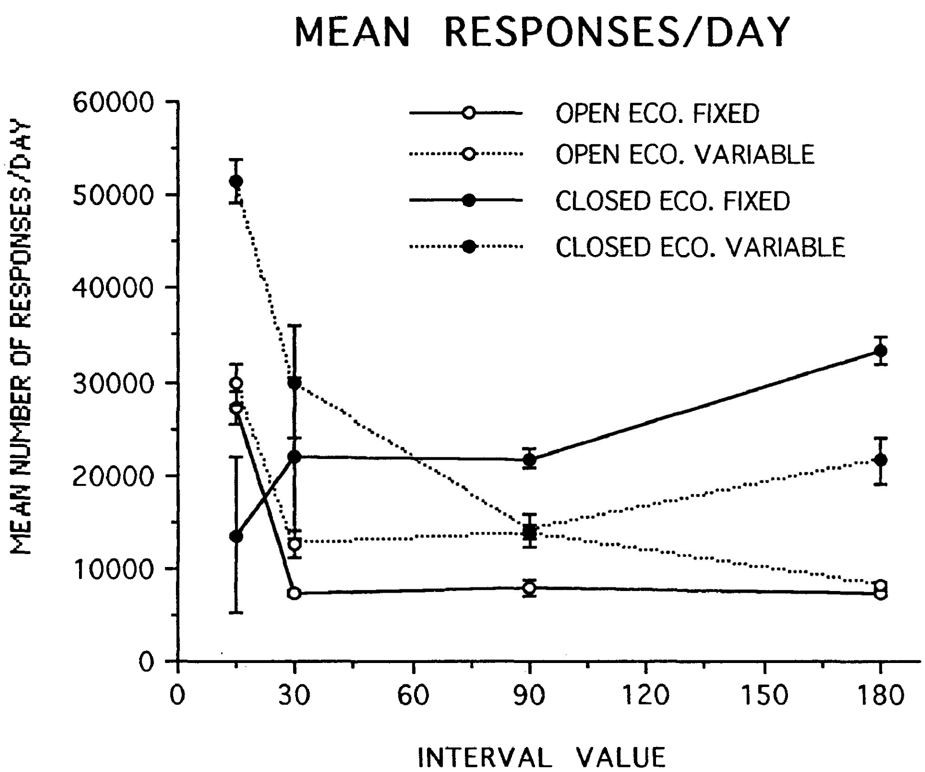


Figure 13. Mean number of responses/day (± SEM) for the fixed and variable stations in both the open and closed economies.

mean responses per day between the open and closed economies. Although the two economies are significantly different, there is some overlap during certain interval values. The mean responses at the variable stations during interval 90 sec. in both economies are nearly identical (open VI90 = 13885.8; closed VI90 = 14016). The mean responses at the fixed stations during interval 15 sec. in the closed economy, is at a level lower than both the fixed and variable stations in the open economy for the same interval value. In the open economy, responses between the fixed and variable stations remain relatively parallel indicating no interaction, where as in the closed economy a definite interaction exists between the fixed and variable stations as the interval value increases in length. During the shorter two intervals more responses occur at the variable stations than at the fixed stations, but this switches to more responses at the fixed stations during the longer two intervals.

The main effect of the 2 x 2 x 4 ANOVA for mean COP per day indicated an overall difference between the open (x = 56.1) and closed (x = 11.99) economies ($F(1, 64) = 738.56$, $p < .01$). Figure 14 displays the comparison of mean COP per day between the open and closed economies. What is most evident from Figure 14 is the rapid increase in COP from interval 30 to interval 180 sec. in the open economy, where as the COP changes very little from interval 15 through to

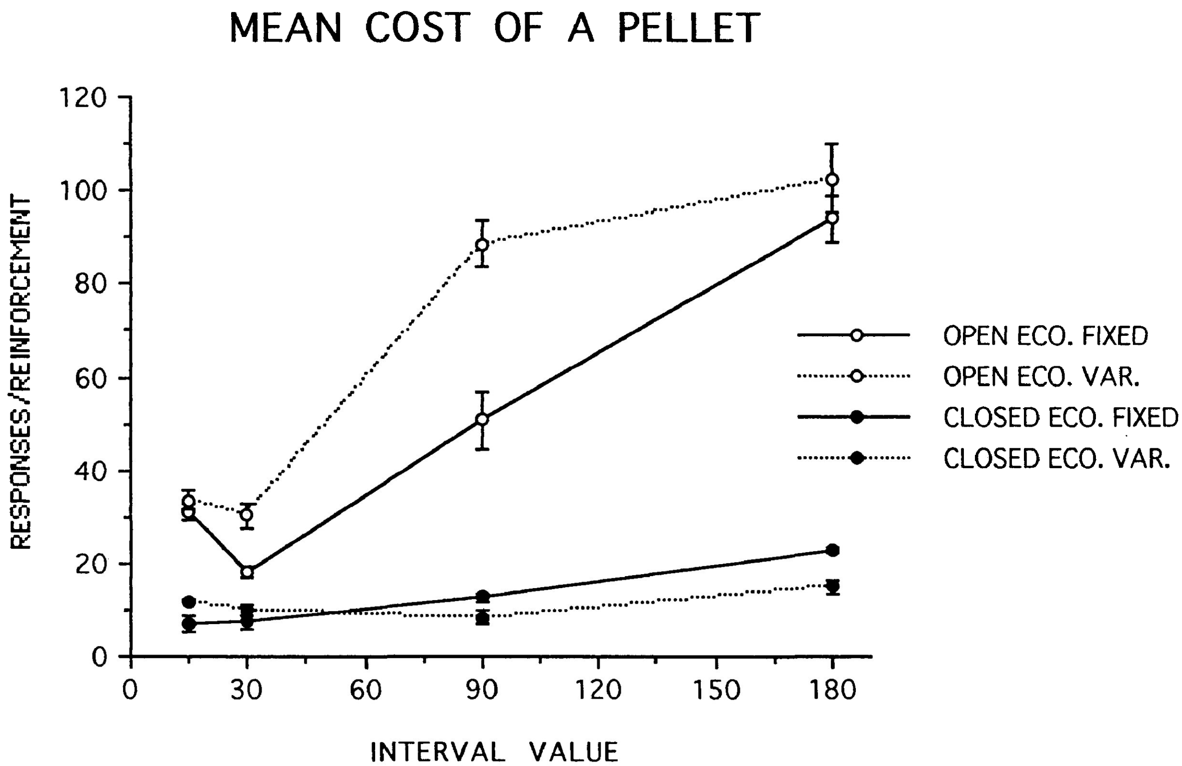


Figure 14. Mean cost of a pellet/day (± SEM) for the fixed and variable stations in both the open and closed economies, during each of the four interval values.

interval 180 sec. in the closed economy. In the open economy the COP is consistently higher at the variable stations during all four interval values, but in the closed economy it starts out the same during the 15 sec. interval but decreases during intervals 90 and 180 sec.

Discussion

The main purpose of this study was to determine whether open and closed economies differentially affect risk-sensitive foraging. The results of this study provide an affirmative answer to this question. In particular, the most revealing measure was the number of rats observed foraging between the fixed and variable stations. During the open economy no preference was evident, while during the closed economy a constant preference for the variable stations was exhibited at all interval values.

The differential effects of open and closed economies were also present for the measure of reinforcements produced between the fixed and variable stations. As with the above measure, no difference in number of reinforcements produced between the fixed and variable stations was evident during the open economy. However, preference for the variable stations was present during the closed economy, but only during the shortest interval length when potential net energetic gain was highest. As the interval length was increased in the closed economy, preference for the variable stations decreased to become approximately equal to that of the fixed stations. Responses and COP were somewhat less revealing in terms of preference, but were good indicators of the differential effects of open and closed economies.

The significance of these results is that under unconstrained conditions, a foraging group of rats will always engage in risk-prone behaviour, preferring to forage in variable food patches rather than in fixed food patches. The source of these constraints comes from the short temporal nature of open economies, and their reliance upon subjects operating under conditions of food deprivation. During the open economy in the present study, the deprivation levels of all the rats was increased jointly, resulting in all eight rats competitively foraging concurrently when the bars were made available. Since there was only four variable stations to choose from, the increased competition and deprivation levels led to the utilization of the concurrently available four fixed stations. The closed economy effectively eliminated these constraints, thus reducing deprivation levels and conspecific competition. In addition the closed economy provided a more direct link between performance and reinforcement, a condition which Hursh (1984) notes is largely absent in the open economy. This resulted in the rats freely foraging in a manner that more readily revealed their preference for the variable stations, and provided greater generality to the natural environment.

Based on the results of the present study, the author feels preference be given to closed economies over open economies during investigations that involve the analysis of foraging behaviour. What follows is a step-by-step discussion of the results during both the open and closed economies.

The number of rats observed to forage at either the fixed or variable stations in the open economy indicated no overall preference, however a chi-square comparing the fixed and variable stations during the 180 sec. interval did indicate a significant difference, but this was due to an apparent avoidance of the fixed stations, as an increase in the number of rats foraging at the variable stations was not observed (see Figures 2, 10 and 11). When the constraint imposed by the open economy was removed by use of the closed economy, the number of rats foraging at either the fixed or variable stations revealed a constant preference for the variable stations, although the preference became less as the interval length increased (see Figures 6, 10 and 11).

Reinforcements produced between the fixed and variable stations was also differentially affected by open and closed economies. In the open economy the reinforcements produced at the fixed and variable stations was virtually identical at all four interval values (see Figures 3 and 12), whereas during the closed economy, as the interval length decreased, the difference in the number of reinforcements produced at the variable stations over the fixed stations increased (see Figures 7 and 12). This implies that as the amount of available resource increased in the closed economy, producing a corresponding increase in net energetic gain, the rats foraged more at the variable stations over the fixed stations, a pattern that is contrary to Caraco's (1980) risk - sensitivity theory.

Responses were affected differentially by the open and closed economies in a very different manner than the above two measures. During the open economy the number of responses made at the variable stations was significantly higher than at the fixed stations. T-Tests revealed the difference to be during intervals 30 and 90 sec. (see Figures 4 and 13). During the closed economy, responses at the variable stations were significantly higher than at the fixed stations during the 15 sec. interval, but as the interval length increased, it resulted in a reversal where significantly more responses were now made at the fixed stations during intervals 90 and 180 sec. (see Figures 8 and 13).

When reinforcements and responses are investigated in terms of the average response per reinforcement, or cost of a pellet (COP), the pattern within the open and closed economies, between the fixed and variable stations, is similar to that of the mean responses per day. However, during the open economy the COP is significantly higher than during the closed economy. Furthermore, interval value has a direct effect upon the COP in both economies, but during the open economy the COP increases at an accelerated rate compared with the rate of increase during the closed economy.

The prevalence of risk-indifference during the open economy may have been the result of conspecific competition for available resources. In Berklund's (1988) study, which utilized ratios instead of intervals, a group of foraging rats in the operant arena displayed an overwhelming tendency to be risk-averse at all ratio levels. She reported that risk-aversion became less pronounced as the ratio values increased.

On the surface, this may be evidence for the effectiveness of the discriminative stimuli in the present study to enhance the foraging group's ability to discriminate between the fixed and variable stations. Although this should not be ruled out, it is more likely that it was more the result of increased competitiveness in the present study over Berklund's. Both studies utilized eight foraging stations, but differed in population size. In our study the size of the group was eight, whereas in Berklund's study it was four. This twofold increase in competition might have been a significant factor in producing the observed risk-indifference. This is surprising, since the increased competition has the effect of reducing the amount of available resource per individual, and as a result, according to Caraco's (1980) risk-sensitive theory, this should produce an increase in risk-prone behaviour at all levels of resource availability.

Barnard had predicted increased risk-prone behaviour in common shrews when in the presence of an apparent competitor (Barnard, 1990; Barnard & Brown, 1985). This species is normally risk-averse when meeting net energetic requirements and risk-prone when not. In open economy experiments Barnard reports that the common shrew becomes risk-indifferent at all levels of net energetic gain when in the presence of an apparent competitor. His results are very similar to the findings during the open economy sessions of the present study.

Since there was a preference to congregate at the variable stations during the closed economy, the present study appears to indicate that foraging choice between competitive foragers, is masked by use of open economy procedures. In addition, when considering the results of Berklund (1988), who used an open economic design, indifference may be increased when the total number of foraging animals is equal to the total number of available fixed and variable food patches. Why Berklund's study found a prevalence of risk-aversion and the present one did not, could be seen as evidence of the effectiveness of the additional discriminative stimuli which had been utilized in the present study to increase differentiation of patch variance.

The reduction of preference in the closed economy as interval length increased, may be due to patch distance interacting with interval value duration. In typical concurrent interval experiments where an animal has the choice of responding on one of two independent interval schedules, a changeover delay (COD) is often imposed when a switch is made from one schedule to another (Houston & McNamara, 1981). The COD is similar to separating the patches spatially so that switching is not reinforced (Herrnstein, 1961). Such a procedure is not viable in the operant arena since when one rat switches from one patch to another, there may already be a second rat currently working at the patch the rat switches to. If a COD were imposed, it would unfairly penalize the rat that had made no switch. Therefore in the operant arena, the spatial distance between patches and the average time to travel this distance, is relatively the same for all interval values used.

Interval schedules can be thought of as simulating patches with renewing resources. Once a reinforcement has been obtained, a period of time must elapse before the bar is set to payoff again. The shorter the interval, the faster the rate of renewal and therefore the more abundant is the prey in that patch. The marginal value theorem predicts that optimal foragers should leave a patch once the mean level of available resources within that patch falls to the overall level of the environment (Charnov, 1976). Since patch distance is an unchanging variable in the operant arena, increases in the interval schedules length will have the effect of reducing the relative cost of travel time between patches. This change has the effect of reducing a patches mean amount of available resource to an amount that is equal to the overall mean of the environment. In order for a rat to be an optimal forager in such an environment, the animal should leave the patch once it obtains a reinforcement. Conversely, short interval values will have the effect of increasing the relative cost of travelling between patches, resulting in longer giving-up times (ie. less switching) for a foraging rat. Further support of this premise comes from theoretical comparisons of equal concurrent variable interval - variable interval schedules (Houston & McNamara, 1981). Houston and McNamara point out that when the COD is equal to or greater than the interval value, it is never worth switching.

The pattern of reinforcements produced in the closed economy is also attributable to an interaction of patch distance and interval value. The significant number of reinforcements produced during the short interval value at the variable stations over the fixed stations, supports the preference to be risk-prone rather than risk-averse. However the elimination of this difference when the interval length was increased requires explaining.

One of the purposes of using a closed economy design, was to allow the individual rats to forage during periods of time that was different from their conspecifics. Theoretically, if one rat is foraging while the other seven are engaged in other activities (sleeping, grooming, drinking, etc.), the individual now has the choice to forage between four fixed or four variable stations. Therefore when working at a variable station during short mean interval values, and by random a long interval value is selected from the distribution around the mean, the rat can simply move to another variable station which, given the short interval length, is likely set to payoff upon the next response. Again as the mean overall interval length is increased, it becomes more optimal to forage over a wider range of food patches, or in this case available number of variable *and* fixed foraging stations. This results in a relatively equal distribution of reinforcements obtained between the fixed and variable stations at higher interval values, as was the case in the present study. By contrast, when ratio schedules are used in place of intervals, it would be expected that the pattern of reinforcements produced between the fixed and variable stations, would more readily exhibit a constant preference for the variable stations with increasing ratio costs since reinforcement frequency is under the control of the foraging animal. In a companion study to the present one, which is currently under analysis, results for ratio schedules indicate significantly more reinforcements produced at the variable stations over the fixed stations during both small and large ratio values in the closed economy.

Past research has found differential effects of open and closed economies upon response rates. Several researchers report finding a direct relationship between response rate and reinforcer magnitude in open economies, while in closed economies they report an inverse relation between response rate and reinforcer magnitude (Hall & Lattal, 1990; Kendall, 1991; La Fiette & Fantino, 1988; Lucas, 1981). The general agreement is that the future food supplement provided in open economy experiments, causes a decrease in responding as reinforcement frequency is reduced over the experimental sessions.

Not everyone agrees with this explanation, for example Timberlake, Gawley, and Lucas (1987) have demonstrated that food available more than 16 minutes in the future had no effect in decreasing the rate of response during a session. Furthermore, Timberlake and Peden (1987) claim that by manipulating the percentage density of reward, both direct and inverse relations can be produced in both open and closed economies. They contend that past studies of open and closed economies have not used large enough ranges of reward density to obtain this bitonic function of both direct and inverse relationships between responding and reinforcement.

In the present study, response frequency between the four interval values in the open economy followed a direct relationship for both the fixed and variable stations, with a higher number of responses occurring at the variable stations over the fixed. The decrease in responses was however greatest when the interval changed from 15 to 30 sec., after which responses remained relatively constant across increasing interval sessions. During the closed economy an inverse relation between responses and reinforcer magnitude was evident for the fixed stations, but not the variable stations. Initially a direct relationship was observed at the variable stations as reinforcer magnitude decreased from interval 15 sec. to 90 sec., but then an inverse relationship occurred as the reinforcer magnitude was reduced further from interval 90 sec. to 180 sec. It should be noted that the bitonic (decrease then increase in responding) relationship at the variable stations is the reverse pattern (increase then decrease in responding) reported by Timberlake and Peden (1987). In the present study it appears that choice between concurrent fixed and variable stations in the closed economy, upsets the normal relationship due to offsetting work output between the fixed and variable stations, a direct consequence of preference choice.

The difference in the COP's between the two economies has been observed in other studies that utilized interval schedules (La Fiette & Fantino, 1988). La Fiette & Fantino (1988) compared the effects of component duration on multiple-schedule performance in open (one hour duration) and closed (23.5 hour duration) economies. Pigeons responded to varying component durations, but constant variable interval schedules of either 30 or 90 sec. The overall mean COP in the open economy was 29.75 and 33.45 for VI30 and VI90 respectively, while in the closed economy mean COP was 12.8 and 14.1 for VI30 and VI90 respectively (values determined from La Fiette & Fantino, 1988, Table 2, pp 462-463). It can be concluded that economic context also has differential effects upon the mean number of responses per reinforcement during interval schedules of food presentation.

To conclude, a foraging animal tends to prefer to forage in a risk-prone manner, during high and low levels of net energetic gain. However the economic context under which the animals are tested can impose differential effects upon the expression of their foraging choices. Open economies impose constraints that come primarily from their short temporal nature. During open economies animals are propelled to exert relatively the same amount of behaviour they would during 24 hour periods, but in much shorter periods of time. In the present study the eight rats, in an attempt to acquire an equal share of the resources because of equal deprivation levels, had to competitively forage concurrently at all eight food patches, which resulted in a masking of any possible preferences that the group may have. Use of the closed economy removed this constraint by allowing the group to individually spread out their behaviour over the continuously present response bar time period. This allowed the group to more readily exhibit foraging preferences through exclusive foraging in one or the other type of food patch. In the present study, this preference was to forage more at the variable stations than at the fixed stations, regardless of reinforcement frequency.

One further note regarding risk-sensitivity in this study is that during both economic contexts, mean grams of food per day per rat during all experimental sessions was sufficient enough for the rats survival (see Appendixes 2 and 6). Since risk-prone foraging behaviour was exhibited by the rat population during the closed economy, risk-sensitive foraging theory may be enhanced by giving more emphasis to the variance imposed by the schedules of reinforcement and less emphasis to the mean amount of reinforcement. During concurrent equal mean schedule choices, the schedule with the greater variance around the mean will be preferred over the schedule with the lesser variance around the mean. What makes this position more compelling is when you consider that risk-sensitive foraging theory would have predicted constant risk-aversion under conditions when daily net energetic intake is sufficient enough for the animals survival.

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Appendix 1

Open Economy (Dispersion of Base Loadings)

The five day means and totals of the number of times rats were observed, at one minute intervals, to be working at either the fixed or variable stations during the AM and PM sessions in the open economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
AM	599	580	603	566	600	575	534	609
PM	550	605	582	588	578	594	493	589
TOTAL	1149	1185	1185	1154	1178	1169	1027	1198
AM MEAN	119.8	116.0	121.6	113.2	120.0	115.0	106.8	121.8
PM MEAN	110.0	121.0	116.4	117.6	115.6	118.8	98.6	117.8
MEAN/DAY	229.8	237.0	237.0	230.8	235.6	233.8	205.4	239.6

T-Tests comparing the number of rats observed working during the AM sessions with the PM session, for the fixed and variable sides separately.

FI15; $t(8) = 2.57$, $p < .01$, VI15; $t(8) = 1.54$, N.S.

FI30; $t(8) = 0.48$, N.S., VI30; $t(8) = 0.44$, N.S.

FI90; $t(8) = 1.54$, N.S., VI90; $t(8) = 1.07$, N.S.

FI180; $t(8) = 1.84$, N.S., VI180; $t(8) = 0.35$, N.S.

2(variance) x 4(interval) ANOVA.

Variance; $F(1, 32) = 2.19$, N.S.

Interval; $F(3, 32) = 0.87$, N.S.

Variance x Interval; $F(3, 32) = 2.17$, N.S.

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3, 16) = 3.69$, $p < .01$,

VI; $F(3, 16) = 0.16$, N.S.

Chi-squares individually comparing the fixed stations with the variable stations.

I15; $\chi^2(1, N = 2334) = 0.56$, N.S.

I30; $\chi^2(1, N = 2339) = 0.41$, N.S.

I90; $\chi^2(1, N = 2347) = 0.04$, N.S.

I180; $\chi^2(1, N = 2226) = 13.29$, $p < .01$

Appendix 2

Open Economy (Reinforcements)

The five day means of the totals of the number of reinforcements produced at the fixed and variable stations during the AM and PM sessions during the open economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
AM MEAN	445.2	437.4	207.6	207.2	78.4	77.8	39.2	40.8
PM MEAN	428.4	447.2	193.0	209.6	77.4	79.0	39.4	38.8
MEAN/DAY	873.6	884.6	400.6	416.8	155.8	156.8	78.6	79.6

Mean grams/day/rat including the supplemental feeding and reinforcements produced.

Interval Value

15	30	90	180
22.4	17.1	14.3	15.9

T-Tests comparing the reinforcements produced in the AM sessions with the PM sessions for the fixed and variable sides separately.

FI15; $t(8) = 1.32$, N.S., VI15; $t(8) = 0.97$, N.S.

FI30; $t(8) = 1.11$, N.S., VI30; $t(8) = 0.15$, N.S.

FI90; $t(8) = 0.79$, N.S., VI90; $t(8) = 0.44$, N.S.

FI180; $t(8) = 0.20$, N.S., VI180; $t(8) = 0.79$, N.S.

2(variance) x 4(interval) ANOVA.

Variance; $F(1, 32) = 0.89$, N.S.

Interval; $F(3, 32) = 2161.32$, $p < .01$

Variance x Interval; $F(3, 32) = 0.24$, N.S.

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3, 16) = 1454.24$, $p < .01$,

VI; $F(3, 16) = 864.77$, $p < .01$

T-Tests comparing the number of reinforcements produced between the fixed side and the variable side in the open economy.

I15; $t(8) = 0.71$, N.S.

I30; $t(8) = 0.61$, N.S.

I90; $t(8) = 0.31$, N.S.

I180; $t(8) = 0.42$, N.S.

Appendix 3

Open Economy (Responses)

The five day means of the total number of responses made at the fixed and variable stations in the AM and PM sessions during the open economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
AM MEAN	12818.4	15564.0	3373.6	6714.6	3845.6	7006.6	3778.4	3892.4
PM MEAN	14289.8	14188.8	3809.0	5992.0	4047.0	6879.2	3621.4	4218.2
MEAN/DAY	27108.2	29752.8	7182.6	12702.2	7892.6	13885.8	7399.8	8110.6

T-Tests comparing the number of responses made during the AM sessions with the PM sessions, for the fixed and variable sides separately.

FI15; $t(8) = 0.98$, N.S., VI15; $t(8) = 0.74$, N.S.

FI30; $t(8) = 1.36$, N.S., VI30; $t(8) = 0.66$, N.S.

FI90; $t(8) = 0.29$, N.S., VI90; $t(8) = 0.20$, N.S.

FI180; $t(8) = 0.44$, N.S., VI180; $t(8) = 0.74$, N.S.

2(variance) x 4(interval) ANOVA.

Variance; $F(1, 32) = 18.90$, $p < .01$

Interval; $F(3, 32) = 124.57$, $p < .01$

Variance x Interval; $F(3, 32) = 2.12$, N.S.

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3, 16) = 88.62$, $p < .01$,
VI; $F(3, 16) = 48.39$, $p < .01$

T-Tests comparing the number of responses made between the fixed side and the variable side in the open economy.

I15; $t(8) = 0.95$, N.S.
I30; $t(8) = 3.76$, $p < .01$
I90; $t(8) = 5.00$, $p < .01$
I180; $t(8) = 1.17$, N.S.

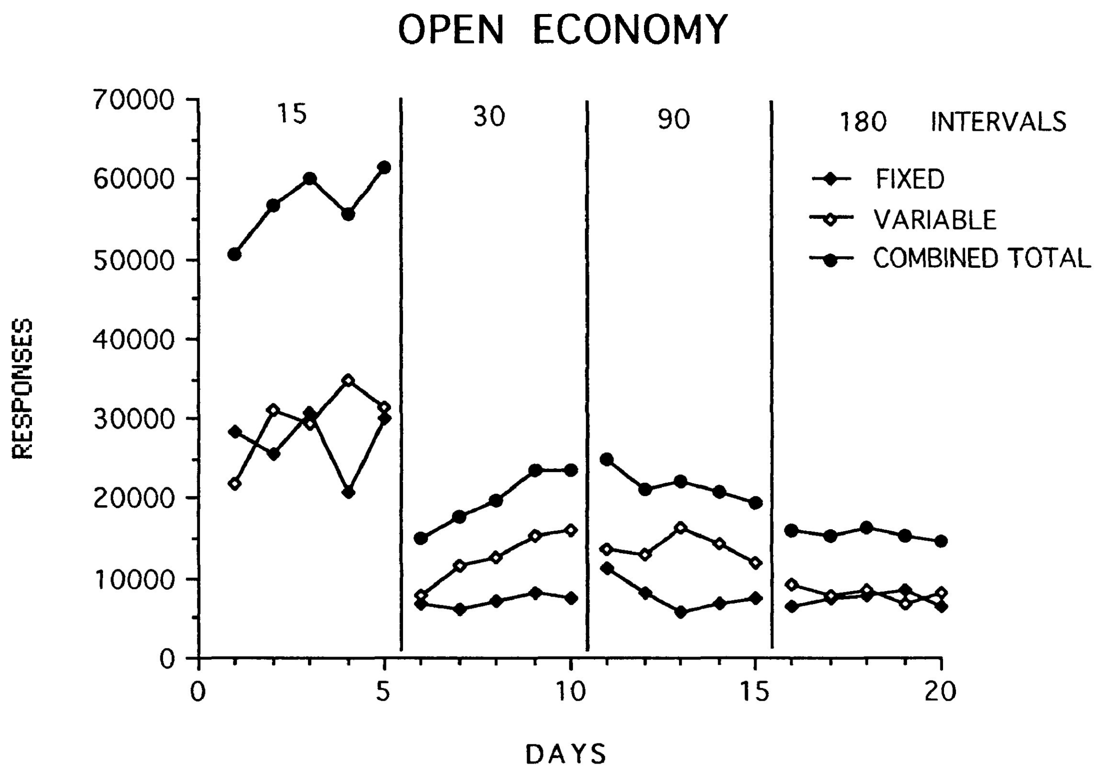

Figure 15. Daily totals of the number of responses at the fixed and variable stations during each of the four interval schedules in the open economy, as well as the daily totals of the fixed and variable stations combined.

Appendix 4

Open Economy (COP)

The five day means of responses/reinforcements, or cost of a pellet (COP) produced at the fixed and variable stations during the open economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
MEAN/DAY	30.98	33.54	18.05	30.24	50.75	88.65	94.04	102.59

2(variance) x 4(interval) ANOVA.

Variance; $F(1, 32) = 24.02, p < .01$

Interval; $F(3, 32) = 121.63, p < .01$

Variance x Interval; $F(3, 32) = 6.23, p < .01$

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3, 16) = 65.16, p < .01$

VI; $F(3, 16) = 62.98, p < .01$

T-Tests comparing the COP between the fixed side and the variable side in the open economy.

I15; $t(8) = 0.93$, N.S.

I30; $t(8) = 4.49$, $p < .01$

I90; $t(8) = 4.82$, $p < .01$

I180; $t(8) = 0.96$, N.S.

Appendix 5

Closed Economy (Dispersion of Base Loadings)

The five day means and totals of the number of times rats were observed, at ten minute intervals, to be working at either the fixed or variable stations in the closed economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
TOTAL	140	581	322	571	304	389	529	707
MEAN/DAY	28.0	116.2	64.4	114.2	60.8	77.8	105.8	141.4

2(variance) x 4(interval) ANOVA.

Variance; $F(1, 32) = 48.48$, $p < .01$

Interval; $F(3, 32) = 13.31$, $p < .01$

Variance x Interval; $F(3, 32) = 4.86$, $p < .01$

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3, 16) = 11.46$, $p < .01$,

VI; $F(3, 16) = 6.95$, $p < .01$

Chi-squares comparing the fixed stations with the variable stations in the closed economy.

I15; $\chi^2(1, N = 721) = 269.74$, $p < .01$

I30; $\chi^2(1, N = 893) = 69.43$, $p < .01$

I90; $\chi^2(1, N = 693) = 10.43$, $p < .01$

I180; $\chi^2(1, N = 1236) = 25.63$, $p < .01$

New totals and Chi-squares comparing the fixed stations with the variable stations in the closed economy when a 2% error towards non-significance is utilized. This was the estimated error between the one minute and ten minute samplings, as derived from the four days sampled at one minute intervals.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
TOTAL	154.42	566.58	339.86	553.14	317.86	375.14	553.72	682.28

I15; $\chi^2(1, N = 721) = 235.61$, $p < .01$

I30; $\chi^2(1, N = 893) = 50.94$, $p < .01$

I90; $\chi^2(1, N = 693) = 4.73$, $p < .05$

I180; $\chi^2(1, N = 1236) = 13.37$, $p < .01$

Appendix 6

Closed Economy (Reinforcements)

The five day means of reinforcements produced at the fixed and variable stations during the closed economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
MEAN/DAY	1474.4	4326.6	2419.0	2854.8	1738.8	1674.6	1460.8	1422.4

Mean grams/day/rat produced during the closed economy.

Interval Value

15	30	90	180
32.6	29.7	19.2	16.2

2(variance) x 4(interval) ANOVA.

Variance; $F(1, 32) = 20.22$, $p < .01$

Interval; $F(3, 32) = 15.90$, $p < .01$

Variance x Interval; $F(3, 32) = 15.36$, $p < .01$

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3, 16) = 2.01$, N.S.

VI; $F(3, 16) = 69.56$, $p < .01$

T-Tests comparing the number of reinforcements produced between the fixed side and the variable side in the closed economy.

I15; $t(8) = 5.60$, $p < .01$

I30; $t(8) = 0.90$, N.S.

I90; $t(8) = 0.77$, N.S.

I180; $t(8) = 0.72$, N.S.

Appendix 7

Closed Economy (Responses)

The five day means of responses made at the fixed and variable stations in the closed economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
MEAN/DAY	13602.8	51556.0	21886.0	29911.6	21769.2	14016.0	33417.6	21592.0

2(variance) x 4(interval) ANOVA.

Variance; $F(1, 32) = 3.54$, N.S.

Interval; $F(3, 32) = 3.02$, $p < .05$

Variance x Interval; $F(3, 32) = 10.37$, $p < .01$

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3, 16) = 1.81$, N.S.

VI; $F(3, 16) = 20.83$, $p < .01$

T-Tests comparing the number of responses made between the fixed side and the variable side in the closed economy.

I15; $t(8) = 4.45$, $p < .01$

I30; $t(8) = 0.76$, N.S.

I90; $t(8) = 3.81$, $p < .01$

I180; $t(8) = 4.03$, $p < .01$

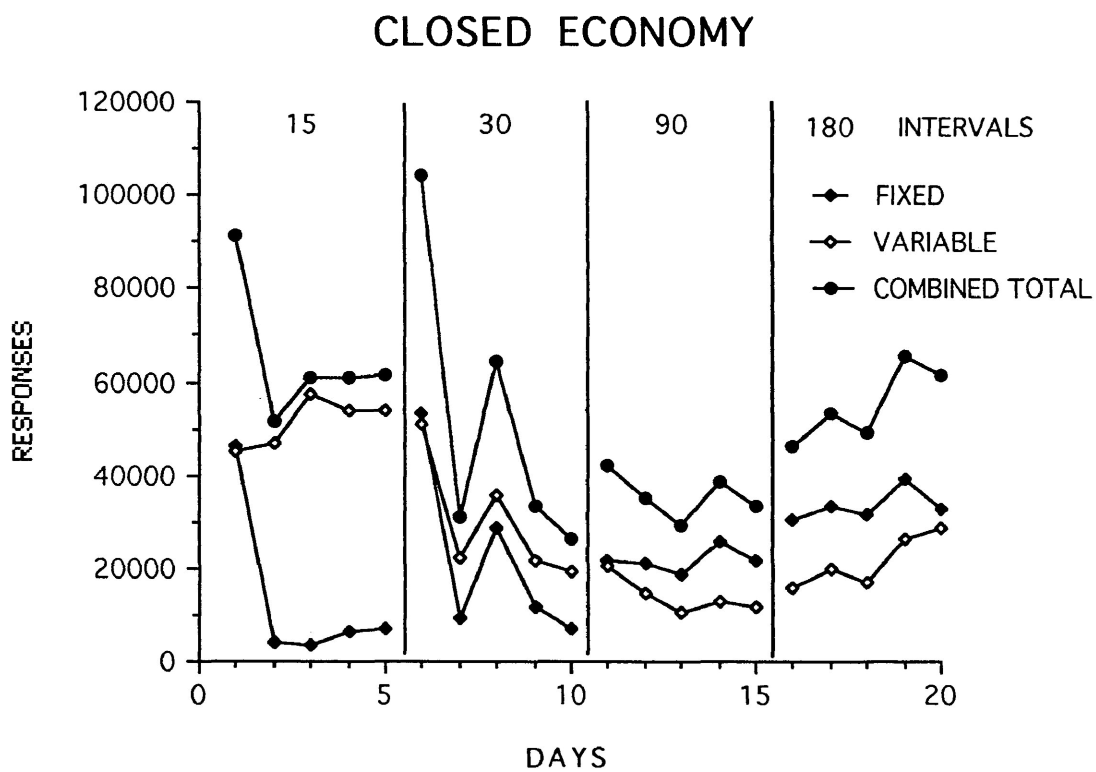

Figure 16. Daily totals of the number of responses at the fixed and variable stations during each of the four interval schedules in the closed economy, as well as the daily totals of the fixed and variable stations combined.

Appendix 8

Closed Economy (COP)

The five day means of responses/reinforcements, or cost of a pellet (COP) produced at the fixed and variable stations during the closed economy.

Interval Value

	15		30		90		180	
	F	V	F	V	F	V	F	V
MEAN/DAY	7.01	11.93	7.87	10.12	12.59	8.46	22.86	15.09

2(variance) x 4(interval) ANOVA.

Variance; $F(1,\ 32) = 1.78$, N.S.

Interval; $F(3,\ 32) = 221.03$, $p < .01$

Variance x Interval; $F(3,\ 32) = 10.62$, $p < .01$

Oneway ANOVA's comparing interval values at the fixed and variable stations.

FI; $F(3,\ 16) = 27.89$, $p < .01$

VI; $F(3,\ 16) = 6.35$, $p < .01$

T-Tests comparing the COP between the fixed side and the variable side in the closed economy.

I15; $t(8) = 2.80$, $p < .01$

I30; $t(8) = 1.03$, N.S.

I90; $t(8) = 2.92$, $p < .01$

I180; $t(8) = 4.61$, $p < .01$