

RISK SENSITIVE FORAGING BY RATS

IN THE OPERANT ARENA

BY

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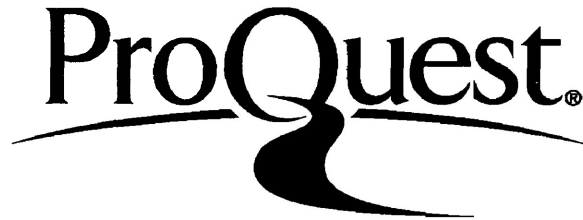
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ABSTRACT

The operant arena was used as the framework in which to study the theory of risk-sensitivity. A small colony of hooded rats was exposed to increasing work demands while given the choice between simultaneous fixed ratio (risk-averse) and variable ratio (risk-prone) schedules.

The four rats were maintained in a large arena with access to eight feeding stations for two 30-minute sessions per day. Stations on one side of the arena were programmed to pay off on a fixed ratio, while those on the other side paid off on a variable ratio. The subjects were exposed to ratio value schedules 5, 10, 20, 40, and 80 in an ascending sequential order; each schedule was in effect for seven consecutive days.

Dispersion patterns, transition types, reinforcements, and the observed preference for working on the FR or VR side of the arena were studied. Throughout the experiment the rats showed an overwhelming preference for the FR side of the arena. However, there was a gradual decrease in the magnitude of the preference for the FR side of the arena over the course of the experiment. It is therefore concluded that as the cost of food increased rats became more risk-prone in their foraging preference. It is also suggested that had the animals been allowed to experience a negative net energy budget (i.e., starvation) a more powerful effect would have emerged.

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The behavior of animal populations can be conceptualized in two ways: optimization theory and contingencies of reinforcement. Optimization theory, which developed most completely in the science of ecology (Schoener, 1971; Charnov, 1976), basically proposes that a foraging animal distributes its behavior so as to maximize net energy per unit foraging time. Prior to the advent of this theoretical approach, ecologists attempted to account for the behavior of populations by focusing on availability of resources, competition for these resources, weather, and geographical structure as the most important determinants of how a species was dispersed within an environment (Krebs, 1978). In the early 1970's, a number of papers appeared in which it was suggested that these factors operate within an optimization framework. Within this framework organisms were conceived of as energy exchange systems that would optimize the expenditure of energy in the acquisition of resources. It follows then, that a species foraging for food would have an exclusive preference for that resource which would yield the greatest net energy.

Behavioral researchers view population changes as controlled by operant conditioning and therefore subject to the laws of learning. The behavior of

animal populations can then be investigated objectively using the behavioral methodology which has been developed in the psychology of learning. From the operant perspective, an animal foraging for food in a group is under the control of a complex schedule of reinforcement. For example, a pigeon foraging in a park is controlled by cues which are correlated with the availability of food. The presence of other foragers in a group is often a signal that food is there, and so fellow foragers become discriminative stimuli. Once at the site where conspecifics are feeding, the presence of competitors generally has the effect of increasing the work/time required to acquire food, which increases the ratio or schedule of food availability.

Both the optimization theory and operant research approaches are concerned with the concept of choice. Organisms must "decide" where and when to forage and also "choose" their prey. Both approaches study the factors which interact to govern how these choices are made.

In what follows attention will be focused on one approach from the optimization perspective - risk sensitive foraging. Caraco (1980) presented a model of foraging which deviates from the deterministic foraging models. This model goes beyond a total emphasis on the maximization of net energetic rewards, and includes mixed strategies which take into account variation in

the distribution of resources, and the manner in which these variations can shape an animal's foraging preferences. The probability of an animal's being present in an area of the environment at a given time is affected by the rate at which the animal is reinforced by that environment. As internal and external variables change, an animal will choose a food source which is more suitable to the new environmental conditions.

Two ways of responding within Caraco's (1980) model are described as "risk-averse" and "risk-prone" behaviors. A risk-averse forager will tend to avoid food sources with relatively high variation and exploit resources with small variation, even if the average reward obtained is less than that of a more variable food source. Risk-prone behavior is the preference for a more variable food source based on the possibility of getting a relatively large food reward. In risk-prone behavior there is a possibility of the net energetic benefits being greater than those obtained in risk-averse behavior. However, Caraco says that animals exhibiting risk-prone behavior also accept the possibility of relatively low energetic rewards and eventual starvation. These two patterns of behavior are not mutually exclusive and may be observed in the same individual depending upon the prevailing environmental conditions.

In an exploration of foraging preferences Caraco,

Martindale and Whittam (1980) found that yellow-eyed juncos (Junco phaeontus) were risk-sensitive. By analyzing such variables as the energetic value of the millet seeds consumed by the birds and their oxygen consumption, Caraco et. al. were able to estimate a 24 hour expected energy requirement budget for the birds. The juncos were then given a choice between fixed (2 seeds per session for 20 trials) or variable (4 seeds per session for ten trials and 0 seeds per session for 10 trials) patches under 2 different experimental conditions.

In the first situation the birds were exposed to 1 hour of starvation and a 30 second delay per seed. Under these conditions the birds could expect a non-negative net energy budget. All birds showed a preference for risk-aversion, with a decreasing risk-aversion response over time.

The second experimental condition exposed the juncos to 4 hours of starvation and a 1 minute delay per seed. A negative net energy budget could be expected under these conditions. In all cases the variable reward was preferred with decreasing risk-proneness over time.

The results of this study show that the risk response depends upon a comparison of energy intake with energetic expenditures. The juncos were able to recognize environmental stochasticity and to respond to this variation in the mean and variance of food

rewards.

In a 1981 article Caraco discussed foraging group size as another variable which interacts with foraging benefits and costs. Specifically, Caraco discussed avian flocking and how risk-sensitivity might affect the formation of these foraging groups. In a patchy environment, food patches are found at a rate which generally increases as flock size increases. Foraging time variation is dependent on flock size.

Another aspect of flocking is the dominance/subordination of the individual members of the group. Dominant members are more likely to acquire a greater portion of any food found. Although a subordinate animal may get a smaller than average portion of food found, the probability of an individual acquiring any food at all increases with flock size.

When an animal expects a positive net energy budget it is likely to behave in a risk-averse manner, avoiding variation in foraging time and therefore favouring flocking. In the case of a negative net energy budget an individual will tend to be more risk-prone, seeking more variation in foraging time and favouring either smaller foraging groups or solitary searching. This bimodal reactivity is similar to r-selective (diversification and productivity) and K-selective (specialization and efficiency) manners of budgeting time, matter and energy exhibited by organisms in nature as discussed by Pianka (1970).

In an extension of Caraco's theories, Stephens (1982) shows that the expected energy budget rules can proceed from a minimization of the probability of starvation. Rather than accepting the greater probability of starvation (Caraco, 1980) a risk-prone forager may decrease its probability of starvation in some situations as shown in Stephens' model. Risk sensitive behavior can be explained by measuring an organism's expected 24-hour energy budget. If the budget is positive, risk-averse behavior is favoured; if it is negative, risk-prone behavior is favoured.

The concepts of "risk" and "choice" can also be found in a study by Krebs, Kacelnik and Taylor (1978) which used great tits (Parus major) as subjects. It was found that the birds will, on average, act in such a way as to optimize exploration and exploitation of two foraging patches when given a choice. The authors define exploitation as immediate maximizing by instant with little risk, while exploration is defined as a long-term maximization over total foraging time with an element of risk. The foraging patches in this case compared reward values 50, 40, 35 and 30 to 0, 10, 15 and 20 consecutively, using a pseudo-random variable ratio schedule. The birds initially sampled the 2 food perches at a rate which slightly favoured the less profitable perch. After this initial sampling period, the birds remained on the perch which paid off a higher rate for approximately 95% of the trials; this was true

for each of the different pairs which were compared.

Lea (1979) structured a choice situation for key pecking in pigeons and manipulated reward ("prey") density, size and delay of reward, and post reward detention in an investigation of the optimality theory. Lea found that birds consistently chose the key with the lower rate of pre-reward delay, but that the probability of the birds pecking at the alternate key varied among the conditions. This non-optimal result showed that the birds tended to sample alternative behaviors at an approximately constant rate when to do so is not too costly. Lea concludes by proposing "that the laws of operant behavior have evolved to ensure efficient, if not optimal, foraging." (pg. 885).

Both the concepts of exploitation and exploration are necessary to the theory of risk-sensitivity; an animal explores its environment and then exploits the most efficient resource. Risk-sensitivity is this ability to recognize variability in energetic rewards and to respond to this variability. In studies done by Krebs, Kacelnik, and Taylor, and by Lea the animals behaved in a risk-averse manner. Further manipulation of the food patches could have yielded other patterns of responding.

The following studies give an operant perspective, and focus on that literature most closely related to the risk sensitive relationship between fixed ratio and variable ratio schedules of reinforcements. In these

studies animals have been given the choice between alternative methods of responding while under various schedules of reinforcement. These schedules can approximate predictable (fixed) and unpredictable (variable) environments.

Pigeons showed a consistent preference for variable-ratio over fixed-ratio schedules even when the mean response requirement of VR was considerably higher (Sherman and Thomas, 1968). A chaining procedure with a switching key was utilized in this experiment and the ratio values for both fixed and variable ratio schedules were 1, 30, 60, 90, 120, 150, 180, 210 and 240. The birds were presented with the option of switching to a variable ratio schedule after each reinforcement, if they pecked at the switching key they were automatically given the variable-ratio schedule. The birds preferred the VR schedule although they had to work to get access to it. Only when the work requirement was significantly increased or when a delay was instituted did the switching behavior decrease.

In a study by Rider (1979) rats were given a choice between fixed ratio (25, 35, 50, 60 and 99) and mixed ratio (MR; equiprobable 1 and 99) or fixed ratio and variable ratio (VR50 made up of 11 possible ratios). In general the rats showed a preference for whichever of the two concurrent ratio schedules had the smaller average response requirement. However, a preference for the FR schedule occurred only when the

FR value was at least 2.5 reinforcements more per minute than the VR schedule. When the response requirements were the same for either schedule the animals responded most often on the VR or MR as compared to the concurrent FR schedule. There seemed to be a slight preference indicated for aperiodic (providing reinforcement after variable ratios or intervals) rather than periodic (providing reinforcement after fixed ratios or intervals) schedules.

In a later article, Rider (1983) investigated the choice for aperiodic or periodic ratio schedules in a comparison of concurrent versus concurrent-chains procedures. When FR35 was compared to MR with equiprobable 1 and 99 under a concurrent schedule, FR35 was preferred, while MR1,99 was chosen during the chaining procedure. The results of this study show that preference for a FR or MR schedule can be influenced by the procedure used for assessment, and that this should be taken into consideration when comparing studies with different methodologies.

The preceding studies do not take into account the net energy benefits which were earned during the various schedules of reinforcement. Risk-sensitivity may have helped to explain the variability in responding.

In a 1981 article Real discussed the foraging behavior of bees and wasps in an experiment using artificial blue and yellow flowers filled with nectar.

The insects showed a constant preference for the yellow flowers when the amount of nectar contained in each blossom, regardless of colour, was held constant. However, when the yellow flowers paid off at VR2 (mixed 0 and 6) while the blue flowers paid off at a constant FR2, the insects avoided the previously preferred yellow blossoms. When the ratios were switched to yellow FR2 and blue VR2(0,6) the insects preferred the yellow flowers. The preference for consistent reward was greater when the variable ratio paid off at 0 and 6 rather than 0.5 and 5. Real concluded that this showed a trade-off between the expected value of a behavior and its certainty.

Fantino (1967) in an experiment using pigeons, compared mixed-ratio and fixed-ratio schedules by using a chaining procedure which allowed the bird access to one of the schedules. The mixed-ratio schedule consisted of a combination of fixed ratio schedules which had an equal probability of occurring. Ten comparisons were carried out using various ratio values. The birds showed a preference for the MR scheduled MR1;90 or MR10;90 over FR50 although the mean responses were approximately equivalent. The bird's preference for the MR side increased as the range between the FR values increased. The preference for MR remained until the FR level became sufficiently smaller than the MR level.

Another variable to be considered in the study of

foraging is the distribution of the animals themselves in their environment. In the natural environment animals do not forage in isolation, rather they arrange themselves in patterns of dispersion. These patterns have been described as forming regular, random and clumped formations (Brown and Orians, 1970). In regular dispersion, animals distribute themselves in a uniform pattern throughout the environment. Random dispersion occurs when the probability of an animal's being at any place throughout the environment is the same. A clumped formation describes the dispersion of animals in the environment in an irregular non-random pattern.

The operant literature which has been discussed to this point has been based on single subjects, a fact which raises the question of whether operant procedures can be applied to group foraging behavior. The following studies review operant group behavior which has been well documented by Goldstein, who has utilized reinforcement contingencies -- responses, rewards, schedules and discriminative stimuli -- to approximate the conditions found in the natural environment.

Goldstein (1981a) studied schedule control of dispersion and density patterns in rats in an operant arena. By manipulating which bars delivered food and ratio values between bars and sessions, it was found that schedules of reinforcement are a factor in determining the distribution and abundance of animals.

This experiment showed that it is possible to engender all three major dispersion patterns in the same group of rats, in relative independence of food supply.

In a later article Goldstein and Mazurski (1982) investigated the effects of an ascending series of fixed ratio schedules on the dispersion patterns in a colony of eight rats. In two daily 30 minute sessions the rats were exposed to FR 1, 4, 8, 16 and 32 consecutively. As the work requirement increased the dispersion patterns became more regular (non-linearly) and more stable (linearly). Work requirement, food supply, and aggression were discussed as proximal agents underlying dispersion in this article.

The operant arena provides the framework in which risk sensitive foraging approaches to choice can be investigated. This can be achieved in a general way by arranging areas of the arena to correlate with either predictable or unpredictable environments. More specifically, the arena can be divided into areas in which food availability can be unpredictable (variable ratio), or highly predictable (fixed ratio). When working on a variable ratio schedule an animal does not know when its next reinforcement will be earned. An animal working steadily on a fixed ratio schedule, on the other hand, earns rewards on a regular, and therefore predictable basis. In the present study, fixed and variable schedules of reinforcement were independently programmed in the operant arena, provid-

ing a direct test of risk-sensitive foraging.

Risk-proneness was represented by a preference for the variable ratio schedule. By choosing to work on this schedule the subject took the chance that the work required to earn a reinforcement would be lower than on the fixed side, even though there was also the possibility that the work requirement would be higher than on the fixed ratio side. Risk-aversion was represented by a preference for the fixed ratio schedule; the amount of work required to earn a reward was always highly predictable, with no chance of the work requirement being higher or lower than average.

In addition to the uncertainty in obtaining food, a second component of the risk dimension is the change in energetic deficit experienced by the animal. This variable can be manipulated in several ways. In this experiment, the option of progressively increasing the cost of food was used as the energetic cost variable. The purpose of this study was to test whether the increasing cost of food (as represented by progressively increasing ratio values) would cause the animals to become more risk-prone and show an increased preference for working on the VR side of the arena.

METHOD

Animals:

Four mature male hooded rats with a previous history of bar pressing on various schedules of reinforcement in the operant arena were used.

Apparatus:

The rats were maintained throughout the experiment in an arena 3.7 m X 3.4 m X 1.2 m which contained eight feeding stations. There were four stations on each of the two longest walls of the arena arranged in a bilaterally symmetrical arrangement (Goldstein, 1981b) (Figure 1). Each 54 cm long X 22 cm wide 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. A large exhaust fan situated above the pegboard ceiling of the arena ventilated the area; a wire mesh floor helped ventilation and also allowed urine and feces to fall to a trough below. Water discharged through perforated copper pipes rinsed this trough periodically. Hinged Plexiglas doors along the two longest walls of the arena allowed observation of, and access to, the arena. Mirrors on the walls above the floor made it possible

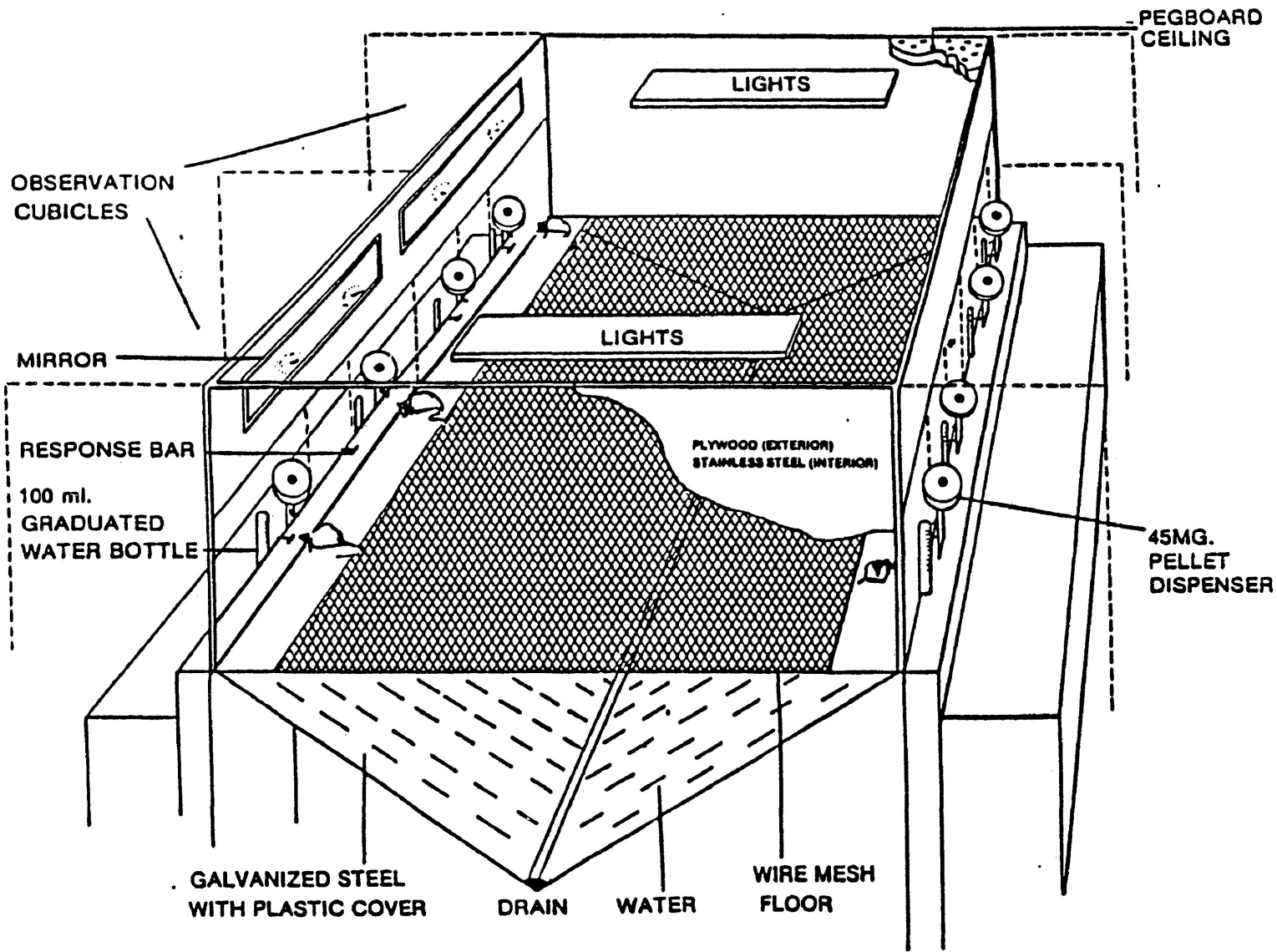


Figure 1

Diagram of the Operant arena.

to observe the arena in its entirety from the experimenter's observation station. Illumination for the arena was provided by two banks of fluorescent lights mounted in the ceiling. Lighting occurred on a 14:10 light/dark cycle.

A PET 2001 microcomputer was programmed to provide station-by-station control of reinforcement schedules, data collection and data analysis (Goldstein, Blekkenhorst and Mayes, 1982).

Procedure:

The four rats were exposed to fixed ratio and variable ratio 5, 10, 20, 40, and 80 in an ascending sequential order. The ascending sequence was used to avoid a breakdown in bar pressing due to "ratio strain" and to simulate a progressive decrease in net energy intake. The stations were independently programmed so that the four response levers on one side of the arena paid off on a variable ratio schedule while the four on the opposite side of the arena paid off on a fixed ratio schedule. Each ratio value was in effect for 7 consecutive days for a total of 14 sessions. The animals were given access to the bars for two 30 minute sessions beginning at 9 a.m. and at 5 p.m. each day. 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 computer recorded the bar press responses and

the number of reinforcements for each station during the sessions. At the beginning of each minute the dispersion pattern of the rats throughout the arena was recorded by counting the number of rats at each station. A rat was counted as "present" at a station if it was within the area 54 cm X 22 cm in front of the Plexiglas partition holding the response bar and dispenser.

At the 40 and 80 ratio value levels a food supplement was supplied for the rats a half hour after the end of each 5 p.m. session to ensure that the rats were healthy and would not starve.

RESULTS

Data analysis

Risk sensitivity was represented by the amount of time the rats were observed on either the fixed or variable ratio side of the arena. The animals were said to be risk averse when they worked on the fixed ratio side of the arena; they were said to risk prone when they worked on the variable ratio side of the arena. A total of 1680 observations were generated for each ratio schedule since observations were made minute by minute during each of the 14-30 minute sessions per ratio schedule for each rat. The percentages of time the subjects were observed on the FR and VR sides of the arena were obtained for each of the ratio schedules. Analysis of variance (ANOVA) was performed comparing the AM and PM means of the observations for the FR and VR sides. Analysis of variance was used to compare the total number of observations of rats on the FR side throughout the entire experiment to the number of rats observed on the VR side over the same time period. The changes in the numbers of rats observed on each side of the arena over the five ratio value

schedules were evaluated using ANOVA.

The number of reinforcements received was averaged per rat to arrive at the AM, PM and daily means for each ratio schedule. In all analyses the identities of the individual rats were not taken into consideration. For this analysis the bars were differentiated only by whether they were programmed to pay off on a fixed or variable ratio schedule. The relative number of reinforcements earned on each side of the arena was plotted against relative usage of the FR and VR sides of the arena.

Dispersion patterns were analyzed by spatial configurations (the manner in which the rats arranged themselves in their environment), with particular emphasis on the frequency of maximal dispersion (in which the rats disperse themselves in a pattern which maximizes the space between individuals) and by the number of rats at each station. The minute to minute movements by the rats were analyzed to count each of the five major types of transitions - Type A Macrostate, Type B Macrostate, microstate, position and identical (Goldstein 1981a).

There were relatively few different types of transition recorded during the experiment. The transitions other than identical transitions were combined so that they could be compared to the identical transitions. This allowed the stable (identical) and unstable (all other types) transitions to be

compared.

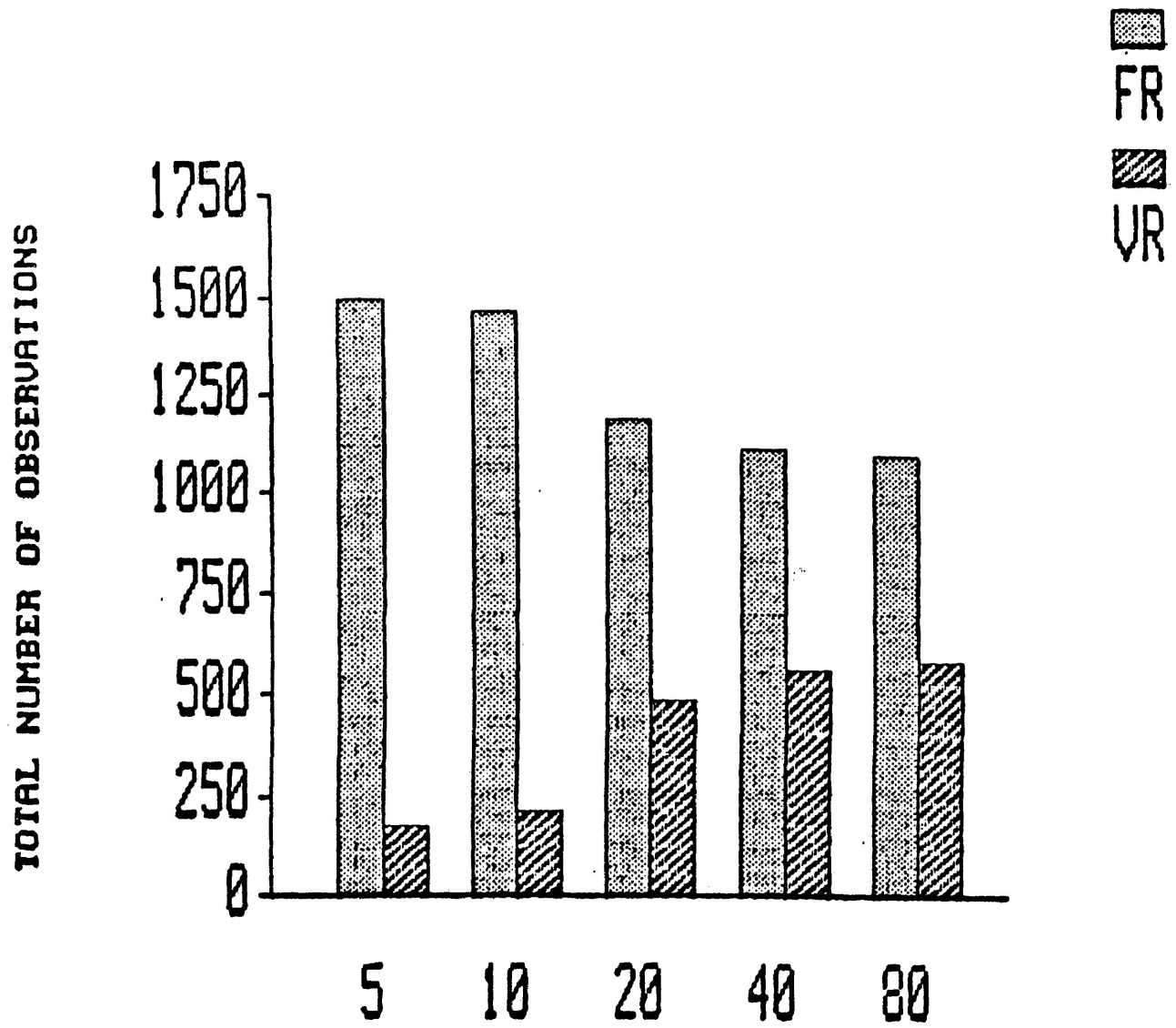
For ease of comprehension most of the data are presented in graphic form where possible, while the corresponding numerical data are found in the appendices. The results are organized into five separate sections, each dealing with one of the main factors which were analysed in this study.

Relative usage of the FR and VR sides of the arena

The AM and PM totals did not differ significantly on either the FR ($F(1,8)=1.7$, $p>0.9$) or the VR ($F(1,8)=1.7$, $p>0.9$) side of the arena, so this was not included as a variable in further analysis (Appendix 1 shows the AM and the PM totals and means).

There was a significant preference for the fixed ratio side of the arena ($F(1,8)=51.8$, $p<0.00009$); of the 8,400 observations which took place over the course of the experiment (1,680 for each of the five ratio schedules), 76.02% were of rats on the FR side of the arena. However, as the ratio value increased the magnitude of the preference decreased ($F(1,4)=25.9$, $p<0.007$). The largest change in preference for the variable side occurred between ratio schedules 10 and 20.

Figure 2 shows the total number of times the rats were observed on the FR or VR side of the arena during each of the five ratio value schedules (for the



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Figure 2

Total number of times that rats were observed on the FR and VR sides of the arena during the five ratio value schedules.

numerical data see appendix 1). The proportion of time spent on the fixed and variable side of the arena for each of the five ratio schedules is shown in Figure 3. These figures describe changes in preference which took place as the ratio value was increased. It can be seen that the changes are fairly minimal except for the change which took place between ratios 10 and 20.

Reinforcements

The mean number of reinforcements earned per day on the FR and VR sides of the arena during each of the 5 ratio value schedules are graphed in Figure 4; the proportions of the total number of reinforcements earned on each of the arena are depicted in Figure 5 (the totals and means are found in Appendix 2). As the work requirements increased the mean daily total reinforcements acquired decreased steadily from almost 2000 at ratio values 5 and 10, to 520 reinforcements at ratio 80. The proportion of reinforcements shown in Figure 5 closely correspond with the proportion of time spent on each side of the arena shown in Figure 3. There is a direct linear relationship between the relative number of reinforcements earned on the FR and VR sides of the arena and the relative usage of the FR and VR sides (see Figure 6).

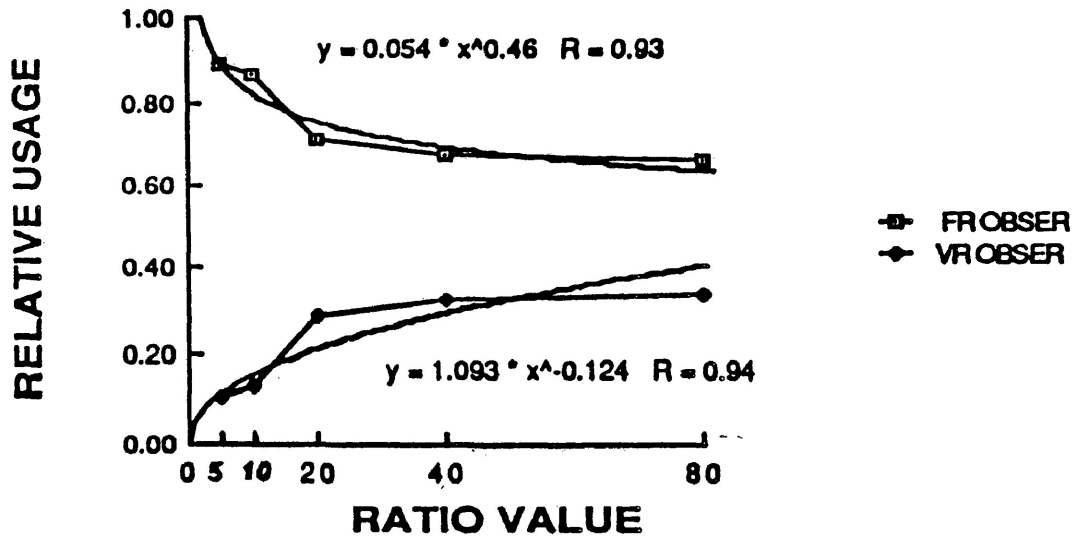


Figure 3

The relative usage of the FR and VR sides of the arena during each ratio value schedule.

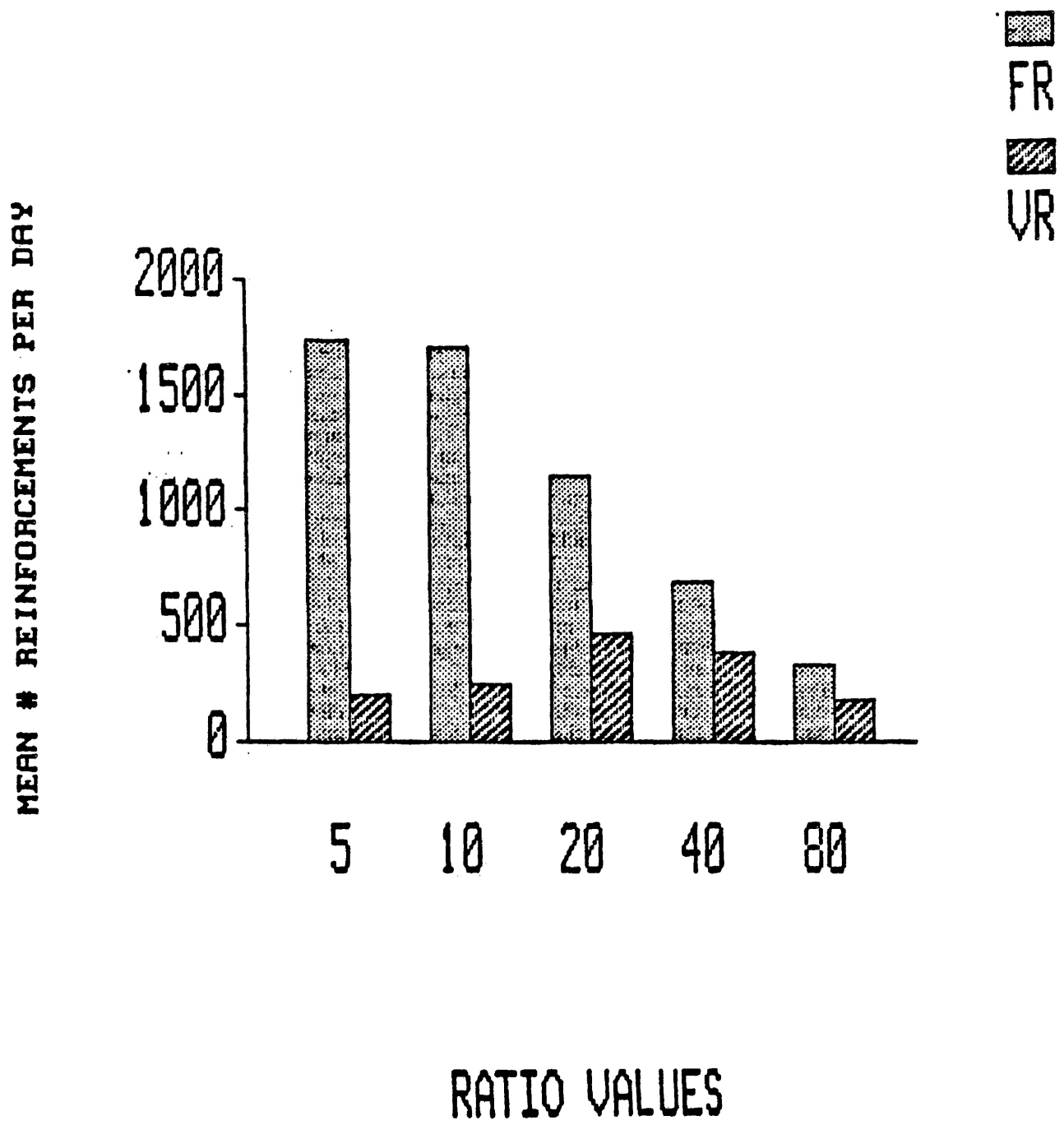


Figure 4

The mean number of reinforcements obtained per day on the FR and VR sides of the arena during the five ratio value schedules.

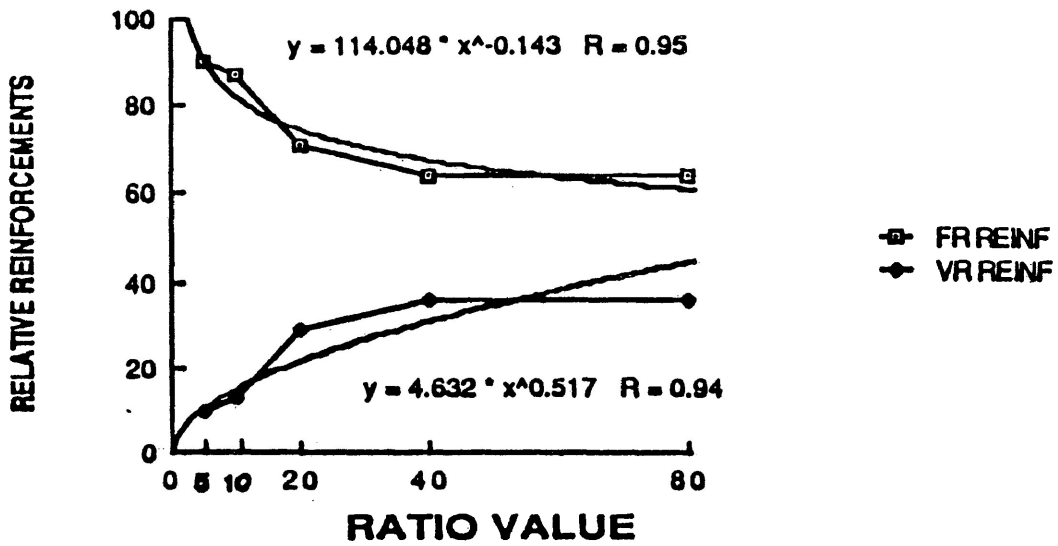


Figure 5

The relative number of reinforcements obtained on the FR and VR sides of the arena during the five ratio value schedules.

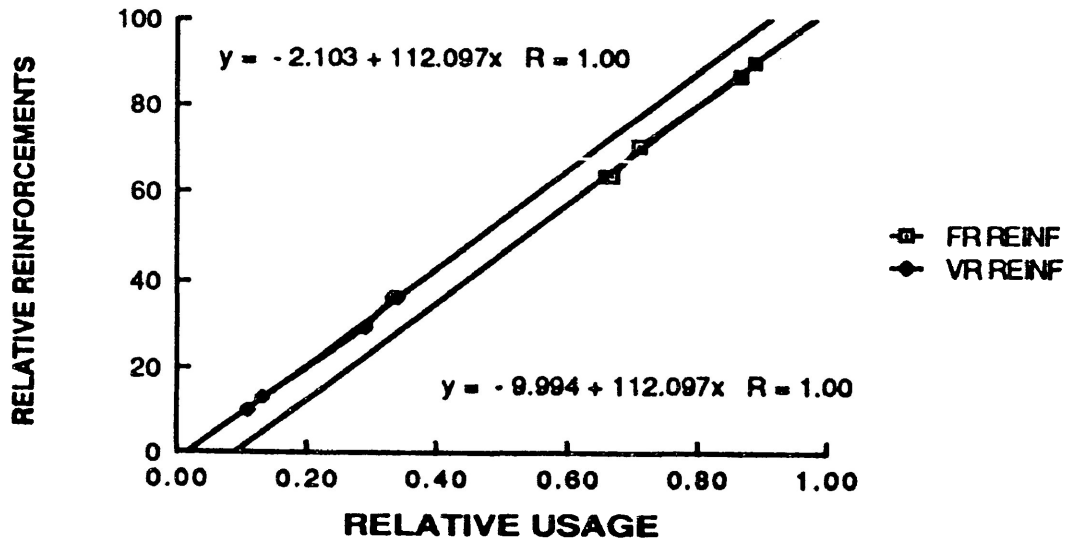


Figure 6

The relative number of reinforcements earned on each side of the arena versus the relative usage of the FR and VR sides of the arena.

Spatial Configurations

Without taking the identity of the individual rats or bars into consideration, there were 12 spatial configurations possible on each side of the arena. The configurations are grouped in classes according to how many rats were working on a particular side, and by how many rats are working at each of the four stations. These configurations and the frequency with which they were observed are depicted in Table 1. In general the rats did not aggregate, preferring to work at separate food stations. There was no observed attrition (fewer than 4 rats working at one given minute in time within the entire arena) during the course of this experiment. The dispersion patterns were the most regular under ratio values 10, 20 and 40, on both the FR and VR sides. On the FR side of the arena the number of different configurations observed ranged from eight during ratio 5, to six at ratios 20, 40, and 80. On the VR side of the arena four dispersion patterns were observed under ratio value 5, seven under ratio values 10, 20, and 40, while six patterns were seen during ratio value 80.

Of the 2,100 dispersion patterns observed throughout the experiment, there were 645 times when all the rats were working on the FR side of the arena; there were only 2 times when all the rats were found working

Table 1

Number of times that each dispersion pattern was observed on the FR and VR side of the arena during each ratio value schedule.

Frequency of each dispersion pattern

	Ratio Value									
	5		10		20		40		80	
	FR	VR	FR	VR	FR	VR	FR	VR	FR	VR
<u>class 0</u>										
0	0	267	0	265	0	52	2	59	0	2
<u>class 1</u>										
1	0	127	8	105	0	249	29	197	7	265
<u>class 2</u>										
2	4	5	1	2	1	1	0	1	3	3
1 1	22	21	41	40	118	118	133	132	143	143
<u>class 3</u>										
3	0	0	0	1	0	0	0	0	0	0
1 2	21	0	5	3	3	0	3	1	16	4
1 1 1	106	0	100	4	246	0	194	28	249	3
<u>class 4</u>										
4	0	0	0	0	0	0	0	0	0	0
1 3	4	0	0	0	0	0	0	0	0	0
2 2	2	0	0	0	0	0	0	0	0	0
1 1 2	61	0	9	0	2	0	0	0	0	0
1 1 1 1	200	0	256	0	50	0	59	2	2	0

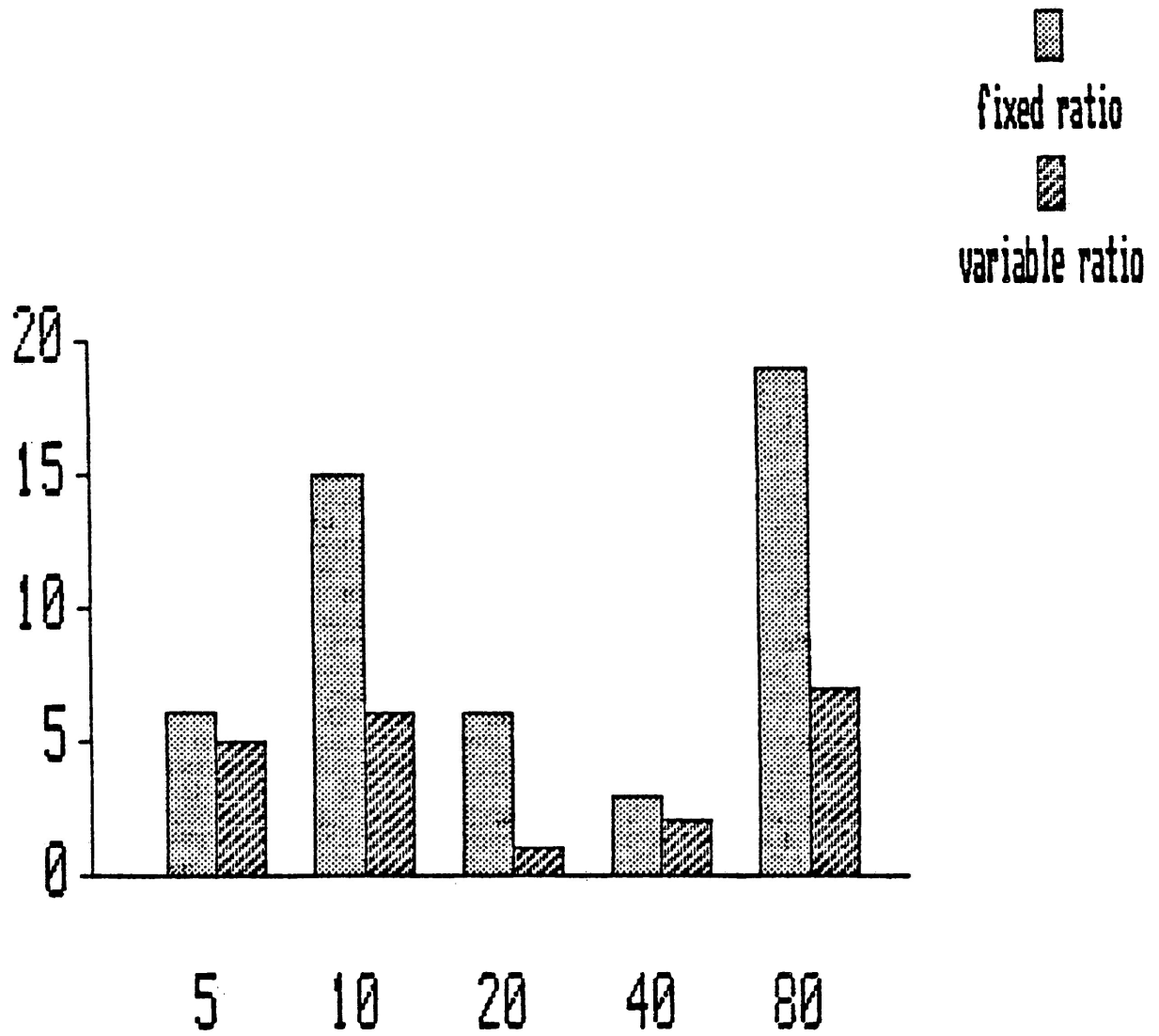
on the VR side.

"Clumping" refers to the occasions when more than one rat was working on a single station. The total number of times that clumping was observed on each side of the arena is graphed in Figure 7. Incidents of clumping were most common during ratio value schedules 10 and 80 on the FR side of the arena. There were generally fewer instances of clumping on the VR side of the arena as compared to the FR side. Clumping is only possible if there is more than one animal working on one side at a time; on the VR side of the arena this was often not the case. When frequency of clumping is compared to the opportunity for clumping to occur (total frequency of clumping per side divided by the total number of times that there was more than one animal on that side), the differences between the FR and VR sides are minimal (see Figure 8).

Transitions

The minute to minute transitions which occurred on each side of the arena are recorded in Table 2. Identical transitions (ITRAN), position transitions (PTRAN), microstate transitions (MITRAN), type A macrostate transitions (MATRAN), and type B macrostate transition (MBTRAN) were observed during this experiment. The same bars being used by the same number of rats from one minute to the next is called an identical

TOTAL OBSERVED CLUMPING



RATIO VALUE

Figure 7

Total number of times that the animals were observed "clumping" on the FR and VR sides of the arena during the five ratio value schedules.

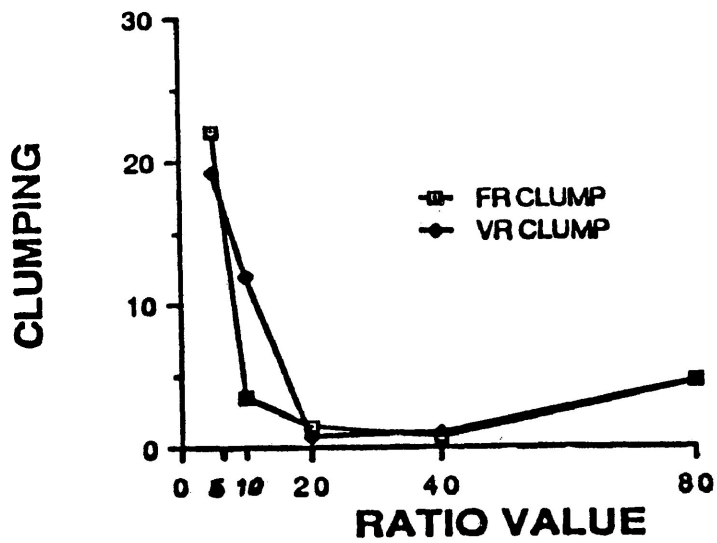


Figure 8

Percentage of "clumping" per opportunity on the FR and VR sides of the arena during the five ratio value schedules.

Table 2

Total number of times each of the different types of dispersion pattern changes (transitions) took place on the FR and VR side of the arena during each of the ratio value schedules.

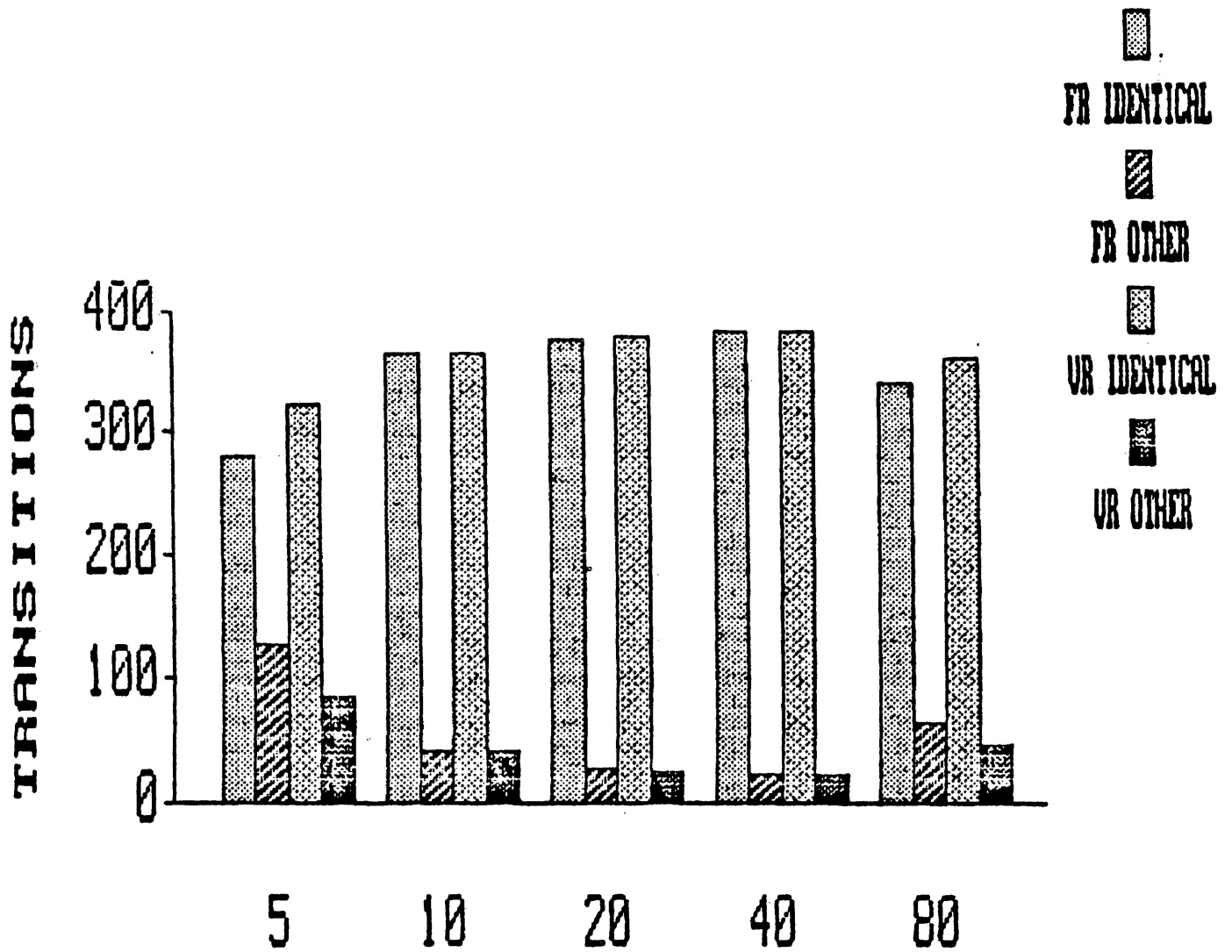
Frequency of each transition

Type of Transition

<u>Ratio Value</u>	ITRAN		PTRAN		MITRAN		MATRAN		MBTRAN	
	FR	VR	FR	VR	FR	VR	FR	VR	FR	VR
<u>5</u>	278	322	12	15	5	0	47	5	64	64
<u>10</u>	365	366	8	15	0	0	15	7	18	18
<u>20</u>	378	381	6	10	0	0	8	1	14	14
<u>40</u>	384	384	11	10	0	0	3	4	8	8
<u>80</u>	342	361	19	15	0	0	20	5	25	25

transition. When different bars are being utilized it is called a position transition. A microstate transition means that the same bars are occupied but there are different numbers of rats at the bars. In a Type A Macrostate transition the number of bars occupied changes but all of the rats continue to work. Type B Macrostate transitions occur when one of the rats stops working, or when a rat begins to work that was not working during the previous observational period.

The majority of transitions which occurred on each side of the arena were identical, 86.1% on the FR side and 89.4% on the VR side. The small numbers of other transitions were combined so they could be more easily compared to the identical transitions (see Figure 9 and Appendix 3). There was a trend towards greater stability as the ratio value increased; on both sides the greatest level of stability was reached under ratio value 40. The percentage of identical transitions which took place on the FR side increased from 68.5 at ratio value 5 up to 94.6 at ratio 40, before decreasing to 84.2 at ratio value 80. On the VR side, the percentage of identical transitions increased from 79.3 at ratio value 5 to 94.6 at ratio 40, and then decreased to 88.9 during the final ratio value schedule.



RATIO VALUES

Figure 9

Comparison of ITRAN's versus all other transitions which occurred on the FR and VR sides of the arena.

Maximal dispersion or "corner-seeking"

The stations in the arena were numbered 1 through 8; the bars 1-4 were on the variable ratio side while bars 5-8 were on the fixed ratio side of the arena. As the ratio requirements were raised, the rats were prone to maximize the area between themselves by moving to the furthest corners of the arena. The bars numbered 1,4,5 and 8 were situated at the four corners of the arena. When the rats were seen working at 1 and 4 it was scored as maximum dispersion on the VR side of the arena, when they worked at stations 5 and 8 it was counted as maximum dispersion on the FR side; when stations 1,4,5 and 8 were used simultaneously it was counted as a concurrent maximum dispersion. The total number of times the rats were observed to be maximally dispersed is graphed in Figure 10. These data were compared to the number of opportunities which the rats had to seek the corners of the arena (a maximum dispersion could only take place when there were two rats on each side of the arena)(see Figure 11). There were few occurrences of maximal dispersion on either side at ratio value 5, however by ratio 80 there were 117 observed on the FR side of the arena, 107 on the VR side, and 86 times when the animals were maximally dispersed on both sides of the arena concurrently. The high proportions shown in Figure 10 are even more

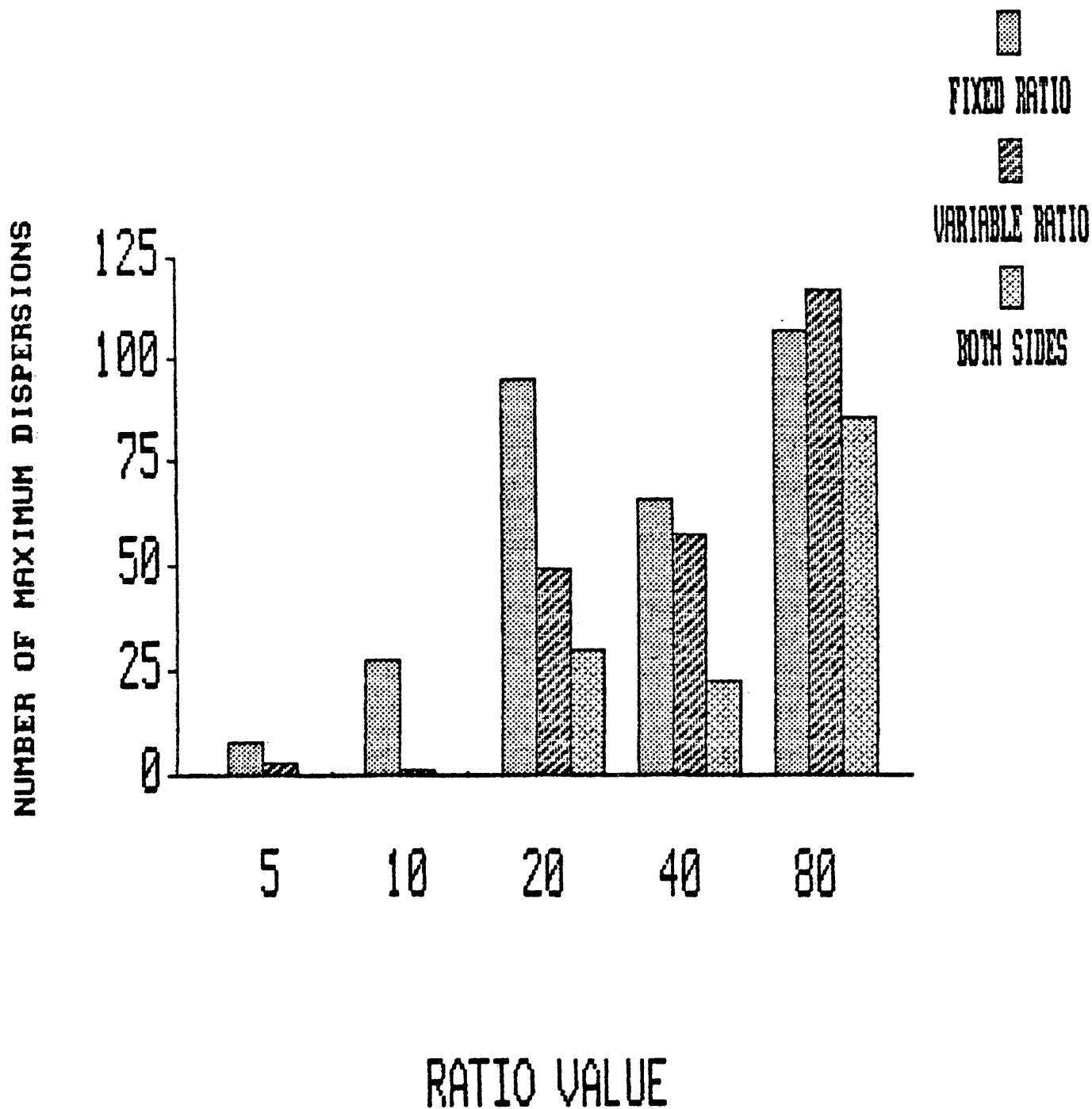


Figure 10

Total number of times rats were observed maximally dispersed, or "corner-seeking", during each ratio value schedule.

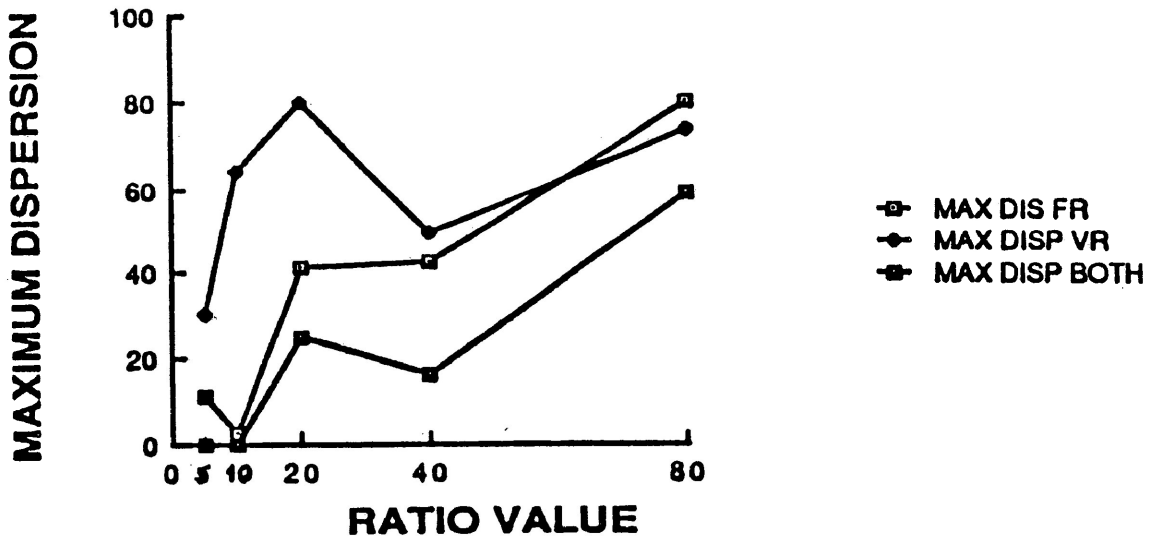


Figure 11

Percentage of maximum dispersions per opportunity for maximum dispersions during each ratio value schedule.

interesting when it is realized that maximal dispersion is only one of a possible six patterns (i.e., stations 1,2; 1,3; 1,4; 2,3; 2,4; or 3,4 could be used) which could occur when two rats are working separately on one side of the arena, and only one of a possible 36 patterns which could occur when both sides are considered concurrently.

DISCUSSION

Irrespective of the ratio value, the rats showed a consistent, strong preference for the fixed ratio side of the arena. From the risk-sensitive perspective this preference would be seen as a reflection of risk-averse behavior, and a preference for a more conservative foraging style. The magnitude of this almost exclusive preference which the rats showed for the fixed ratio bars gradually became smaller as the net energy benefits earned during work sessions decreased, although there remained a preference for the FR side. The shift towards increased work on the variable ratio (risk-prone) side as food resources became scarce, is consistent with Caraco's theory (1980) that risk-proneness is more likely when an animal is unable to meet energy requirements with a more risk-averse (represented by the fixed ratio schedule) foraging strategy.

A closer examination of the change in preference for side as related to increased ratio value and number of reinforcements earned helps to clarify this point. During the first two ratio schedules the mean daily reinforcements earned were approximately equiva-

lent in spite of the potential for the rats to earn as many as twice the number of reinforcements on the first schedule with its lower response requirements. Each rat needs approximately 20 grams of food per day (Barnett, 1963) which is equivalent to 444 pellets (each pellet weighs 45 mg.). Therefore, the four rats would require a total of 1776 pellets of food per day. The animals were able to earn in excess of this amount during the first two ratio schedules. However, after this point there was not enough time available in the sessions for the rats to complete the increased number of bar presses required to procure the same number of reinforcements. It is at the point between ratio 10 and ratio 20 that the first decrease in net energy benefit takes place; this is also the point at which the greatest increase in preference for the variable ratio side of the arena takes place. Under the last two ratio value schedules the magnitude of the change in preference for the VR side is maintained, but further increases in this preference are minimal.

This failure to show a further shift can be explained as follows. During these last two ratio value schedules the animals were given a food supplement following the evening sessions. By this stage in the experiment the number of reinforcements which could be earned per day was not sufficient to meet the rats' nutritional requirements. The food supplements were given to avoid exposing the animals to the long term

risk of starvation. By giving food supplements the effect of a decreasing net energy budget required to produce the risk-prone behavior (preference for the variable side) was moderated. The tendency to behave in a risk-prone manner may have been much more pronounced had the supplements not been provided.

Most operant studies using individual subjects have found a stronger preference for variable schedules rather than fixed schedules when given a choice (Fantino, 1967; Sherman and Thomas, 1968; Rider, 1979). In contrast, Real (1981) found that bumblebees and wasps avoided uncertainty when given the choice of foraging among flowers which had constant and variable energetic rewards.

The choice the animal makes is often dependent upon the procedure used to implement the choice. For example, in a later article Rider (1983) showed that animals could be made to behave very differently depending upon the methodology used in the experiment. It was discovered that when FR 35 was compared to MR 1,99 using a concurrent-chains schedule (the schedules are mutually exclusive and access to the schedule not currently being offered is contingent upon a "choice" response) the MR was preferred. However, when the same ratios were compared using a concurrent schedule (both schedules are available simultaneously) the rats showed a preference for the FR schedule.

Other methodological differences could also affect

the results of these studies and make comparisons difficult. For example, many of the studies use a mixture of only two values for their VR schedules (Fantino, 1967; Sherman and Thomas, 1968; Rider, 1979 and 1983; Real, 1981), and the specific values used for the mixed schedules also differ among the experiments. The choice of subjects also varies across experiments. In Real's study (1981) the bumblebees displayed a greater avoidance of variability than did wasps under the same experimental conditions.

The present study has the added variable of working with a group of animals rather than with single subjects. This is a closer representation of a natural setting since animals usually do not forage in isolation. Because the animals are foraging in a group, the interaction of animals at stations creates variability, and the competition which exists between the subjects creates an element of risk. These interactions of the animals within the group can also affect the manner in which foraging choices are made.

Using a population of animals allows the analysis of dispersion and density patterns to be included in the study. A pattern of increasing stability and decreasing clumping toward mid-ratio values, followed by decrease in regularity of the dispersion patterns was found in this experiment. This pattern describes the curvilinear effect of ascending ratio schedules on regularity found by Goldstein, Ward and Johnson

(unpublished) in their study of fixed-ratio and variable-ratio control of dispersion patterns. This effect holds true for combined fixed-ratio and variable-ratio schedules, as shown in this study. The increasing frequency of observed maximum dispersion or "corner-seeking" can be thought of as a more detailed analysis of population dispersion. This phenomena may have been the animals' way of trying to optimize their utilization of the resources in their environment.

The increased variability in behaviors, which occurred at the highest ratio level when net energetic benefits were at their lowest, could be further evidence of the animals taking risks when a more conservative strategy was not able meet their energy needs.

The different, often contradictory information which exists on the subject of preference between fixed (predictable) and variable (unpredictable) schedules of reinforcements points to the necessity for consistent experimental procedures before adequate comparisons can be made among studies. The operant arena provides an important tool for researching how variables interact to control animal behavior, from both operant and ecological perspectives.

Appendix 1

Total and mean number of times that each rat was observed working on either the FR or VR side of the arena during the AM and PM sessions for each ratio value schedule.

	Total number of observations									
	Ratio Value									
	5		10		20		40		80	
	FR	VR	FR	VR	FR	VR	FR	VR	FR	VR
AM	729	111	779	61	660	180	509	331	524	316
PM	772	68	688	152	533	307	613	227	579	261
Total	1501	179	1467	213	1193	487	1122	558	1103	577
AM Mean	104	16	111	9	94	26	73	47	75	45
PM Mean	110	10	98	22	76	44	88	32	83	37
Total Mean	214	26	210	30	170	70	160	80	158	82
	Proportion between FR and VR									
AM	.87	.13	.93	.07	.79	.21	.61	.39	.62	.38
PM	.92	.08	.82	.18	.63	.37	.73	.27	.69	.31
Total	.89	.11	.87	.13	.71	.29	.67	.33	.66	.34

Appendix 2

Total and mean number of reinforcements earned on the FR and VR sides of the arena during the AM and PM sessions for each ratio value schedule.

	Frequency of reinforcement									
	Ratio Value									
	5		10		20		40		80	
	FR	VR	FR	VR	FR	VR	FR	VR	FR	VR
AM	5890	904	6385	544	4545	1254	2326	1506	1161	729
PM	6262	520	5514	1199	3494	2030	2473	1207	1179	570
Total	12152	1424	11899	1743	8039	3284	4789	2713	2340	1299
AM Mean	841	129	912	98	649	179	332	215	166	104
PM Mean	895	74	788	171	499	290	353	172	168	81
Total Mean	1736	203	1700	249	1148	469	686	388	334	186
AM %	87	13	92	08	78	22	61	39	61	39
PM %	92	8	82	18	63	37	67	33	67	33
Total %	90	10	87	13	71	29	64	36	64	36

Appendix 3

Comparison of identical transitions versus all other types transitions combined on the FR and VR sides of the arena during each of the ratio value schedules.

<u>Transition type</u>	Frequency of dispersion pattern				
	Ratio Value				
	5	10	20	40	80
FR ITRAN	278	365	378	384	342
FR all others	128	41	28	22	64
% FR ITRAN	68.5	89.9	93.1	94.6	84.2
VR ITRAN	322	366	381	384	361
VR all others	84	40	25	22	45
% VR ITRAN	79.3	90.1	93.8	94.6	88.9

Appendix 4

Observed maximum dispersion and percentage of maximum dispersion per opportunity on the FR and VR sides of the arena, and both sides concurrently.

Frequency of Maximum Dispersion

Ratio Value

	5	10	20	40	80
FR side	3	1	49	57	117
VR side	8	27	95	66	107
Both sides concurrently	0	0	30	22	86
Opportunities	26	42	119	133	146

Maximum Dispersion per Opportunity

FR side	11.5	2.4	41.2	42.9	80.1
VR side	30.8	64.3	79.8	49.6	73.3
Both sides concurrently	0	0	25.2	16.5	58.9

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