

DENSITY DEPENDENT EXTINCTION

PHASE II

By

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Thesis

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ABSTRACT

In two separate experiments, an 8 rat 8 station operant arena was used to study resistance to extinction to test learning and optimal foraging theories of behaviour. The learning theory, called the generalized decrement theory (GDT) assumes that increased resistance to extinction will occur with increased partial reinforcement schedules. It becomes more difficult to distinguish the acquisition phase from the extinction phase as the time interval increases and as a result less generalized decrement is observed during extinction. An extension of optimal foraging theory called the skill pool effect (SPE) describes a foraging group as composed of either active producers (active participants in locating food) or scroungers (passive participants who specialize in following others to food sites). The producers determine when to leave a food patch and move on. The GDT and SPE were tested by allowing the population access to all stations with some bars capable of producing food reward and others as not producing food reward. For three consecutive sessions the population was exposed to either 1,2,4 or 8 bars functioning and then extinguished under the same conditions. In Experiment 1, an attempt was made to provide an equal distribution of food as the number of functioning bars decreased. This was done by enriching schedules of reinforcement as the functioning bars decreased. In Experiment 2, the schedule of reinforcement was held constant at a VI of 120 in order to control for any schedule differences. According to the GDT, the population should manifest the greatest number of responses with the least amount of bars working, during extinction. However, the SPE would anticipate the greatest number of responses occurring with the most amount of bars functioning. The results showed the greatest number of responses occurring with 4 bars functioning. This occurred in both experiments. The findings did not support either the GDT or the SPE. It appears that additional work is needed to account for the above phenomenon.

INTRODUCTION

Operant research has shown that schedules of reinforcement are linked to dispersion patterns (Goldstein, 1981) and optimal foraging (Grott, 1974). For a majority of this research, the central issue has been how individual animals adjust their foraging behaviour in response to the distribution of their food. While most of the researchers have concentrated on the effects of schedules and acquisition on foraging (Cheney, Bonem, & Bonem, 1985; Illersich, Mazmanian, & Roberts, 1988) few have explored the effects of extinction.

Briefly, extinction is defined as a decrease in the frequency of operant responding to the operant level, after the removal of the reinforcement (Jenkins, 1950; Haggbloom, 1983). Experimental studies maintain that a subject who is reinforced continuously will extinguish faster than a subject reinforced on an intermittent schedule. The extinction which occurs from this latter schedule is said to have a greater resistance to extinction.

The concept of resistance to extinction may be applied to foraging behaviour. It has been demonstrated

that animals in a natural setting manifest foraging behaviours which are similar to those simulated by reinforcement schedules in a laboratory (Lea, 1981; Kamil, 1981; Dallery, 1991). It follows that the extinction principles applicable to partial reinforcement schedule should be useful in explaining foraging behaviour. For example, in a natural environment it may not be possible to always secure food sources and foragers are often required to make choices i.e., a forager must decide when to stay with a food patch or move on. Partial reinforcement schedules may play an influential role in this decision.

While there have been many theories available to explain the concept of resistance to extinction the most accepted has been the generalized decrement theory (GDT) proposed by Hull (Gleitman, 1954; MacIntosh, 1987). "The generalized decrement hypothesis assumes that the heightened resistance to extinction following partial reinforcement occurs because such training increases the similarity in the stimulus situation between the learning and extinction, with the result that there is less generalized decrement when the extinction occurs"

(Sheffield, 1949 p.1).

This theoretical construct takes on great importance when it is applied to a foraging situation. For example, when an animal is foraging for food in it's natural environment, choices must be made regarding whether or not to remain with the patch of food or move on. The GDT predicts that an animal exposed to a variable patch will spend a longer period of time at the site when food runs out than will an animal which has a history of exposure to a constant patch.

Social Facilitation and Resistance to Extinction

While some versions of optimal foraging theory assume social interactions, research supporting the GDT, has typically neglected research concerned with social facilitation (Gleitman, 1954; Katz, 1954; Hearst, 1986).

Grott and Neuringer (1974) outlined the significance of operant schedules in group interactions. In their study, subjects were either placed in groups of three or kept alone. Two groups and one individual were then placed in a chamber where they were exposed to a variety

of intermittent schedules. Behavioral measures for satiation, extinction, and discrimination learning were taken for each group and for isolated individuals. The experimenters determined that animals in a social context had fewer pauses between eating sessions and ate longer than the individuals for both extinction and satiation. This occurred regardless of the schedule. The experimenters theorised that the group situation complicated the schedule under investigation. For example, when the groups was placed on a fixed ratio schedule the individuals were really on a variable interval schedule because only one member in three would receive food when dispensed. As was found in this experiment, the GDT predicts that animals in a variable schedule should exploit a food patch for a longer period of time when food runs out, and hence this experiment may be said to support the GDT.

The phenomena discussed above also occurs among humans when they are placed in a social context. Castro (1989) tested the amount eaten by 82 humans when they were in the presences of others. Subjects were not competing for food, but, they ate in the same area.

Subjects were asked to keep a behavioral record which consisted of food ingested, hunger, the amount of individuals present and their emotional state (anxiety, elation). They concluded that the amount of food ingested was positively correlated with the amount of individuals nearby.

Many theories have evolved from a psychological perspective to emphasize the importance of conspecifics on individual performance. Perhaps the most influential of these has been the mere presence theory proposed by Zajonc (1965). Zajonc (1966) asserted that the mere presence of conspecifics, whether as active participants or passive viewers, increased the quality and or quantity of an individual's performance. He postulated that this phenomenon imitated a domino effect. The presence of a conspecific aroused an individual, which in turn increased drive. However, Zajonc contended that this phenomenon did not occur immediately. Initially, individuals were found to perform at a poorer rate when exposed to the presence of others, but with increased trials a reversal took place and the subjects performance improved to a level higher than it would have in

isolation. He attributed the increase in overall performance to a frequency effect. Repetition of task eventually led to improved performance.

In their attempts to confirm Zajonc's (1965) drive theory Treichler, Graham, and Schweikert (1971) studied resistance to extinction in a social context. During the training phase subjects were exposed to an operant schedule either alone (A) or together (T). Subjects in the A and T group were further subdivided during extinction into extinction alone (A) or extinction together (T) so that a total of four groups were formed—AA, AT, TA, TT. Enhanced resistance to extinction was observed in the TA group only. The researchers concluded that the presence of a conspecific during acquisition enhances performance, and this enhanced performance was carried over to the extinction phase. The TT group did not manifest enhanced resistance to extinction.

Other experiments, which utilized the resistance to extinction paradigm, did not support the drive theory of social facilitation but supported the GDT. Haung and Wood (1984) utilized a procedure similar to Treichler (1971) in order to determine whether the drive theory,

the distraction interference theory or the GDT could be used to explain resistance to extinction in a social context. In the presence of a conspecific the drive theory postulates an increment in general arousal, and hence an increase in responding for both acquisition and extinction. Conversely, the distraction/interference theory would predict the opposite, with a decrease in both. For 17 days, Haung and Wood (1984) exposed half of their subjects to a conspecific condition (T) while bar pressing and the other half to an isolation condition (A). On the 18th day all subjects were extinguished with half of each group exposed to a conspecific (T-A and T-T) and the other half remaining alone (A-T and A-A). Haung et al. postulated that an increased rate of responding during acquisition and extinction for T groups would support the drive theory since the presence of a conspecific is said to increase arousal hence drive. A decrease in the rate of responding for groups T-A and T-T would support the distraction interference theory as a conspecific is thought to disturb learning of new material. And a decrement in the rate of responding for animals exposed to change from the acquisition stage to

the extinction stage (T-A and A-T) would support the GDT. Haung et al, reported a significant decrement in responding for groups A-T and T-A favouring the GDT as an appropriate explanation for resistance to extinction in a social context.

Ecological Perspective

Ecological research has also generated research in optimal foraging and extinction. While the psychological perspective has focused on the influence of behaviour schedules on foraging, the locus of the ecological view is divided between mathematical models and field analysis, with both methods emphasizing cost-benefit relationships.

This is not to say that the two disciplines have not overlapped in the methods used to study foraging. Dallery (1991) states that "ecologists have been employing operant techniques and equipment as tools for the study of foraging." Similarly, Roberts (1990) asserts that partial reinforcement experiments and patch sampling experiments are analogous since in both cases a sequence

of reinforcements and non-reinforcements are encountered. Furthermore, Roberts (1991) suggests that the similarity is extended to resistance to extinction. Roberts studied patch sampling on the radial maze. He created a situation where some arms were baited, and within the baited areas the number of food patches varied (b). He found that "just as the number of resistance to extinction increases as b decreases in baited patches, resistance to extinction increases as percentage of reinforcement decreases." It follows, that ecological theories may have a valuable input into psychological explanations of resistance to extinction and its relation to foraging.

Distinctively, the ecological focus highlights foraging as a maximization problem with an animal attempting to obtain the maximum food per unit time (Kamil & Sargent, 1981). This is the basis of optimization theory and is assumed to be central to an animal's survival. The greater the amount of energy obtained by a forager per unit time, the more liberty the animal will have to satisfy other needs such as mating, protecting its food source and offspring (Charnov & Hensch, 1989). Charnov (1976) proposed a marginal value

theorem, otherwise classified as a deterministic foraging model, in his efforts to explain how animals optimize foraging behaviour. He identified the average intake of food by a foraging group and the reduction of energy per unit time, as two prominent factors in a forager's decision-making process. For example, the decision to persist with a certain food patch or embark on a new one is dependent on (1) travel time to the patch and (2) energy expended in obtaining the food or carrying the food. The longer an animal spends foraging for food the more elusive it becomes (since it is unlikely they will find food in the next few moments) and the more energy is used. It is therefore not conducive to the foragers survival for it to remain in an area for too long. Similarly, it is not advantageous for a forager to abandon a food patch when it can still benefit from foraging in that area. An optimal foraging time falls between the above two options. According to the marginal value theorem, a forager will embark on a new patch when the intake of food equals the depletion of energy regardless of the richness of the patch.

While many researchers have supported the findings

of the marginal value theorem (Cowie, 1977; Krebs, 1973; Davies, 1977) common criticisms involve its practical application and its lack of explanation regarding a decision-rule. How many foragers actually retain information pertaining to the amount of energy they have consumed during the exploitation of patches (Cowie & Krebs, 1979; Galef, 1988; Kamil & Clements, 1990)? This has led supporters of the marginal value theorem (Krebs, 1974) to concentrate on the mechanisms involved in the decision-making process. Three hypotheses which have been postulated are (1) foraging by number expectation, (2) foraging by time expectation, and (3) give-up-time (GUT).

Gibb (1958) examined titmice and how they capitalize on the larvae residing in pinecones. He observed that titmice left more food in areas containing pinecones with a high density of larvae than in areas with a lower density. This led him to the hypothesis that foragers look for an expected number of food items (foraging by number expectation) and once they reach the criterion number move on to another patch.

In his efforts to support the number expectation hypothesis, Krebs (1973) discovered that predators use a

much simpler method in deciding which patches to exploit and suggested foragers hunt by time expectation. He suggested that foragers monitor the time they spend within a certain area and argued that what was monitored was the time span between last catch in a patch (the give-up time) for all patches within a habitat.

Ydenburg (1984) compared the give-up time (GUT), the foraging by number expectation and the foraging by time expectation hypothesis to determine which could best support the decision-making process. Three great tits were tested in an experimental room where they were required to hop on a perch to obtain food rewards and then hop back to a station point to reset the perch for the next reinforcement. Rewards were dispensed randomly and once obtained the probability of reward recurrence declined. Ydenburg measured average patch residence times. In examining patch visits, Ydenburg found titmice (1) remained at the perch for greater than 1 but not more than 4 non-reinforcements and (2) departed after successive non-reinforcements. These findings were in accordance to the give-up-time hypothesis. However, an interesting phenomenon was found when Ydenburg examined

the patch residence time. Although give-up-times increased when a reward schedule was poor, when visits were interrupted (by not allowing a reward to occur for 9 fixed responses or by providing additional reward), patch residence time remained significantly longer for the additional reward group than the delayed reward group. Ydenberg suggests that the above finding supports the view that (1) give-up-time rule applies to a clumped distribution of food and (2) other environmental influences affect a forager's decision to leave an area. However, while the great tits had a preference for the GUT rule, they were also capable of using other rules. He concluded that the GUT rule alone cannot explain all patch leaving behavior.

In a natural environment, food distribution is not always clumped. A forager is more likely to forage in an environment where food is discovered by chance (stochastic environment). Often this requires the animal to learn while he forages and what he learns may influence how long he will stay with a patch. Two common criticisms of the marginal value theorem are connected to the above factors. Oaten (1977) and Lima (1984) suggest

that the marginal value theorem assumes animals are familiar with the travel time to and the quality of each patch, but, as suggested above, this may not always be the case.

Lima set out to test how the GUT rule is affected by a stochastic environment (an area where food is discovered by chance). He trained downy woodpeckers to forage for food in logs which contained 24 holes each. He varied the location of food so that some logs contained a substantial food reward others contained marginal reward and yet others no reward at all. The results partially supported the GUT. Lima suggested that along with the GUT rule a more sophisticated strategy was being used in the decision-making process. He found that the woodpeckers used a sampling strategy to locate food. The woodpeckers sampled each area in a systematic fashion, and quickly learned that some areas contained food while others did not. With this knowledge, the woodpeckers were then able to determine a give-up-time. The woodpeckers increased their give-up-time when food was located in a food site.

Krebs (1987) criticized the GUT rule stating that

average rate of food intake is not a reasonable measure of foraging. Instead he suggested that models based on the variation in food intake, i.e., Caraco's risk-prone risk-averse model, may provide a refined explanation for foraging behaviour since it better represents the natural environment.

Caraco (1980) disagreed with the notion that foragers only exploit patches that yield the highest net energy per unit time. He viewed optimization as an extension of deterministic foraging models and emphasized the role of variable food patches and how these patches affect foraging behaviour. According to Caraco, an animal could be classified as risk-averse (favouring relatively consistent patches) or risk-prone (embracing variable food patches for high reward). The natural environment determined whether an animal would act in a risk-prone or risk-averse manner. For example, an environment dictating risk-averse behaviour would provide a subject with all energy costs needed.

Caraco's (1980) risk-sensitive theory has been labelled as impractical. Pyke (1977) argued that foragers find it difficult to discern the energy contents of a

resource. Caraco, himself, has stated that his theory may be unnatural since foragers may not be able to distinguish the parameters of a foraging site in a natural setting.

In an attempt to integrate the models based on (1) learning mechanisms, (2) mathematical models (optimal foraging model), and (3) field studies on foraging, Giraldeau (1984) proposed a skill pool effect (SPE) as an explanation for social foraging. The SPE suggests that foragers within a group take on the role of producer (an active participant in foraging who takes the initiative of locating feeding sites) or scrounger (a passive participant in foraging who depends on producers to locate feeding grounds). Frequency-dependent learning governs the role each member will take. For example, producers have become more interested at locating food sites because they have been rewarded for doing so and they function as producers. Scroungers, on the other hand, have been rewarded for stealing food and they continue to scavenge food. Krebs (1973) proposed that the greater the probability of discovering food in a site, the greater the number of scroungers since foraging

efficiency is enhanced when only a few individuals specialize in the energy demanding task of finding food.

Giraldeau also suggests that flexibility within this frequency dependent paradigm is paramount and that it is this flexibility which will lead to local enhancement (acquiring new feeding sites). In order for the SPE to operate and frequency dependent learning to occur, (1) individual variation, i.e., individual differences among group members (Giraldeau & Lefebvre, 1984) and individual specialization, i.e., heterogeneity of skills within a foraging group (Palameta & Lefebvre, 1984) are required. However, it is paramount that "individual differences are exchangeable as a function of food patch types and group composition" and not as a result of individual learning ability and dominance (Giraldeau & Lefebvre, 1986).

Giraldeau and Lefebvre (1984) give a concrete example of this phenomenon. The scenario involves a group of pigeons (C. Livia) who (1) each possess a specialized skill for locating food, (2) are opportunistic feeders, and (3) commonly locate food at the same feeding site. Giraldeau explains that while the C.Livia share a common feeding site they also feed at different sites and this

is governed by their individual food-discovering skills. When an individual with one specialized food discovering skill (mastered through frequency-dependent learning) encounters a food depleted patch in the common site it will follow another individual with a dissimilar skill to a different specialized food site. Hence, according to this theory it is possible for a producer to become a scrounger (local enhancement since the following will introduce a new food site). However, an interesting question arises: How do scroungers react when food patches begin to run out for a variety of producers? Do they themselves become producers or do they follow producers to another location? While the SPE theory doesn't directly deal with this question, it nevertheless suggests, at least initially, that scroungers remain scroungers and follow producers to another site.

Giraldeau and Lefebvre (1987) studied cultural transmission as it relates to the SPE to determine the underlying mechanisms governing the producer scrounger relationship. Specifically, in a series of investigations they explored (1) the role of dominance and competition in the producer-scrounger relationship, (2) the role

scroungers play in the blocking of learning, and (3), specific mechanisms associated with scroungers and the blocking of social learning. An artificial feeding site was assembled by placing 48 test tubes 5 cm apart. Feral pigeons were to peck on a wooden stick in a downward motion in order to obtain food. Subjects were observed for 27 2-h sessions to determine the pattern of interaction. A scrounger-producer relationship was identified. In order to determine if competition was an important factor in the discovery of food the two most successful foragers were removed from the group and the results showed that the scroungers were flexible and able to switch to producers after a delayed period of time. This suggests that individual learning ability is not a factor affecting scrounging behaviour.

To determine if dominance was a factor the rank of priority to access of food was examined for a period of 4 weeks and correlated with discovery of performance. No significant correlation was observed suggesting that dominance was also not a factor. To determine if the blocking of learning suggested above was a result of individual variation naive individuals were placed in a

position where they could observe individuals experienced at pecking at a tube for food (tutors). Naive individuals were able to learn suggesting that foraging skills are not due solely to individual variation but rather to group composition (i.e., ability for a producer scrounger relationship to occur).

In order to test this hypothesis Giraldeau performed a variety of experiments. When naive subjects were allowed access to the tutors' (individuals pre-trained at pecking for food) food, a preference for scrounging behaviour was observed with very few naive individuals becoming producers. This suggests that it was more beneficial for the naive subjects to become scroungers and depend on producers for food. It also supports the specialization within groups. In a clustered food patch, the congestion is apt to provide an atmosphere where it is easier and therefore preferable for animals to scrounge food. Should a producer leave a food site the scroungers are prone to follow, since they have not learned the specialized techniques for obtaining food at that food patch.

Much of the above mentioned work raises a number of

questions. For example, how quickly will animals extinguish foraging in an area and move onto another site? Goldstein and Harrigan (1991) studied resistance to extinction in a social context in an attempt to determine whether an ecological (SPE) or a psychological perspective (GDT) could be utilized in explaining foraging behaviour. Eight subjects were placed in an octagonal shaped operant chamber with eight reinforcement stations. By manipulating the number of stations available to the subjects, it was possible to control the similarity between the conditions of reinforcement and the conditions of extinction. In such a setting, the GDT predicts the greatest resistance to extinction to occur when these two conditions are most similar. However, these authors found the opposite to be true. They concluded that the skill pool effect (SPE) was a better theory for explaining resistance to extinction. The rationale behind their conclusion was that SPE takes into consideration the social dynamics involved in foraging, as it assumes that skills are readily transmitted through a population (Goldstein, 1991). For example, when one subject realized that food was not available in

the operant chamber, it's behaviour provided cues to the other subjects indicating non-reinforcement.

Analogous to Goldstein and Harrigan (1991) the present study attempted to determine if resistance to extinction is influenced by social context and if the GDT can be used to explain the phenomenon. While Goldstein and Harrigan kept both food production and schedules of reinforcement constant as the number of stations varied, they did not control for accessibility. These researchers tested subjects in a setting which provided concurrent food patches only. However, in the natural environment foragers are usually exposed to depleted and non-depleted food patches and are required to compromise time exploration with food consumption (Kamil, 1978). Hence, this study was designed to compensate for accessibility by allowing subjects access to all stations with some bars acting as food rewards and others as non-rewards. By altering the number of bars functioning it is possible to determine how a forager's extinctive behaviour is affected by his environment—a scarce environment (1 bar functioning) versus a densely food-dispersed environment (8 bars functioning).

This design is more similar to a natural environment since subjects are simultaneously exposed to patches which provide an abundance of food and no food at all. Such an environment provides a controlled climate in which to study what happens after an animal becomes accustomed to a food condition (in this case the number and position of bars dispensing food) and what happens when that food runs out (extinction).

In highly dispersed (8 bars functioning) environments, subjects are expected to acquire food discovering skills, while in stochastic environments (1 bar functioning) subjects are expected to concentrate their efforts on following others to obtain food. Hence, the SPE predicts that during extinction the greatest number of responses would occur when the greatest number of bars were working. The GDT, however, predicts that the greatest number of responses during extinction would occur when the least number of bars were working, since a stochastic environment suggests circumstances similar to extinction. In such an environment, a forager does not know when it will obtain food.

Similar to Goldstein and Harrigan (1991), this study

also controlled for confounding variables. Specifically, food supply and schedules of reinforcement were held constant. In order to rule out food supply as a factor, the food supply was equated, in Experiment 1, by changing schedule values. Specifically, each bar working was assigned a VI schedule of 15. Hence, food was available on an average of 15 seconds for 1 bar functioning, 30 seconds for 2 bars functioning, 60 seconds for 4 bars functioning, and 120 seconds for 8 bars functioning. This ensured constant and equal distribution of food.

However, in order to maintain a constant food supply, it was necessary to vary the reinforcement schedule (as above). In Experiment 2, the schedule of reinforcement was held constant at a VI of 120 in order to control for any schedule differences (food variable).

EXPERIMENT ONE**METHOD**

Subjects: Eight 200-day old male hooded rats, who have had exposure to similar experimental conditions (Goldstein & Harrigan, 1991) in a pilot study served as subjects. They were commercially bred and purchased from a Montreal supplier, and upon their arrival in Thunder Bay were housed together in an octagonal arena.

Apparatus: Subjects were housed in an operant arena with the following measurements—area of 16.2m²; diameter of 4.6m; perimeter of 14.6m; 1.8 m on each side and 1.2 m in height. It was constructed of plexiglas with a stretch metal floor and wire mesh ceiling. The light-dark cycle of the facility in which this chamber was housed was 14 hours of light and 10 hours of dark.

Surrounding the arena, approximately 2m apart were eight Noyes 45 mg pellet dispensers. These would hold 45 mg rat pellets. Each pellet dispenser served as a reinforcement station and was equipped with a retractable manipulandum, controlled by a PET computer command

program (Goldstein, Blekkenhorst, & Mayes, 1982). Adjacent to each dispenser was a 100 ml graduated cylinder which served as a water bottle.

Four video cameras surrounded the arena and recorded the activities at each station. In turn, these activities were monitored on a television in an adjacent room. A VCR recorded each session on an mm video cassette.

The PET (4062) microcomputer, as described by Blekkenhorst and Goldstein (1983), recorded the total number responses per station, reinforcements per station, and a mean post-reinforcement pauses per station. In addition, the number of responses per station per minute and the number of subjects per station per minute were recorded manually on a record sheet.

Procedure: Subjects were previously trained and familiarized with the different reinforcement schedules (Goldstein & Harrigan, 1991).

For three consecutive sessions the subjects (2 sessions per day - 8:30 a.m. and 5 p.m. - each 30 minutes in length) were trained on a VI schedule and then extinguished. The extinction phase persisted until a 5 minute period of no response was observed.

The above paradigm was repeated for four different situations (number of bars functioning = 1, 2, 4, and 8) and the order in which these conditions were presented was determined randomly. In each situation, the subjects were exposed to all eight bars with only a specified number of bars functioning. Specifically, for the 1 bar condition, bar 5 was functioning; for the 2 bar condition, bars 1 and 6 were functioning and the for the 4 bar condition, bars 2, 3, 7, and 8 were functioning. During acquisition, the reinforcement schedule varied in accordance with the situation - number of bars functioning - in order to maintain a constant food production. Consequently, the reinforcement schedule for bars 1, 2, 4, 8 was VI 15, VI 30, VI 60, and VI 120, respectively.

Rat chow was fed to the subjects approximately 2 hours following the evening session.

EXPERIMENT 2

METHOD

Subject: The specifications were the same as Experiment 1.

Apparatus: The specifications were identical to those of Experiment 1.

Procedure: The paradigm replicated Experiment 1 with the exception of the reinforcement schedule in the acquisition phase. The reinforcement schedule was kept constant. For three consecutive sessions, subjects were trained on a VI schedule of 120 and then extinguished. Due to other experimental commitments, the acquisition phase for the 4 bars functioning was only kept to one session.

RESULTS

Data Analysis

The response pattern was determined by the total number of bar presses accumulated at each bar for each session and the number of bars functioning (1, 2, 4, 8) during acquisition represented the treatment phase. Resistance to extinction was evaluated in single sessions and measured by total number of bar presses per station for functional and non-functional bars. A trend analysis was employed in order to determine the changes in the number of responses during extinction when the number of bars were varied.

Data analysis did not concentrate on the acquisition phase, as the focus of this experiment was on what happens when a subject becomes accustomed to a condition and then the food runs out (extinction). However, an analysis of variance was performed to identify differences due to stations and trials for acquisition.

The total number of rats at each station represented the dispersion pattern. A microstat package as defined by Goldstein (1981) was used to survey the dispersion of

animals within the operant arena. The number of rats per station were recorded and this information was used to determine the magnitude of spatial movement within the arena (D stat). Generally, the higher the D stat the greater the movement within the spatial arena.

Experiment 1

Acquisition

Analysis of variance was used to identify differences due to stations (functioning versus non-functioning bars, for Experiments 1 and 2) trials (acquisition1, acquisition2, acquisition3) and their interactions. A strong main effect of stations ($\eta = .93$) shows a significant difference in mean responses for bars functioning and non-functioning ($F = 100.688$, $p < .01$). Specifically, the number of responses were greater for bars functioning (4018.70 versus 1143.91). Stations did not interact significantly with trials.

An analysis of covariance was used to determine if the total number of responses for stations (bars functioning versus non-functioning) were independent of

trials. No significant difference was found ($p > .05$) indicating that stations did not influence number of responses.

Similarly, an analysis of covariance was used to determine if the total number of responses for stations (bars functioning versus non-functioning) were independent of condition (food constant versus food variable). No significant difference was found between Experiments 1 and 2 indicating that the total number of responses were not influenced by whether food was held constant or allowed to vary.

Resistance to Extinction

Figure 1 illustrates the total number of responses for treatment for Experiment 1 (food constant). A trend analysis indicated a quadratic trend with an equation of $y = 50.504 x + 354.609$ ($r^2 = .176$). Hence, the change in total number of responses can not solely be explained by the number of bars functioning ($r = .420$). Interestingly, 4 bar functional condition showed the greatest resistance to extinction, while the 1 bar functional condition

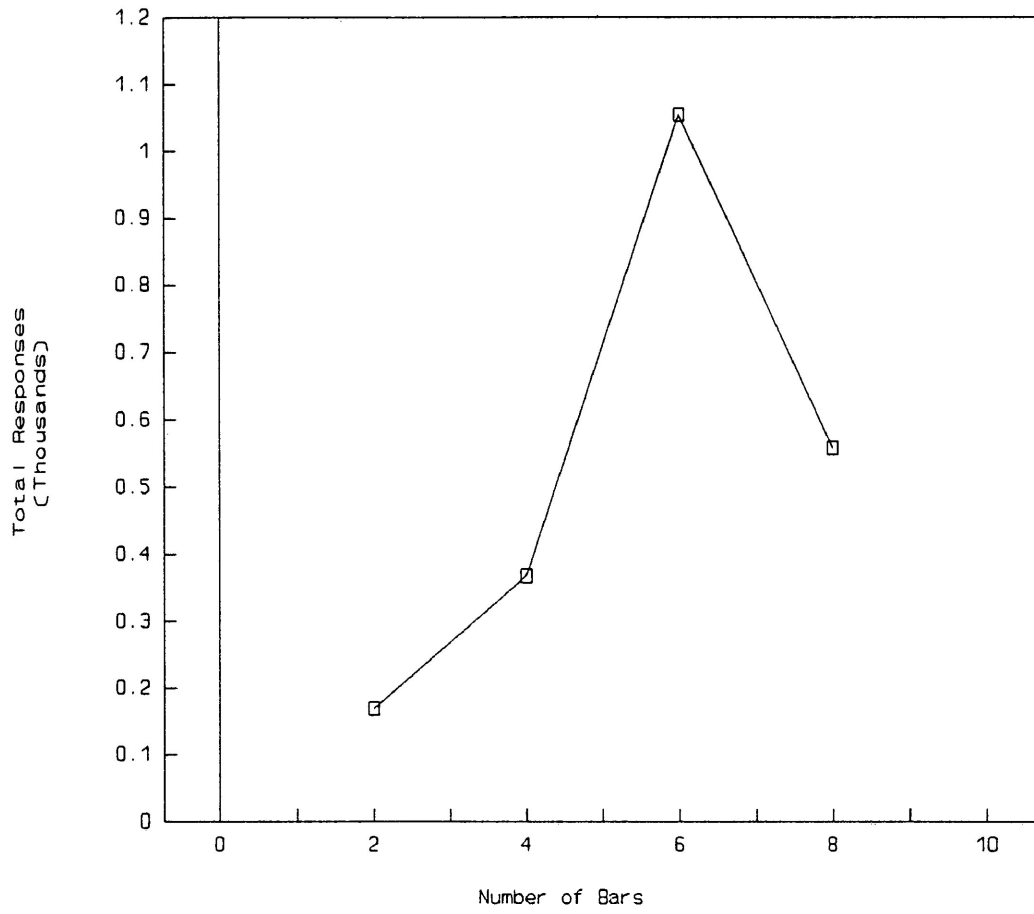


Figure 1 Total number of responses for treatment when food was kept constant (schedule varied)

showed the least resistance to extinction. Initially, with number of bars functional equal to 1, 2, 4, it appears that the graph is approaching a linear trend. However, a relatively large drop in number of responses occurs when 8 bars are functioning.

Different results were obtained when total number of responses for functional and non-functional bars were separated for Experiment 1. The total number of responses are shown in Figure 2, for functional versus non-functional bars. A trend analysis for functional bars indicated an upward trend with an equation of $y = 160.3913 + 66.4957 x$ ($r^2 = .44275$) for the line of best fit. There was a moderate relationship ($r = .6654$) between the number of bars functional and the total number of responses. This means that the total number of responses increased as the total number bars functional increased. These findings are analogous to Goldstein and Harrigan (1991).

However, a trend analysis for the non-functional bars indicated a quadratic trend.

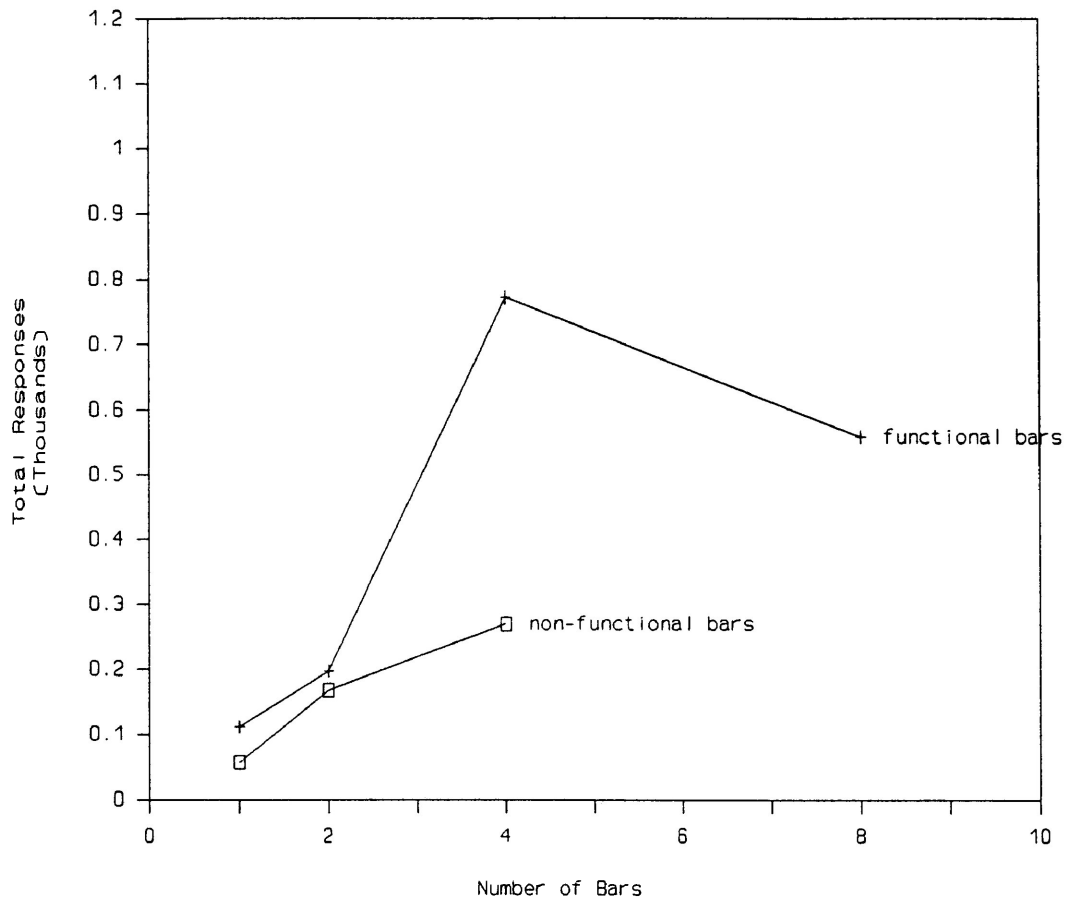


Figure 2 Total number of responses at functional & non-functional bar when food was controlled (schedule varied)

Dispersion Patterns

Figure 3 reflects the dispersion pattern for the three acquisition trials for Experiment 1 (food held constant). The percentage for D stat figures range from 65.52 to 96.55. These figures are relatively high indicating a significant amount of movement or instability within the operant chamber.

The D stat percentage (Goldstein, Blekkenhorst, & Mayes, 1982) for the treatment condition for Experiment 1 are shown in Figure 4. The greatest amount of movement occurred with 4 bars functional (83.33) while the least amount of movement occurred with 8 bars functional (66.67).

Figure 5 compares the D stat for Experiment 1 (food kept constant) and Experiment 2 (food varying) for extinction. In all cases, the D stat was greater when food was not held constant (D = 78.57, 73.68, 83.33, and 66.67 for 1, 2, 4, and 8 bars functioning, respectively). However, the difference is not large. The greatest difference for percentages between food varying (28.57) and not varying (83.33) was evident when four bars were functional with the food constant cycle manifesting a

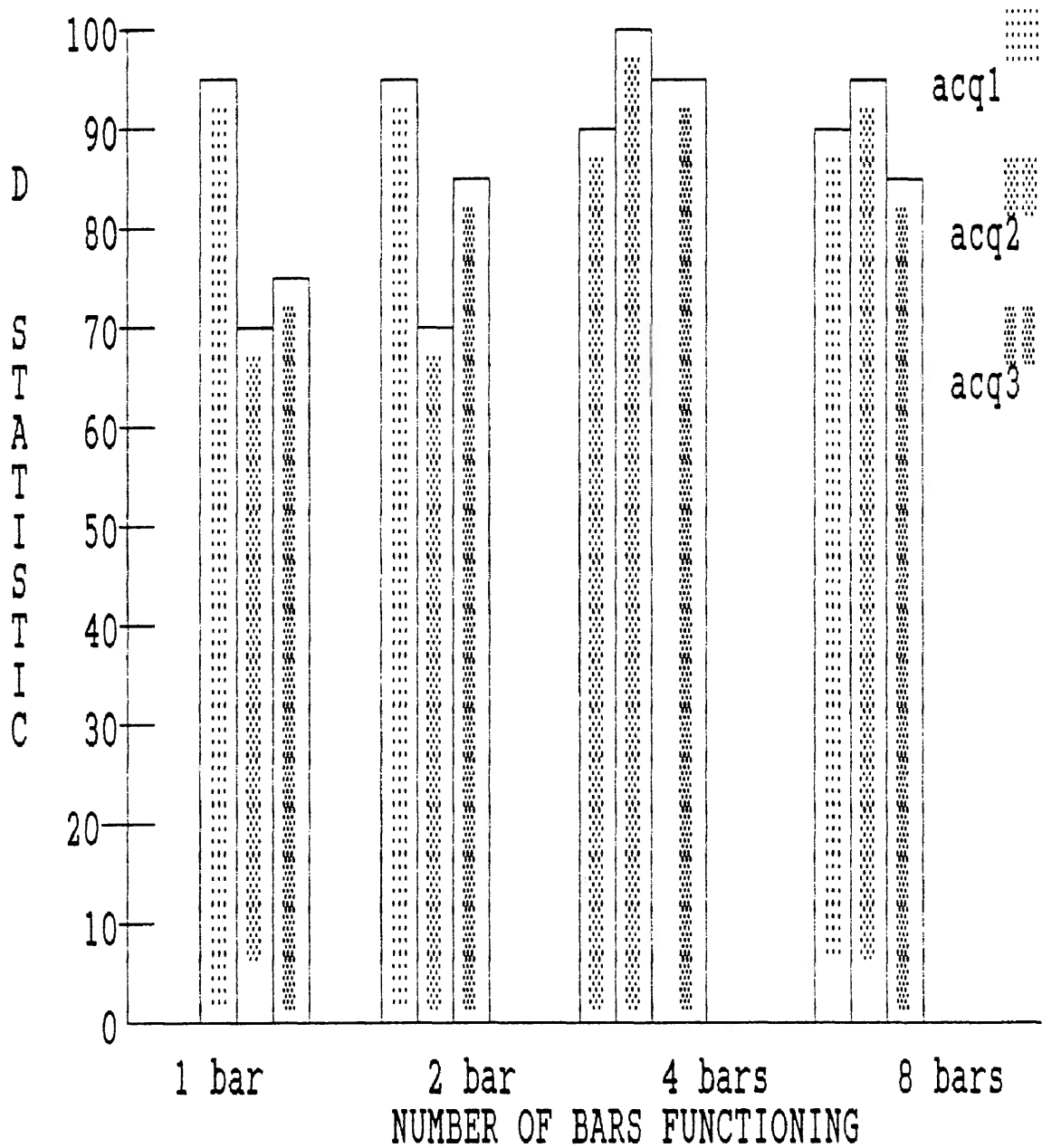
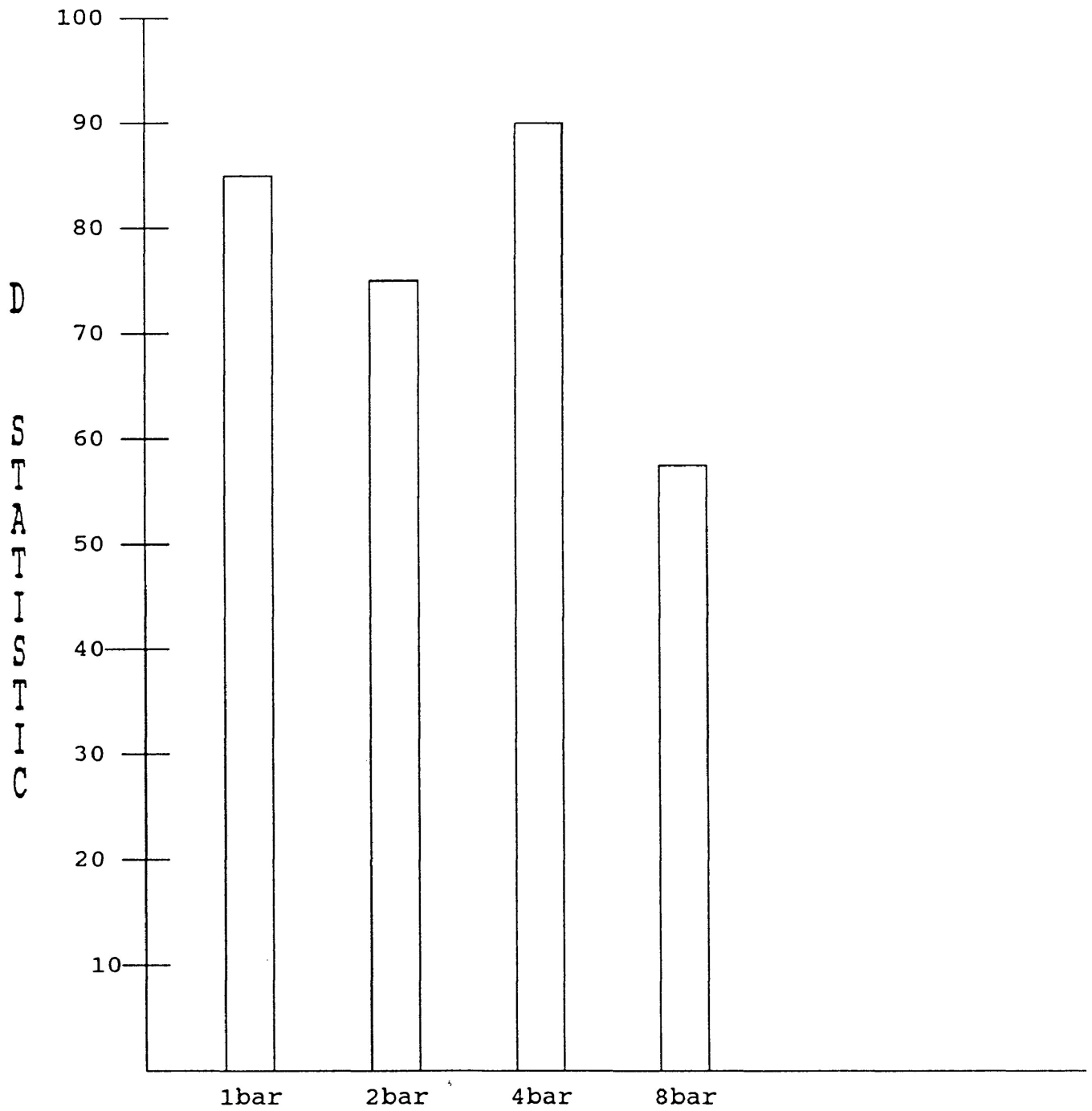


Figure 3

The dispersion statistics for the 3 acquisition phases (acq1 acq2 acq3) for food constant.



NUMBER OF BARS FUNCTIONING
 FIGURE 4

The dispersion patterns during extinction for treatment when food was kept constant (Experiment one).

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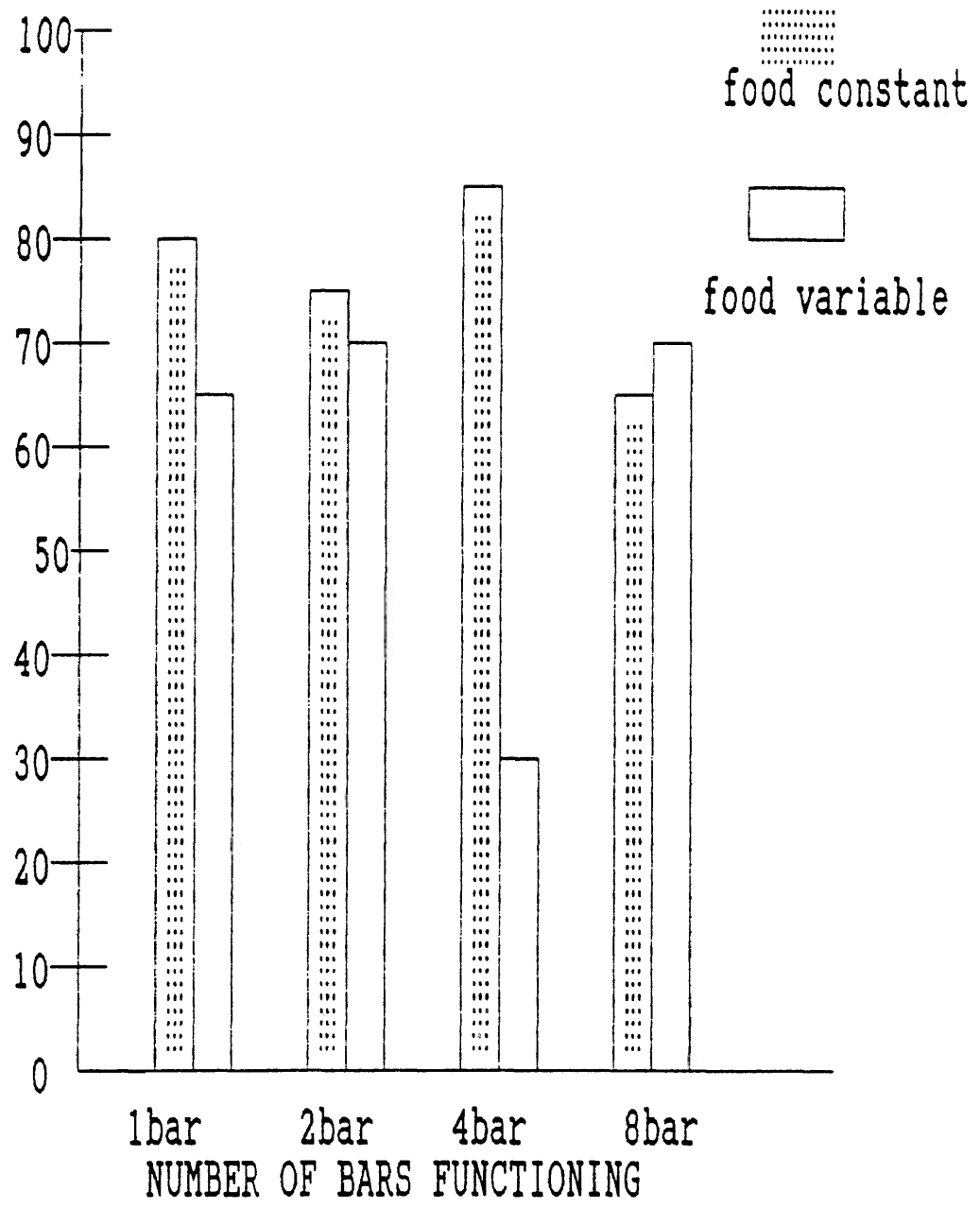


FIGURE 5

The dispersion patterns for extinction for food kept constant and kept variable

greater D stat percentage.

Figure 6 illustrates the total of rats working (measured by the total number of visits per bar) when food was held constant for both functional and non-functional bars in extinction. For the functional bars, the greatest amount of rats were observed working when 4 bars were functional, while the least amount of rats were seen working with two bars functional. Similarly, for the non-functional bars, the most amount of rats working was observed with 4 bars functional, while the least amount of rats working was observed with two bars functional.

Figure 7 represents the number of responses at non-functional bars during the acquisition and extinction phases for all conditions, i.e., 1, 2, 4, and 8 bars. The greatest amount of responses for acquisition occurred with 4 bars functional and the least with two bars functional. During the extinction phase, the most responses occurred with 4 bars functional and the least with 1 bar functional for non-functioning bars. Interestingly, the greatest difference in number of responses between the acquisition phase and the extinction phase occurred with 1 bar functional.

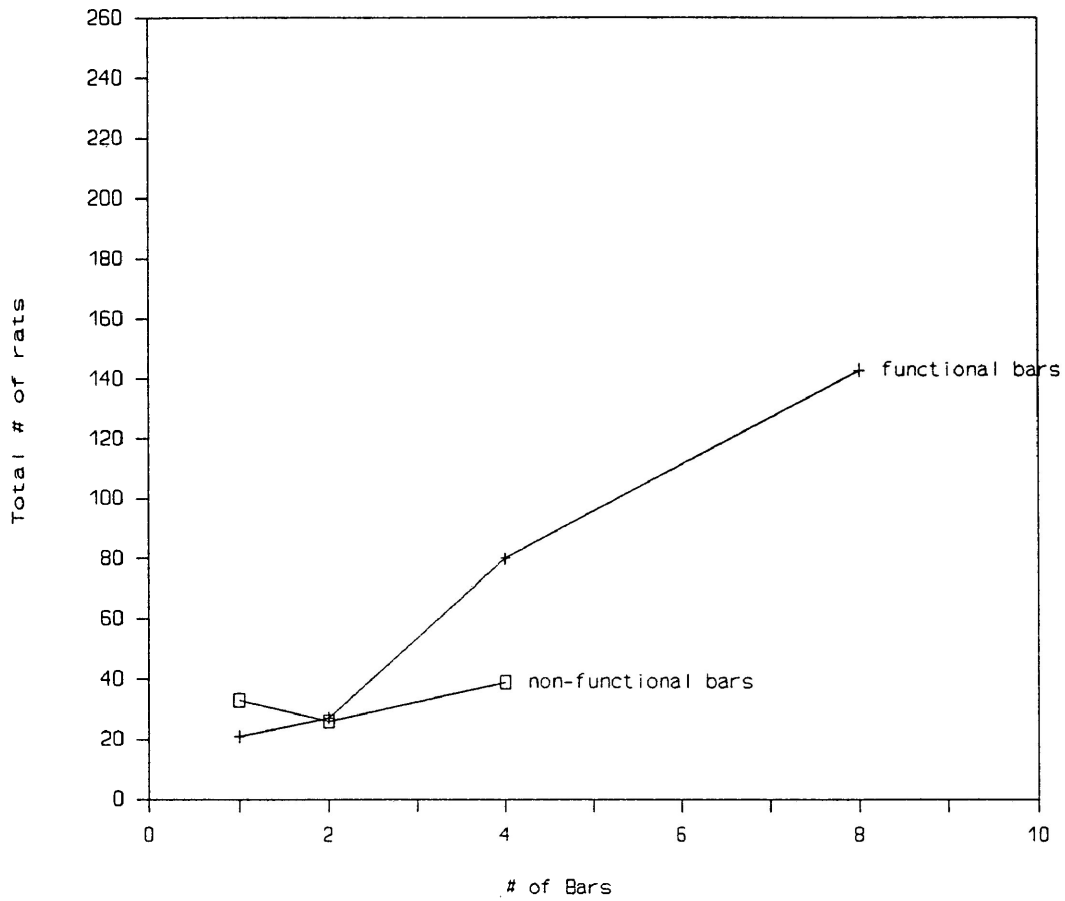


Figure 6 Total number of rats working when food was held constant (schedule varied) for both functioning and non-functioning bars.

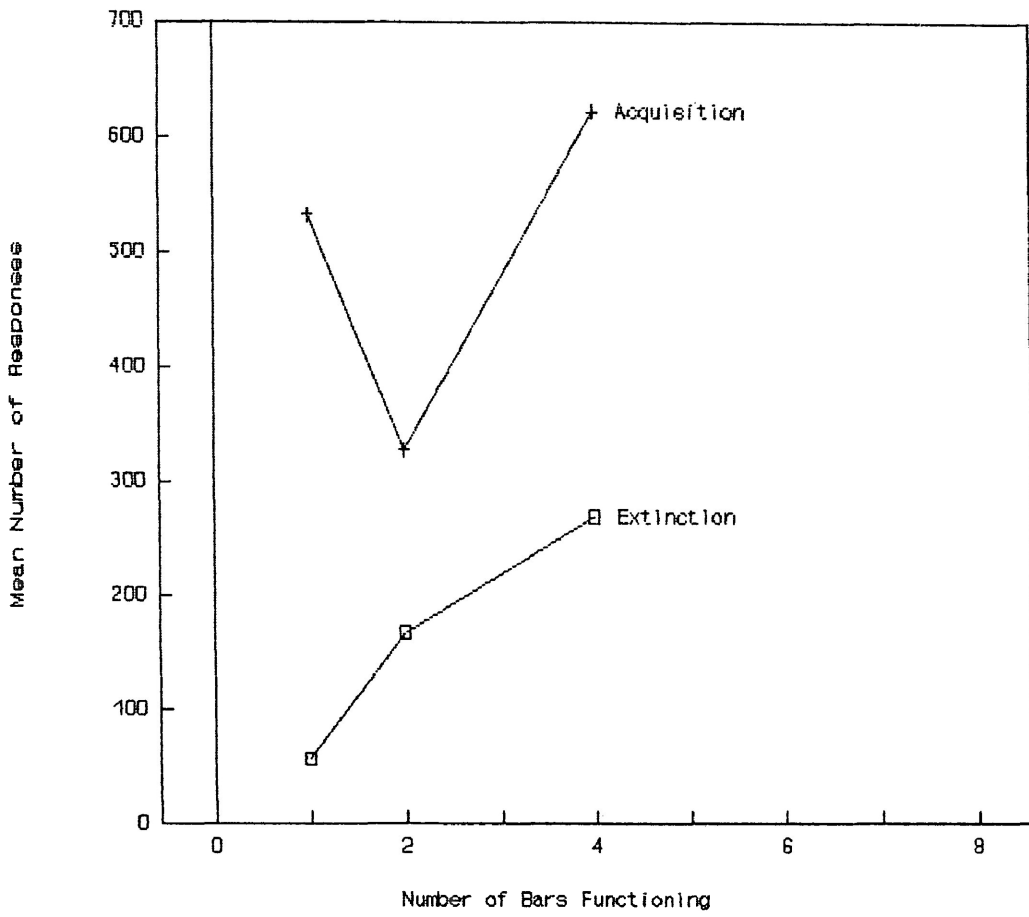


Figure 7 Mean number of responses for non-functioning bars during acquisition & extinction.

Experiment 2

Resistance to Extinction

The total number of responses for treatment during extinction for Experiment 2 (food variable) are shown in Figure 8. A trend analysis indicated an upward trend, with an equation of $y = 108.1913x + 186.783$ ($r^2 = .8836$) for the line of best fit. There was a strong relationship ($r = .94$) between the number of responses and the number of bars functional.

Hence, the total number of responses increased as the number of functional bars increased. This is analogous to the results in Goldstein and Harrigan (1991).

Figure 9 compares the total number of responses for functional versus non-functional bars during extinction when food was variable. A trend analysis for the functional bars indicated a linear trend with an equation of $y = -118.3044 + 146.347x$ ($r^2 = .9337$) for the line of best fit. A strong relationship ($r = .96628$) was shown between the number of responses and the number of bars functional. This indicates that the total number of responses increased as the number of bars functional increased. This is also analogous to the findings of

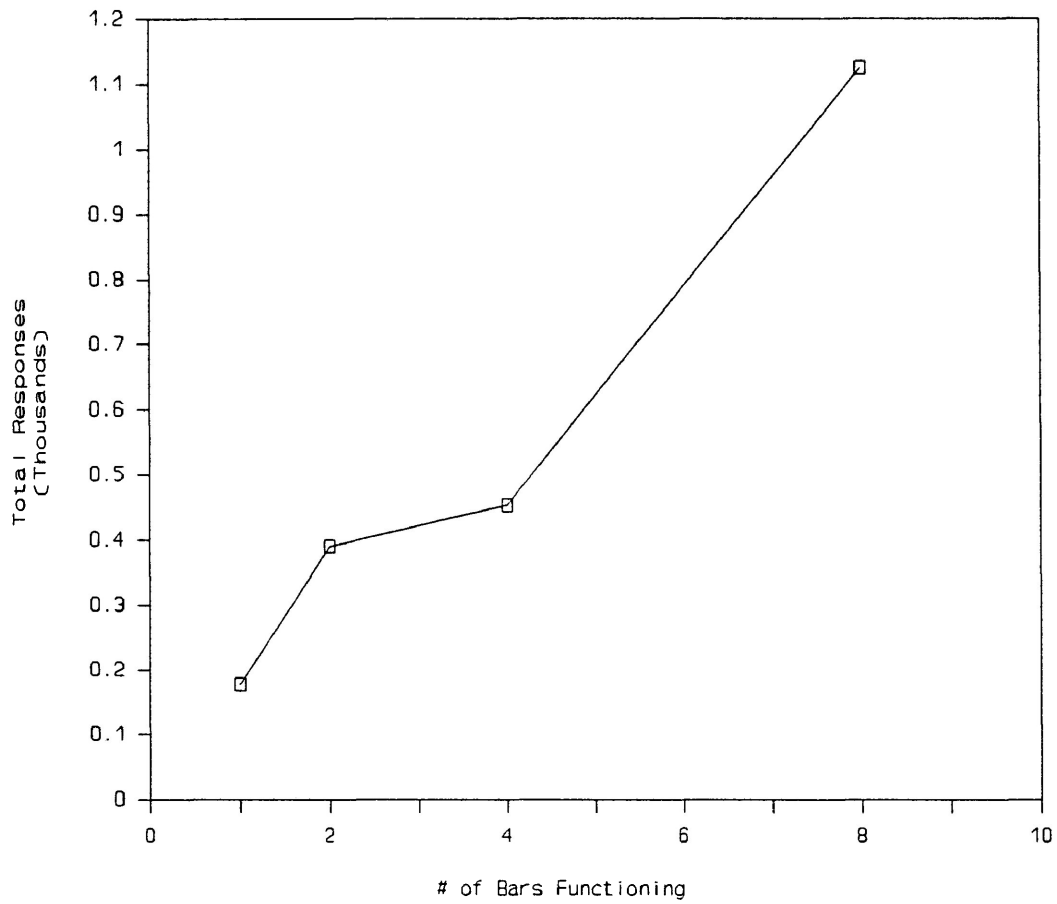


Figure 8 Total number of responses for treatment during extinction when food varied (schedule constant).

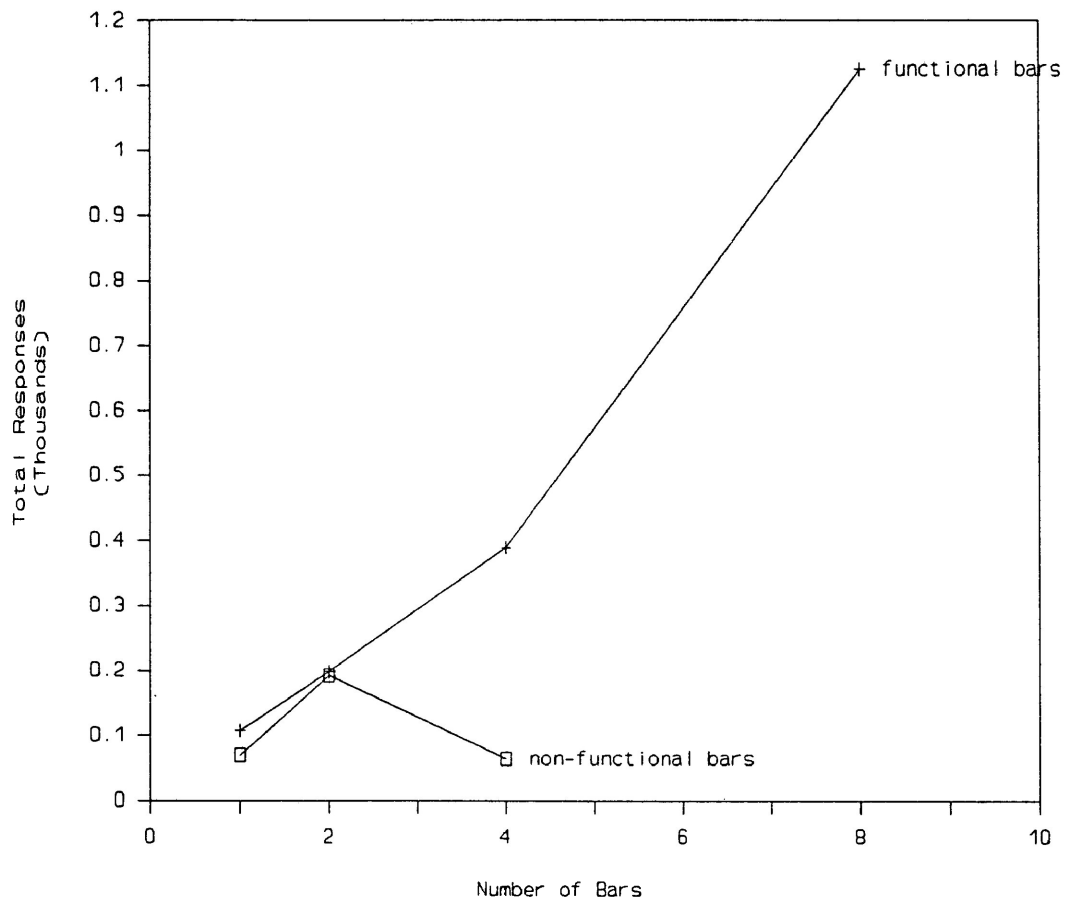


Figure 9 Total number responses for functioning and non-functioning bars during extinction when food was allowed to vary.

Dispersion Patterns

Figure 10 illustrates the dispersion pattern of the three acquisition trials when food intake was not controlled. The percentage for D stats ranged from 58.62 to 96.55 for acquisition. The acquisition figures are relatively high, once again suggesting a significant amount of movement.

Figure 11 compares the total number of rats working for the different conditions for functional versus non-functional bars in extinction. For the functioning bars, the greatest amount of rats working was observed with 8 bars functional, while the least amount of rats working was observed with 4 bars working. The most amount of rats working at non-functional bars was observed when 1 bar was working, while the least amount of rats working at non-functional bars was observed when 4 bars were working.

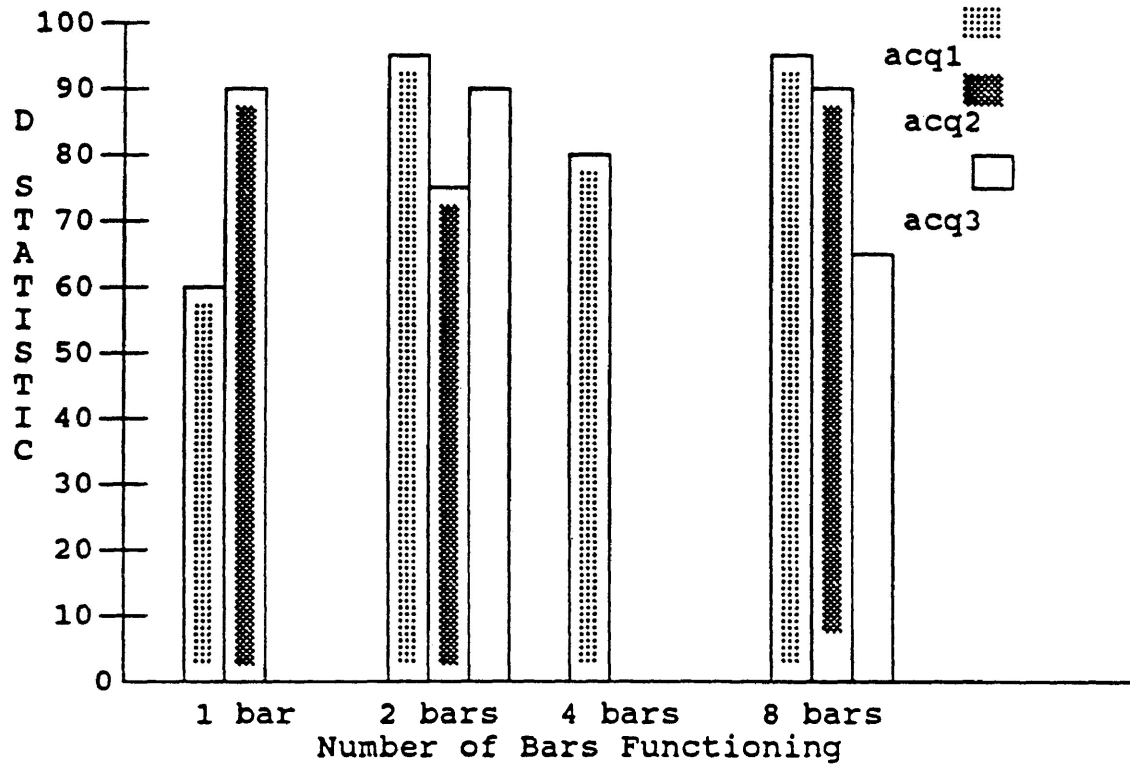


Figure 10.

The dispersion statistics for the 3 acquisition phases (acq1 acq2 acq3) for food varied.

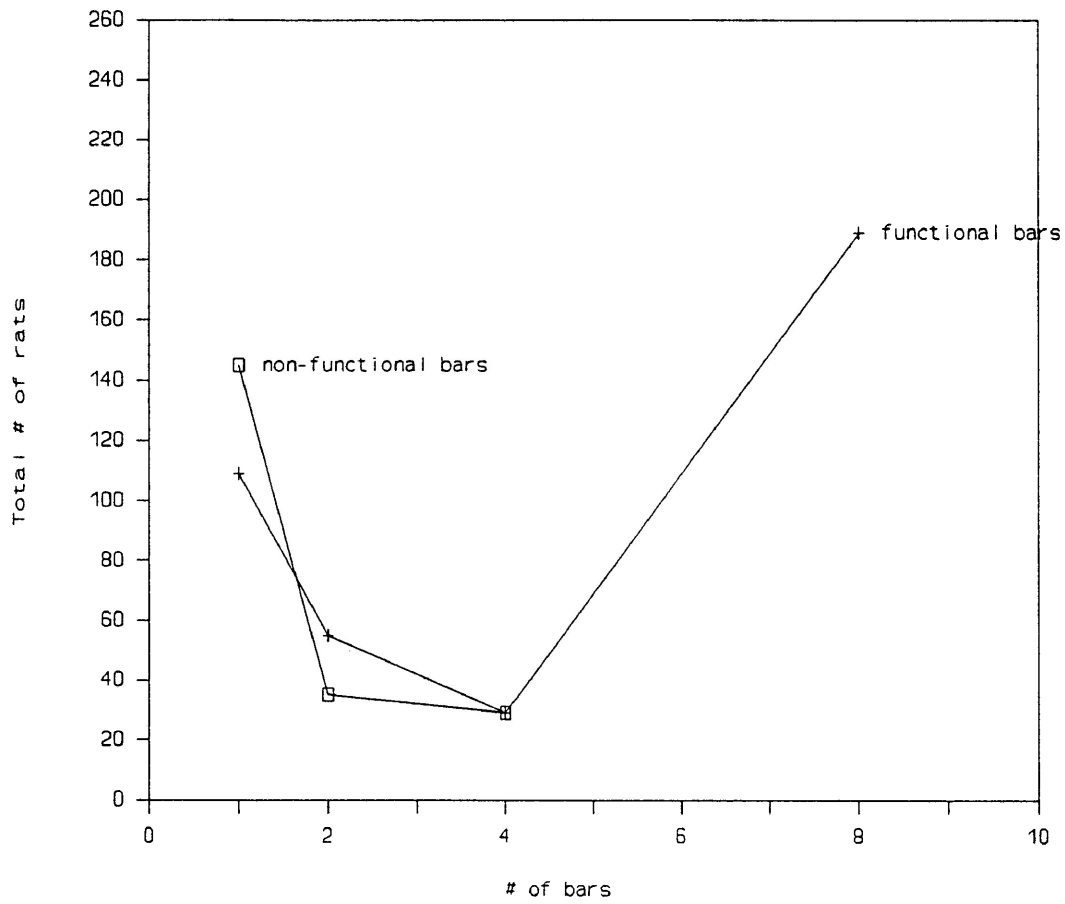


Figure 11 Total number of rats working when food was allowed to vary for extinction for both functioning and non-functioning bars.

DISCUSSION

The analysis of the acquisition phases suggests that the subjects learned to distinguish rather quickly between the functional and non-functional bars. This suggests that the population established a discrimination, regardless of whether food was found in a dispersed environment (8 bar condition) or a stochastic environment (1 bar condition). This occurred for both conditions (food constant and food variable) suggesting that learning took place regardless of the amount of food available or the magnitude of the interval schedules of reinforcement.

For resistance to extinction, the overall analysis did not support the findings of Goldstein and Harrigan (1991). Goldstein and Harrigan found a significantly strong predictive factor for number of bars functional and resistance to extinction (number of responses). That is, with increased number of bars functioning during acquisition, an increased number of responses during extinction was observed. They concluded that the results supported the SPE. They explained when 8 bars were

functioning during extinction, food was densely dispersed and hence subjects were required to use their own skills to obtain food. However, when 1 bar was functioning food was scarce and subjects were required to rely on each other to obtain food.

In the present study, subjects did not appear to use the strategy suggested above. A steady increase in the number of responses as the number of bars functioning was not observed in Experiment 1 (schedule varied), but observed in Experiment 2 (schedule constant).

The previous results are similar to those found by researchers studying the stochastic models of foraging (Krebs, 1974; Lima, 1984; Oaten, 1977). To recall, stochastic models of foraging assume that food will be found at different locations within the environment. A common methodology utilized by researchers studying the stochastic models involves baited versus non-baited patches (Roberts, 1991; Lima, 1984). When an environment contains food in one area but not the other, foragers must distinguish food enriched patches from empty patches.

Ydenberg (1984) determined that subjects use a give-up time strategy (GUT) to aid them in making the

above distinction. According to the GUT theory, the give-up time increases as the reward schedule becomes less prosperous. In other words, foragers leave a food patch much quicker when food reward is poor. However, the rate at which subjects leave a food patch and the method used is also dependent on the distribution of prey between patches. If it is evenly distributed then subjects use a number expectation strategy in determining when to leave a patch. If, on the other hand, food is clumped then subjects use a give-up time strategy.

If the above theory serves as an explanation for this study, then subjects would be using a give-up time strategy when food reward resembled a stochastic environment (1, 2, or 4 bars functioning) during the acquisition phase. If a give-up time strategy were used in a stochastic environment then the number of responses would be small, because foragers leave a food patch quicker when food reward is poor. The more impoverished the reward the quicker subjects would leave a patch. During the extinction phase, subjects would give-up even more quickly because food is not distributed and the food reward is exceptionally poor. Hence, with 1, 2, and 4 bars functional, a steady increase in the number of

responses would be expected with an increase in the number of bars functioning. Figures 1 and 8 illustrate the above relationship.

However, when food is evenly distributed (8 bars functional) foragers use a different strategy (i.e., the number expectation strategy) in determining when to leave a patch. The number of expectation strategy assumes that regardless of the amount of food available, subjects will remain in a food area until they receive a given amount of food. If this occurred in this study, then during acquisition, subjects would remain at a station until they had acquired a given amount of food. When the extinction phase was introduced, subjects could no longer rely on the number of expectation strategy and they changed foraging techniques.

If the above is correct, then how may the difference in Experiments 1 and 2 be explained?

For Experiment 1, when a composite graph (Figure 2) was created to compare the total number of responses for the functional and non-functional bars, a linear trend was found for functional bars supporting Goldstein and Harrigan. However, while Goldstein and Harrigan found a strong relationship between number of bars functional and

number of responses, this experiment showed a moderate relationship ($r = .6654$). This suggests that other factors may be influential in explaining what is happening.

By examining the number of responses at non-functional bars and comparing this to Lima's (1984) study, an explanation for the difference in results of the two studies may be suggested. To recall, Lima studied give-up-time in an environment where subjects were exposed to different food conditions. He found subjects moved frequently within the environment sampling the various food sites available. He said this sampling behaviour was responsible for the subjects ability to learn the location of food quickly. Once the location of food was established, subjects then determined a give-up-time for the food site producing food. This give-up-time was established by the time spent between catches.

The design of the present study is somewhat similar to Lima's in that (1) there are various food sites available in the apparatus and (2) the amount of food available in these areas varies from substantial (8 bars functional), marginal (1, 2, and 4 bars functional) to none (extinction). Since the environmental conditions are

similar (as above) subjects may have also initially used a sampling strategy to determine the location of food.

In this experiment, subjects were quick to distinguish functional bars from non-functional bars. It is possible that a sampling strategy was used. During the early parts of the acquisition sessions, it was not uncommon to observe a high degree of movement among individual rats. Once the sampling strategy helped these rats determine the location of food sites, they remained in the anticipated food site area for a given amount of time.

But how exactly did this occur? When 1, 2, and 4 bars were working for acquisition, subjects were simultaneously exposed to extinction conditions, i.e., not all bars were working. In extinction, when food could not be obtained the subjects reverted back to a sampling strategy to determine which food sites were operational. Hence, they tested the non-functional bars once again. They quickly abandoned these bars because they had not been functional during the acquisition phase and still were not during the extinction phase. This second experience with non-reinforcement facilitated the avoidance of the stations.

Figure 7 compares the mean number of responses for non-functional bars for acquisition and extinction for Experiment 1. The comparison suggests that during the extinction phase, subjects were quick to learn that non-functional bars were still not working. In all cases for non-functional bars, the discrimination training or acquisition phase yielded at least double the responses than did the extinction phase. Once again, this suggests that subjects knew the bars were not producing reinforcements.

But how was the give-up-time determined? The give-up time is determined by the time spent between the last catch and the last patch of food, so that energy can be maximized. With one bar functional, the chances of obtaining a food catch are small, and hence, subjects gave up earlier (less responses). With four bars functional, the chances of obtaining food are greater, the give-up-time was longer and the number of responses were high.

This effect does not apply to the 8 bars functional. Instead, the behaviour of the subjects during all bars functioning may have been a result of another factor. When 8 bars were functioning subjects were not

simultaneously exposed to extinction during the acquisition phase because all bars were functioning. Hence, the 8 bar condition may be said to have greater generalized decrement and fewer responses. This methodological difference between Goldstein and Harrigan (1991) and the present study may explain the response rate difference for the 8 bar condition.

The above explanation also suggests that the environment which an animal forages will influence the strategy used in deciding to stay or leave. For experimental research, this may suggest that the environment which a subject is exposed to or observed in will influence the outcome of the studies. Mellgren (1991) suggests that the experimental measurements, i.e., whether response time or number of responses are used to measure the dependent variable, influence the outcome of an experiment in resistance to extinction studies. Further, Mellgren makes a distinction between searching and procurement in foraging behaviour. He suggests that experiments which place subjects in an operant arena with one or two bars functioning, are said to be testing procurement involved in foraging (Dunham, 1986; Sheffield, 1949), while maze studies are said to study

searching behaviour (Baum, 1983; Ilersich, 1988; Olton, 1979). According to Mellgren, evidence supporting the GDT would be based on studies designed to study procurement, while studies on SPE would be based on designs constructed to study searching strategies. The procedure used in Goldstein and Harrigan could be said to study both procurement and searching behaviour. However, in this study the experimental procedure complicates the searching behaviour by making it more difficult and less predictable.

Contrary to Experiment 1, the upward trend in Experiment 2 supports the SPE and the findings of Goldstein and Harrigan (1991). It appears that as the number of bars functional increased, the number of responses also increased. However, the greatest resistance to extinction did not occur when the food was most dense, as suggested in the hypothesis. When the food was held constant for extinction, the most responses occurred when 4 bars were functional. However, the difference in total responses for bar 4 and 8 was not significant.

In contrast, the least amount of movement occurred when 4 bars were functional and the most occurred with 8

bars functional – the opposite of Experiment 1. By examining the graphs for extinction, it becomes evident that there is an upward trend in responses for bars 1, 2, and 4 bars functional, but when 8 bars are functional there is a slight decrease. The line of best fit suggests that the total number of responses can be explained mainly by the total number of bars functional.

When a composite graph is produced (Figure 8) to illustrate the difference between the total number of responses for bars functional and non-functional for food varied, a linear trend appears for number of bars functional and number of responses. Hence, when the bars functional are separated from the bars not functional, the number of bars functional can still explain the total number of responses.

The above findings are different from Experiment 1. Interestingly, in the case of 4 bars functional, the bars which were functioning (1, 2, 7, 8) were in close proximity. The close proximity, in itself, suggests a densely food populated area, even in comparison to 8 bars functional. The uneven distribution of food when 4 bars were functional may have affected the response to 8 bars functional for resistance to extinction. When examining

the raw data for distribution, it becomes apparent that the number of rats at each bar were more evenly distributed than Experiment 1 for extinction (Appendix 1). The total responses were greater for the four bars which were functioning in the previous condition (bars 1, 2, 7, and 8) for the 8 bar condition.

In addition, with 4 bars functional, all in the same area, the chances of a subject obtaining food are great (probably 1 in 2 chances) and the amount of movement need not be great. Unfortunately, the apparatus does not allow the monitoring of individual behaviour. If the tracking of individuals within the arena were possible, it would be possible to determine the movement of individual foragers, to see if the group dynamics involved a scrounger/producer relationship.

To determine if the differences found in Experiments 1 and 2 were due to experimental conditions, the experiments should be repeated within a 16 bar operant arena with 1, 2, 4, 8, and 16 bars functioning. If the 8 bar condition manifests more responses than its lower numbered counterparts and the 16 bar condition manifests results similar to the 8 bar condition in this study, then perhaps the findings in this study have supported

the optimal foraging theory. In other words, if the results are similar to Goldstein and Harrigan, and a linear trend is found, the results will be supportive of the SPE. However, if the results are similar to this experiment, then perhaps the dynamics involved in foraging are more complex. A multidimensional approach may be needed to explain foraging behaviour with both psychological and ecological theories playing an integral role.

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Appendix 1

The D stat percentage for acquisition and extinction when one bar, two bars, four bars, and eight bars were working.

D Stat percentage

Food Varied

	Acquisition1	Acquisition2	Acquisition3	Extinction
1 bar functioning	93.10	65.52	72.41	78.57
2 bars functioning	93.10	65.52	82.76	73.68
4 bars functioning	89.66	96.55	93.10	83.33
8 bars functioning	86.21	89.72	82.72	66.67

Food Constant

1 bar functioning	58.62	86.21	---	63.41
2 bars functioning	89.66	75.86	86.21	67.65
4 bars functioning	78.96	---	---	28.57
8 bars functioning	89.29	83.33	96.55	68.97

Appendix 3

The percentage of responses for bars functioning and non-functioning for both food constant and food varying conditions.

food constant	non-functioning bars	functioning bars
1 bar	42.857%	57.14%
2 bars	45.65%	42.66%
4 bars	27.42%	73.25%
food varied		
1 bar	60%	40%
2 bars	49.36%	50.64%
4 bars	14.10%	63.87%

Appendix 4

The percentage of rats working at functioning and non-functioning bars for food constant and food varied.

food constant	functioning	non-functioning bars
1 bar	57.40%	38.89%
2 bars	75.47%	25.45%
4 bars	50.71%	49.29%
food varied		
1 bar	60.67%	39.33%
2 bars	61.11%	32.22%
4 bars	87.88%	12.12%