VARIABLE RATIO SCHEDULE CONTROL OF DISPERSION IN A PATCHY ENVIRONMENT

MASTER OF ARTS - THESIS DISSERTATION

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ABSTRACT

Current ecological theory suggests that foraging animals are controlled by the distribution and abundance of food resources. Contemporary ecological research focuses on optimizing resources through the maximization of cost-benefit trade-offs. Operant psychological research suggests an alternative, but not mutually exclusive approach. Dispersion patterns, foraging processes, and animal distribution, are the products of naturally occurring contingencies of reinforcement. The purpose of the present study was to determine whether population patterns could be controlled and explained by operant procedures and principles. The study was designed to examine the effects of an ascending series of variable ratio schedules on the dispersion patterns of a colony of 8 male hooded rats in an environment in which the resources were patchily distributed. The use of such food patches constituted a unique feature of this operant research. The 8 rat population was exposed to 8 feeding stations in an operant arena in which each station could deliver a specific quantity of food per delivery. The 8 dispensers delivered 3,6,25,40,55,75,90, and 105 pellets respectively. Two daily feedings for 10 days each under VR3, VR10, VR20, VR40, and VR80 schedules of reinforcement were employed. The ascending variable ratio schedules applied in the patchy environment produced increasingly clumped dispersion patterns which were highly unstable in nature. Analysis of these results showed the continued feasibility of operant approaches to the study of dispersion.

An integration of theoretical perspectives in the fields of operant psychology, ecology, and economics has recently evolved due to a common interest in the study of the foraging behavior of individuals (Abarca and Fantino,1982; Baum,1982; Bernstein,1981; Collier and Rovee-Collier, 1980; Killeen, Smith and Hanson, 1981; Lea,1979; Mellgren, 1982; Rashotte, O'Connell and Baidler, 1982). Organisms are however more likely to forage in groups and these groups display various types of dispersion patterns (Brown and Orians, 1970; Gains and McClenaghan, 1980). The dispersion of organisms has important effects on population dynamics, population genetics and the evolution of species (Krebs and Davies, 1978). In addition, dispersion may act as a mechanism by which genes extend their range or species colonize new areas (Wiens, 1976). The study of dispersion is therefore of great importance to many new areas of current research.

Wynne-Edwards (1962) defined dispersion as the placement of individuals and groups of individuals within the habitats they occupy and the processes by which this is brought about. Dispersion should be differentiated from dispersal which refers to the movements of organisms rather than to their positions (Johnson, 1961). There are three basic types of dispersion patterns: regular, random, or clumped (Brown and Orians, 1970). If the points at which individuals are found within a defined area are spaced as far apart from each other as possible, they are exhibiting a regular dispersion pattern. The random pattern occurs when the probability of finding an organism at one point is the same for all other points. When there is a high probability of not only finding other individuals within a small distance, but finding a high frequency of unoccupied spaces, a clumped dispersion pattern is occurring (Brown and Orians, 1970). Identifying dispersion patterns in populations is useful as a descriptive tool but knowledge of the underlying mechanisms which create these patterns is of functional significance in understanding the origin and purpose of dispersion behaviour and why organisms aggregate into particular patterns. As Goldstein, Johnson, and Ward (1989) point out, the dynamics of organization into aggregate groups raises several questions such as: Why has a specific locale attracted an aggregate?; Why do they leave?; What determines aggregate density?. and why do individuals in an aggregate disperse over the locale in specific ways? The study of organism dispersion patterns and dispersal is important for answering these questions.

There is some disagreement between various schools of research as to the governing agents behind dispersion. Ecologists and ethologists have focused on environmental factors, mainly the food supply, as important in determining the distribution of animals during foraging (Goss-Custard, 1977; Smith and Dawkins, 1971; Smith and Sweatman, 1974; Watson and Moss, 1970). Optimization models view the situation in terms of energetics. Animals foraging optimally attempt to increase the benefits of their work through an increase in energy (in calories) obtained and a decrease in cost in obtaining the energy (Krebs and Davies, 1978, 1981). Dispersion patterns are viewed from this position as products of optimal utilization of resources. Operant psychologists view the situation in terms of contingencies of reinforcement. Dispersion patterns which are created during foraging are the products of schedules of reinforcement. The schedule itself is fabricated by the existing natural environment and the behaviour of the individuals in that environment in the presence or absence of conspecifics (Goldstein, 1981a). Studies supporting each of these perspectives will be examined.

Two critical features of food supply are density and distribution. The density of food varies in degree from sparse to abundant. The distribution patterns of food on the other hand vary in type ranging from uniform or regular, through random, to clumped or patchy (Boughey, 1968; Poole, 1974). Early studies emphasized food supply as the determinant of dispersion. Lack (1954) simply suggested that individuals or groups would be more numerous where food was more abundant. Wynne-Edwards (1962) went further in suggesting that the density of population varied with variations in available food resources and that organisms would reach an "optimal population density" for a given environment. Coloniality and territoriality, the equivalent of clumped and regular dispersion patterns, are responses to the temporal and spatial distribution of resources. Ward (1964) proposed that the function of flocking in a species of birds Quelea, was connected with the efficient exploitation of an unevenly distributed food supply. Emlen (1968) proposed that when food supply is regularly distributed, foragers tend to assume a regular dispersion pattern. Royama (1970) determined that clumped dispersions occur in patchy food environments.

Goss-Custard (1970, 1977) also found the density of foragers to be proportional to food supply in a given area. From this early research basic relationships between organism density and food supply were observed.

More recently ecologists have focused on the cost-benefit analysis of food supply as a determinant of dispersion (Krebs and Davies, 1981). The assumption here is that animals are well adapted to their environment and that particular behaviours will contribute to the inclusive fitness of the species. Optimization models seek to predict which particular trade-off between costs and benefits will give the maximum benefit (Krebs and Davies, 1978). All prey items have a cost, calculated in terms of time spent foraging, energy expended in seeking out and capturing the prey item, and a benefit, measured by the actual energy value, in calories obtained, of the prey item. Food value is an important variable in optimization (Emlen, 1984). Food value (profitability) is the net value of food per unit time. Net value is generally defined in terms of the calories (energy) gained after subtracting those lost in acquiring the prey. Calories are lost by the energy expended in activities such as searching for the food, handling it and digesting it. Maximizing net food value produces greater health, larger resources for sustaining life and improved reproductive capacity (Emlen, 1984).

Research involving optimization models has yielded a number of general findings on how optimal foraging behaviours influence dispersion. In an abundant environment, foods with high energy value are selected over foods with a lower energy value (Estabrook and Dunham, 1976; McNair, 1979, 1980). A study by Krebs, Erichsen, and Webber (1977) presented Great Tits (Parus major) with a choice between a relatively profitable prey and an unprofitable one. When the number of prey encountered was high the birds were selective, preferring the more profitable prey. As the encounter rate decreased, the birds did not select one prey over the other. This optimal selection under depleted conditions lends support to optimal foraging theory and also provides parameters for the selection of prey (depleted vs. abundant resource conditions).

When discussing maximization of net food value energy expended in travelling time is an important consideration. Levy, Moermond and Denslow (1984) conducted an experiment with six species of sub-tropical birds.

Their hypothesis was that, as the distance between two foraging sites increased, the birds would be less selective in their choice of fruit. They found that as distances between food sites increased, the birds indeed became less selective, choosing to eat both preferred and non-preferred fruits before moving to a new site. A critical point was passed where the preferred fruit at a second site was less profitable than the less preferred fruit at the existing site. Thus ease of access in the availability of food is important in determining net food value.

Royama (1970) suggested that animals foraging optimally should not only select more profitable prey but should also aggregate in more profitable patches, avoiding less profitable alternatives unless the desirable patches are limited. Foraging animals do tend to aggregate in the most profitable patches and they will rank these patches in order of profitability (Hassel and May, 1974). Krebs, Kacelnik, and Taylor (1978) found that Great Tits (Parus major) would aggregate in the more profitable of 2 patches 95% of the time after being allowed to sample both. Other studies involving Largemouth Bass (Anderson, 1984), Downy Woodpeckers (Lima, 1984) and individual parasites (Nemeritis canescens Hymenopteron) (Hassel, 1971), have found similar results. Others, Smith and Sweatman (1974) and Smith and Dawkins (1971), have found that foraging time in single subjects was also greatest in areas with the highest food density although not all subjects foraged optimally, suggesting that other factors than optimal profitability are at work here.

An alternative but not mutually exclusive approach to optimality theory in explaining dispersion comes from operant psychology. Operant approaches state that the behaviour of foraging organisms is regulated by contingencies of reinforcement and that these contingencies are the determinants of dispersion, not necessarily abundance or depletion of resources or optimal foraging strategies (Goldstein, 1981b). The contingencies of reinforcement consist of responses (foraging behaviours), the consequences of the behaviour (resource acquisition) and the prevailing circumstances (environmental conditions) in the presence or absence of conspecifics. The analysis of these reinforcement contingencies, operating on populations, may provide an additional - if not alternative - framework by which population dispersion patterns may be studied (Goldstein, Johnson, and Ward, 1989).

The operant model suggests that whenever an animal goes about the buisness of procuring food, either actively pursuing or passively waiting for it, a ratio or interval schedule of reinforcement prevails. The magnitude of these schedule values is set both by the amount of work or the amount of time required to catch a prey and the benefit a particular prey affords (Goldstein, 1981b). With respect to optimal foraging, the animal is foraging optimally when the lowest value schedule of reinforcement is used.

Early operant research provided the basis for studying dispersion in a contingency framework. Herrnstein (1961) showed that organisms will tend to distribute their responses in relation to the relative rate at which these responses are reinforced. This relationship has been named the Quantitative Law of Effect or more simply the Matching Law (Fantino and Logan, 1979). In mathematical form it is expressed as

$$\frac{R_1}{R_1 + R_2 \ldots . R_n} = \frac{r_1}{r_1 + r_2 \ldots . r_n}$$

where R_1 represents the rate of responding at a particular station and r_1 is the rate of reinforcement at that station (Herrnstein, 1970). This matching law has been verified as a response predictor in a variety of experiments (Catania, 1963; Baum, 1974; Herrnstein and Loveland, 1975) and over a wide variety of situations (deVilliers, 1977; Green, Rachlin and Hanson, 1983). It has also been shown to apply to groups (Baum, 1974; Graft, Lea and Whitworth, 1977).

Goldstein (1981b) has suggested that Herrnstein's (1970) matching equation can be extended to predict the distribution of groups of organisms in a population. Goldstein's Population Matching Law is denoted as

$$\frac{B_1}{B_1 + B_2 \ldots . B_n} = \frac{R_1}{R_1 + R_2 \ldots . R_n}$$

where B is the number of bar press responses measured or the number of subjects working at a designated station - B subscripts (the bar press work site designation) and where R is the number of rewards (food pellet reinforcements obtained) at that work site (R subscripts). If the probability of rats working at a given station (denoted in future as probability of a rat) is equal to the probability of reinforcement at that station, the relationship is said to match. If, for example, during an experimental session the number of rats working at each of the 8 stations was measured to be; $B_1=20$, $B_2=10$, $B_3=30$, $B_4=20$, $B_5=50$, $B_6=30$, $B_7=30$, $B_8=10$ then the probability of a rat working at station B_1 could be determined by $B_1/(B_1+B_2+B_3+B_4+B_5+B_6+B_7+B_8)$ or 20/(200)=.10. Similarly if we measured the number of reinforcements obtained at those sites to be; $R_1=100$, $R_2=50$, $R_3=150$, $R_4=100$, $R_5=250$, $R_6=150$, $R_7=150$, $R_8=50$ then a similar probability could be calculated for reinforcements obtained as follows; $R_1/(R_1+R_2+R_3+R_4+R_5+R_6+R_7+R_8)$ or 100/(1000)=.10. Since probability of a rat is equal to probability of reinforcement the relationship is said to match. When the probability of rats is greater or less than that of reinforcement, overmatching or undermatching, respectively, is said to occur. In some recent research this population matching equation has been shown to be useful in predicting group dispersion in rats under various schedule conditions (Goldstein, 1981b; Goldstein and Mazurski, 1982; Goldstein, Johnson and Ward, 1989) and in patchy environments (Goldstein and Carlson, 1984; Smith, 1985).

Using group responding rather than individual responses is a relatively new concept, as the majority of operant studies have been structured using individual behaviour as the dependent variable (Grott and Neuringer, 1974). To test the efficacy of using group responding, a group of rats were placed in a single lever operant chamber and subjected to a variety of schedule conditions. With the exception of fixed interval schedules all schedules showed the characteristic patterns of responding that are produced by using individual subjects (Grott and Neuringer, 1974). Since group dispersion, group dispersal, and aggregate density are the subjects of interest in this study, it seems logical to study group activity measures as the dependent variable.

Previous experiments involving schedule control of dispersion have yielded evidence that contingencies of reinforcement are a critical variable in determining patterns of group density and organization. Goldstein (1981b) studied an ascending series of fixed ratio values in an eight station - eight rat operant arena. As fixed ratio values increased, the rats dispersed into extremely regular patterns utilizing a maximum number of possible stations. During a progressive extinction phase a greater degree of dispersal was observed when fewer foraging sites were made available and during progressive reacquisition, overmatching of initially selected stations and undermatching of newly added foraging sites occurred. Goldstein and Mazurski (1982) studied an ascending series of fixed ratio values in a colony of 8 male rats to determine how increased work requirements affect dispersion. Although the rats were free to work under the most optimal conditions, involving regular dispersion patterns, they more often worked in varying states of aggregation. At low ratio values simulating a uniform, plentiful environment the rats formed small aggregates and concurrently used 5 or 6 of the available stations. As ratio values increased, simulating a uniform depleted environment, the population formed a more regular dispersion. At the same time stability of the dispersion patterns increased linearly with increases in ratio value. In a similar series of studies involving interval and ratio schedule control of dispersion Goldstein, Johnson and Ward (1989) simulated fixed and variable food patches by using fixed and variable reinforcement schedules and simulated varying energy budgets through ascending ratio values. The schedules were found to have systematic effects on the population dispersion, independent of energy output. They also found that the colony of rats preferred foraging in variable patches when exposed to increased ratio schedules but not with interval schedules. In the phases involving ascending ratio conditions, the rats became more risk prone. avoiding unoccupied stations and clumping at occupied sites with increased fixed ratios relative to variable ratio phases. The term risk prone has an obvious everyday connotation which should be distinguished from the more technical use of the term in optimal foraging theory. In the latter, risk refers to the potential loss or gain from foraging in a particular way. An organism is said to exhibit risk prone behaviour when it forages in a space where the uncertainty of reinforcement is great. Risk averse behaviour occurs when the uncertainty value of foraging in an area is low.

Further research is required to explore the effects of schedules under other potential environmental contingency conditions. The present study is designed to examine the effects of ascending variable ratio schedules of reinforcement on rat density, dispersion patterns and dispersal in a patchy resource environment.

In natural environments, ratios are randomized by both competitors and by the behaviour of the prey item. Variable ratios were selected in this study in an attempt to simulate more natural conditions.

In the previously mentioned studies on schedule control of dispersion, reinforcement (food) was available in small regular quantities. To a large extent this was a consequence of the absence of an adequate technique to simulate the patchy manner in which resources are normally available in the natural environment. To overcome this problem with the existing operant arena research a special multiple pellet dispenser was designed and built to deliver different quantities of food. With such a multiple pellet dispenser it then became possible to investigate the effects of patchy resource distributions with respect to schedules of reinforcement. This approach was adopted for the present study. It would be expected from optimality theory that more clumped foraging patterns would occur in response to this patchy environment (Royama, 1970) and that the larger programmed patches would be the preferred foraging sites (Goss-Custard, 1977; Smith and Dawkins, 1971). A similar outcome would also be expected from the operant perspective.

In addition, as in earlier operant arena research, abundance and depletion of food resources were simulated in the present study by increasing variable ratio values between phases. This provided the opportunity for observations of how rat dispersion patterns, density and dispersal respond to increases in work requirements. Goldstein, Johnson, and Ward (1989) using non-patchy, regular food supply, found increased variable ratio values resulted in increased dispersal and decreased station density. Shifts toward regular dispersion with increments in ratio value were seen as a strategy minimizing the ratio cost of food. Where resources are patchily distributed minimization of the ratio cost of food would be obtained if the population converges on the highest payoff stations as ratio values increased.

Optimality theory views dispersion in terms of the cost-benefit analysis of the food supply and how organisms aggregate to maximize energetics by foraging in different patterns. Operant theories approach dispersion in terms of schedules of reinforcement and how schedules, in the presence or absence of conspecifics determine aggregate density and dispersal. This research was not intended to provide a decisive test of optimality theory using operant techniques as both may be used interactively and interchangably to explain the same phenomenon. The main purpose of the present research was to try to further establish the feasibility of operant approaches in studying complex foraging situations that optimality theory usually deals with, such as the patchy food environment simulated in this study.

METHOD

Subjects

The subjects were 8 male hooded rats approximately 20 months old. All subjects had a history of bar pressing for food in similar studies involving different schedules of reinforcement in the operant arena. All rats were maintained in the special group operant arena throughout the study.

Apparatus

a 3.7m long x 3.4m wide x 1.2m high arena constituted the permanent work and living area for the 8 rats (see Figure 1). The arena contained 8 feeding stations each consisting of an automatically insertable response bar, a pellet dispenser and a 100ml graduated water bottle. A special pellet dispenser was designed for this study to accurately simulate patchy food resource conditions (refer to figure 1a). Each of the 8 dispensers was set to deliver a different number of 45mg Noyes food pellets using a cylindrical storage tube of a specific diameter. The volume of this storage tube limited the number of pellets available to the discharge tube upon payoff. The 8 dispensers were afixed with different volume storage tubes to dispense 105, 90, 75, 55, 40, 25, 6, and 3 pellets per reinforcement. These 8 simulated patch sizes were fixed throughout the 5 phases of the study. Urine and feces fell through the wire mesh floor of the arena into a urinal system which flushed periodically throughout the night. A day-night timer regulated a 14:10 LD cycle. Variable ratios of reinforcement were controlled by a Commodore Pet series

2001 microcomputer. Responses and reinforcements were recorded by the Pet computer. From these data a matching relationship using Herrnstein's (1961) formula was calculated by the Pet after each experimental session and this data was fed into a series of programs in a VAX 11/780 computer. For further details on the computer programs or apparatus refer to Goldstein, Blekkenhorst and Mayes (1982) and Blekkenhorst and Goldstein (1983).

Procedure

There were 5 phases of the experiment. During each phase two 30 minute sessions were conducted at approximately 9:30 a.m. and 6:00 p.m., 7 days a week, for 10 days of each phase. In phase 1, the rats worked under a variable ratio 3 (VR3) schedule of reinforcement. During phases 2,3,4 and 5, the rats worked under VR10, VR20, VR40 and VR80 schedules respectively.

During each daily experimental session, a record of dispersion patterns was obtained once per minute. Dispersion patterns were obtained by counting the number of rats at each station and recording this data. A rat was counted at a station if it had all four legs in the area marked by the 54cm length of the Plexiglas partition and the 22cm width of the floor. The dispensers were arranged so that each side of the arena was equal in terms of potential payoff in number of pellets per reinforcement.

Phase 5 involving the VR80 schedule of reinforcement was repeated once due to a possible unnoticed equipment failure.

RESULTS

The most frequently recorded sample size involved dispersion patterns with 8 rats concurrently working. This observation increased with increases in variable ratio schedule (Figure 2). With 8 rats working, if the identity of individual rats and feeding stations is ignored, there are 22 possible ways in which rats can disperse in the operant arena. These patterns range from a 1 rat per 1 station pattern (11111111) to an 8 rat per station pattern (8). When all 8 rats simultaneously work at seperate stations, they form the most regular dispersion pattern possible. At the other extreme, when all 8 rats simultaneously work at one station, they form the most clumped or contagious pattern possible (Goldstein, 1981a). Figure 3 shows the frequency of occurence of each type of dispersion patte during each of 5 phases of the experiment. To obtain the curve of dispersion patterns expected by chance (seen in figure 3) a Monte Carlo simulation was run on the computer filling each of 22 possible patterns (displayed in the key on figure 3) at random over thousands of repetitions. During each schedule, the observed dispersion patterns differed from the patterns expected by chance. Chi-square analysis between the expected and observed frequencies of these patterns were highly significant (Chi-square values ranged from 804.06 at VR3 to 3254.98 at VR80

$p<.01$, see table 1). The rats worked in small aggregate groups at the lower schedules (VR3, VR10) and formed larger aggregates and utilized fewer dispersion patterns as the ratio value increased. The most extreme pattern of contagion (8 rats at one station) increased with each variable ratio value from a frequency of 0% at VR3 to a frequency of 57.1% of all observations at VR80 (Figure 4).

The variance/mean ratio is a common measure of dispersion and an indicator of the degree of aggregation (Poole, 1974). A variance/mean ratio value of less than 1.0 denotes a regular dispersion, a value of 1.0 represents a random distribution and a value of greater than 1.0 represents a clumped pattern if the dispersion is assumed to be a poisson distribution (Poole, 1974). However, this statistic is heavily affected by small sample sizes (Taylor, Woiwood and Perry, 1978). It will therefore be used here as a measure of relative tendency rather than for precise statistical measurement. Dispersion patterns during all 5 phases of the study show a tendency towards clumped dispersion (Figure 5) with an increase in contagion with increases in variable ratio value. The variance/mean ratios ranged from 2.2 at VR3 to 4.48 at VR80 and support the observation of progressively more clumped dispersion and single station contagion.

The stability of the dispersion patterns (dispersal) was measured by analysing the minute to minute transitions and grouping these as unstable (DSTAT) or stable (ISTAT) changes. In the ISTAT change the dispersion pattern does not change from one observation to the next although the location of the rats may change. For example, the patterns 21111111 and 11111112 may have different locations, but the actual dispersion remains the same. In the DSTAT change, the number of rats working at a particular station or the number of stations being colonized changes. As Figure 6 illustrates, the dispersal of the rats was unstable throughout the five phases of the experiment. The DSTAT frequency ranged from 78.8% at VR3 to 93.6% at VR80. The frequency of the stable (ISTAT) transitions was quite low throughout the experiment, ranging from 21.2% at VR3 to 6.4% at VR80. There was also a tendency for the instability of dispersal (DSTAT) to increase with increases in the variable ratio values or for the stability (ISTAT) to decrease. These two measures of dispersal can be broken down further into 2 measures of stability and 3 measures of instability. The ISTAT can be broken down into an identical transition, ITRANS (no change in dispersion pattern) or a positional transition, PTRANS (where station locations change but not the pattern). The DSTAT can be divided into a microstate transition, MITRANS (where the number of rats recorded at a given number of bars changes) or a macrostate transition. The macrostate transition is made up of the MATRANS where the number of bars being colonized by a given number of rats changes or the MBTRANS where the number of bars colonized changes as a result of an increase or decrease in the number of rats working. As Figure 6a illustrates, the most frequent changes in dispersal were MBTRANS transitions. Over 40% of the transitions in dispersion were changes in the number of bars occupied due to increases or decreases in the number of rats working. The only transition pattern which steadily increased with schedule was MITRANS (the second most popular transition) which reached 37.8% by VR80. The ITRANS analysis (no change in pattern) steadily decreased in frequency from 14.6% at VR3 to 1.9% at VR80. The fluctuations in the number of rats working and stations occupied between observations indicates high activity and rapid movement amongst the rats from one minute to the next.

The rat density analysis was performed on both the programmed magnitude of reward (simulating various patch sizes) and the actual obtained magnitude of reward for an examination of the effects of a patchy environment on rat aggregation. In analysing programmed payoff magnitude a variation of Goldstein's (1981b) population matching equation was used, where

$$\frac{B_1}{B_1 + B_2 \ldots . B_n} = \frac{R_1}{R_1 + R_2 \ldots . R_n} .$$

with B equal to the number of responses or subjects working and R equal to programmed magnitude of reinforcement at each station and B and R subscripts signifying the station designation.

There was a definite trend towards contagion around stations with a higher programmed payoff magnitude (Figure 7a). The density of the rats shows a dichotomy in dispersion between the 3 stations with the largest payoff magnitude and the 5 stations with the lowest pellet payoff. The rats were most densely dispersed around the stations with the first and third highest proportion of reinforcements. Figure 7b shows the density pattern at each work station during each of the 5 experimental phases. It can be seen that after an initial increase in the use of station 2 there was a steady decrease along with steady increases in density at stations 1 and 3 as the variable ratio value rises until stations 1 and 3 were occupied almost exclusively at VR80. It is possible that the presence of conspecifics influenced density as the conditions became progressively more deprived. This will be discussed further in the discussion section. Figures 7c and 7d are similar to 7a and 7b except that they display the regression lines and correlational analysis of the same data. A coefficient of correlation of .737 was obtained between mean rat density and programmed magnitude of reward (Figure 7c). A relationship between rat density and proportion of payoff magnitude can be seen with overmatching (more rats than the patch can accomodate) at the first and third highest proportions of obtained pellets. This bimodal overmatching decreased the correlation coefficients at VR40 (r=.732) and VR80 (r=.672) from a high of r=.88 at VR20 (Figure 7d). An increase in slope in the regression equations indicates increases in density in comparison to programmed payoff magnitude. The slope of the regression lines progressively increases from 4.86 at VR3 to 9.03 at VR80, indicating a growing density at the larger programmed payoff magnitudes and increased overmatching at stations 1 and 3.

The actual obtained magnitude of reward is a better predictor of rat density than programmed magnitude. Figures 8 and 8a show the relationship between obtained magnitude of reward and rat density. The correlation for the overall analysis (r=.988) and for each schedule were all high, indicating a very good relationship between density and obtained magnitude of reward. As with programmed magnitude, higher obtained magnitudes resulted in increased rat contagion although obtained magnitudes showed a more linear relationship. According to the matching law (Herrnstein, 1975) programmed and actual magnitude of reinforcement should coincide. Since the results of the density analysis showed them to differ slightly, each will be considered seperately in further analyses. However in discussions of the matching law, it is usually the actual amount of reinforcement which is used as the independent variable (Baum, 1981) and this will be kept in consideration.

Figures 9 and 9a once again use Goldstein's (1981b) modification of the matching law to examine the probability of a rat working under various programmed and actual obtained magnitudes of reward. The results of these analyses involving probability of a rat are almost identical to the results from the earlier density analyses. The probability of a rat matched the programmed magnitude of reward (r=.744, Figure 9). Overmatching was once again seen at stations with the highest and third highest programmed magnitudes and this overmatching increased with variable ratio schedule, as seen by the increase in slopes with schedule (Figure 9a). Mean obtained magnitude of reward was seen to be a better predictor of the probability of a rat also (Figure 10). The relationship (r=.980) is an excellent match between the variables and is constantly high (.984 to .999) during each ratio schedule condition (Figure 10a).

The next set of analyses (Figures 11, 11a, 12, 12a) show the relationship of responses to programmed and obtained magnitudes of reward using Herrnstein's (1970) matching law. The results are very similar to those seen in the density analysis. When programmed magnitude of reward is used as the independent variable, a good correlation (r=.671) results with overmatching at the highest and third highest magnitudes (Figure 11). This overmatching is seen to progress as schedule increases (Figure 11a) and the slight increase in regression line slopes with schedule supports this observation. When a similar analysis was done between probability of a response and the obtained magnitude of reward, the relationship between the two was seen to be very strong (r=.993, Figure 12). This was true for all 5 phases of the experiment with correlations ranging from .976 to .999 (Figure 12a).

Figure 13 shows the actual number of pellets consumed during each of the 5 experimental phases. It can be seen that the food intake of the colony of rats decreased with each variable ratio increase until stabilizing at VR40. Figure 14 shows the actual number of responses recorded during each of the 5 variable ratio schedules. There was a steady increase in responding between each schedule. Figure 15 shows the number of pellets obtained per response during each schedule. As variable ratio values increased, the mean number of pellets obtained per response decreased. Responding increased in the presence of a decrease in obtained food and the average reinforcement value of a response decreased as schedule increased.

DISCUSSION

In the present study the ascending variable ratio schedules implemented in a patchy resource environment progressively increased aggregation in the rat population. This clumped dispersion was focused around larger patch sites (stations with a larger programmed pellet payoff). This finding is in congruence with ecological data reporting preferences for larger more profitable patch sites (Anderson, 1984; Hassel and May, 1974; Krebs, Kacelnik and Taylor, 1978; Lima, 1984; Royama, 1970). It can be argued however, that optimal foaging was not occurring in the present study. The number of pellets consumed by the colony of rats decreased steadily (Figure 13) while the energy expended in obtaining these pellets (measured in responses performed) increased (Figure 14). The net value of a response (measured in pellets obtained) steadily decreased with increased schedule conditions. Since responding steadily increased even when food supply decreased, it is unlikely that food supply is the determinant of dispersion related behaviours in the present study. A more optimal strategy would have been to form smaller aggregates and to disperse over the three or four most profitable payoff sites. For example, under the VR80 schedule of reinforcement, optimal dispersion in this patchy environment would have involved dispersion patterns such as

(2,2,2,2) or possibly (3,2,2,1). If 2 rats on average worked at the 4 stations with the highest pellet payoffs, after one payoff round the 8 rats would receive (105+90+75+55) = 325 pellets. Dividing this amongst the rats results in an average of 65 pellets per rat. In fact, however, because the population shifted towards a preference for 2 of the most profitable stations (90 and 75 pellets per payoff) the group received 165 pellets per payoff round or an average of 21 pellets for each of the 8 rats, an amount 3 times less than would be gained by dispering amongst the 4 highest payoff sites. Defying optimal energetics, the rats displayed an almost exclusive preference for two of the most profitable patch sites at VR80 (Figure 7b). The observed pattern involved all 8 rats rushing to a station which had just paid off, accompanied by an increase in the incidence of aggressive behaviour, squealing, jumping over one another, biting, and occasionally rearing postures and fighting.

A possible explanation for the group preference of the 2 stations with payoffs of 90 and 75 lies in the arena arrangement. These 2 stations were closer in proximity to one another and both were situated in the more profitable left side of the arena. However, this is unlikely given the example in the paragraph above of how energetics could have been more optimally maximized with dispersal amongst 4 stations. If energy variables, such as decreased travelling time between stations or increased station proximity, were critical factors in these results a pattern of dispersion such as (2,2,2,2) would likely have resulted and would have been a more optimal pattern for the group.

The results of the disperion analysis in this research contradict Puliman's (1974) proposition that optimal foragers would behave more efficiently in deprived conditions. The rats not only behaved in a less than optimal manner, they continued this pattern of foraging in the presence of aggressive competition. Other recent research in accordance with this study indicates that foragers will behave less optimally under adverse conditions (Blaine and Rohe, 1984; Snyderman, 1983).

When the data from this study was analysed from the perspective of operant psychology it was clearly seen that operant models can describe the behaviour of the rats. Both programmed and actual magnitudes of reinforcement matched rat density, probability of observing a working rat, and probability of a bar press response. Both programmed and actual magnitude of reward can be accurately used to predict rat density or responding, although actual magnitude of reward was a more accurate predictor than programmed patch sites, suggesting that contingencies of reinforcement are superior for predicting animal dispersion to optimality theories.

These non-optimal distributions can be accounted for with operant theories involving conditioning effects and the presence or absence of conspecifics. At VR3 clumped dispersion was already quite prevalent under relatively abundant resource conditions (Figure 3). The observed pattern was a tendency for the rats to aggregate around stations with a larger payoff magnitude (Figure 7b). It is possible that a conditioned association was developing at the stations with a larger pellet payoff. The discriminitive stimuli accompanying a payoff, including the click of the dispenser, the dropping of pellets, the rush of rats to the station, high activity levels and squealing around the payoff site, all have reinforcing effects on a rat searching for food (Goldstein, 1981b; Husted and McKenna, 1966; Royama, 1970). This along with extinction at stations with very few pellets as a payoff would result in an early selection of sites with the larger programmed magnitudes of reward as seen in this study (Figure 7b). This conditioned association to discriminitive stimuli at larger patch sites is the likely reason why clumped dispersion was maintained even as conditions became more deprived towards VR80. It is proposed here that the increase in variable ratio values, especially from VR20 to VR40 and VR40 to VR80, had the effect of temporarily extinguishing reinforcement due to an abrupt increase in response costs and the presence of conspecifics competing for the reinforcements. A rat working in a small aggregate group at a station has to compete with other rats for the reinforcement payoff. This decreases the profitability of the pellets obtained and increases the schedule value under which the rat is working. This has extinction-like effects on the worker who then leaves the work site and moves to another site, a phenomenon verified by the highly unstable nature of the dispersion patterns recorded in the results section.

As the rats adapted to the work requirements of a higher schedule, a reacquisition of the conditioned association occured with a resultant overmatching at those stations where conspecific stimuli were most prevalent - those sites with higher programmed payoff magnitudes. The obtained magnitude of reward appeared to be immune to conspecific conditioning effects and was therefore a better predictor of rat density and responding. The intent of the present research was not to refute optimality accounts of foraging. It was to demonstrate the feasibility of operant approaches in complex foraging situations. Presumably some version of optimization could eventually be derived to account for the preferences found in this research.

One question posed by this study remains to be answered; Why the rats foraged at the first and third most profitable patch sites and excluded the second most profitable site as work requirements increased? This less than optimal strategy can also be explained by employing operant theory. Each station site in this study could accomodate 4 rats comfortably side by side. The observed pattern was for all 8 rats to rush to a station which had just paid off with a large patch of pellets. The resultant convergence of rats at a single station resulted in inadequate space for all to forage without excessive aggression. The overflow of rats would colonize other available patch sites. The stations with the first and third highest payoff magnitude were closest in proximity to one another. The conspecific stimuli mentioned earlier, ie. activity level, squealing, pellet payoff sounds, were enhanced due to the proximity of these stations. The observed pattern was of increased running activity between these two stations and our stability of dispersion measure confirmed this observation. Dispersion patterns became increasingly unstable as schedule increased and the instability was mainly due to changes in either the number of bars colonized due to an increase or decrease in the number of rats working or the number of rats at a fixed number of bars changing. By VR80 the rats worked almost exclusively at the two stations due to the effect of schedule induced conditioning at these sites. They exhibited a less than optimal solution to the increased schedule demands. Further research in a more symmetrical patchy environment is necessary to determine how much we can attribute this result to the effects of contingencies of reinforcement and whether this result was the product of the conditions used in the present study.

Behavioral theorists have advanced alternative views to optimization to deal with evolution and behaviour. Skinner (1984) proposed that an operant response from a hungry organism is reinforced by the receipt of food. The food decreases hunger and contributes to it's survival. The operant does not occur because it reduces hunger, it is produced because behavioural processes have evolved where this reduction in hunger contributed to the survival of the species. The behaviour is not reinforced by the optimization, or maximization of a food supply, but through the processes of selection (Skinner, 1984). While the results of this study do not totally refute optimization models, they do suggest a more constructive and insightful method of studying the mechanisms of dispersion and provide an alternative framework from which to view the problem. This study supports previous research (Goldstein, 1981b; Goldstein, Johnson and Ward, 1989; Goldstein and Mazurski, 1982) in the importance of studying contingencies of reinforcement as a determinant of dispersion and the application of Herrnstein's (1970) matching law and Goldstein's (1981b) population matching law as indicators of foraging behaviour. The present study confirms the existence of clumped dispersion in response to a patchy environment previously observed using different reinforcement schedules (Carlson, 1984; Smith, 1985), as well as providing a conditioning model for explaining these findings.

REFERENCES

Abarca, N. & Fantino, E. (1982). Choice and foraging. Journal of the Experimental Analysis of Behavior, 38, 117-123.

Anderson, O. (1984). Optimal foraging by largemouth bass in structured environments. Ecology, 65, 851-861.

Baum, W. (1974). Choice in free ranging pigeons. Science, 185, 78-79.

Baum, W. (1982). Instrumental behavior and foraging in the wild. In M. W. Commons, R. J. Herrnstein, & H. Rachlin, Quantitative Analysis of Behavior. Vol.II. Matching and Maximizing Accounts. Cambridge, MA: Ballinger.

Bernstein, R. B. (1981). Ecology and economics: complex systems in changing environments. Annual Review of Ecology and Systematics, 12, 309-330.

Blaine, F. & Rohe, M. (1984). Effects of search costs on foraging and feeding: A three component analysis. Journal of the Experimental Analysis of Behavior, 42, 211-221.

Blekkenhorst, H. J. & Goldstein, S. R. (1983). A Pet interface to control reinforcement delivery. Behavior Research Methods and Instrumentation, 15, 398.

Boughey, A. S. (1968). Ecology of Populations. New York: McMillan.

Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. Annual Review of Ecology and Systematics, 1, 239-262.

Carlson, J. (1984). Magnitude of reward and schedule control of dispersion patterns in rats. Lakehead University honours thesis.

Catania, A. (1963). Concurrent performances: Reinforcement interactions and response independence. Journal of the Experimental Analysis of Behavior, 4, 267-272.

Collier, G. H. & Rovee-Collier, C. K. (1980). A comparative analysis of foraging behavior: laboratory simulations. in A. C. Kamil and T. D. Sargent (eds.). Foraging Behavior: Ecological, Ethological and Psychological Approaches. New York: Garland Press.

deVilliers, P. (1972). Choice in concurrent schedules and a quantitative formulation of the Law of Effect. In W. Honig and J. Staddon (eds.). Handbook of Operant Behavior. Englewood Cliffs, New Jersey: Prentice Hall.

Emlen, J. (1984). Population Biology: The Coevolution of Population Dynamics and Behavior. New York: MacMillan.

Estabrook, G. & Dunham, G. (1976). Optional choice as a function of absolute abundance, relative abundance, and relative value of available prey. American Naturalist, 110, 40-413.

Fantino, E. & Logan, C. (1979). The Experimental Analysis of Behavior: A Biological Perspective. San Francisco: Freedman.

Gains, M. & McClenaghan, C. (1980). Dispersal in small animals. Annual Review of Ecology and Systematics. 11, 163-196.

Goldstein, S. (1981a). An operant arena for rats. Behavioral Research Methods and Instrumentation, 13, 37-39.

Goldstein, S. (1981b). Schedule control of dispersion and density patterns in rats. Behaviour Analysis Letters, 1, 283-295.

Goldstein, S. Blekkenhorst, M. & Mayes, L. (1982). Computerization of the operant arena. Behavior Research Methods and Instrumentation, 14, 369-372.

Goldstein, S. & Carlson, J. (1984). Operant foraging in a patchy environment. Paper presented at the International Congress of Psychology, Acapulco, Mexico.

Goldstein, S. Johnson, P. & Ward, G. (1989). Schedules of reinforcement as regulators of dispersion patterns. paper in revision.

Goldstein, S. & Mazurski, E. (1982). Fixed-ratio control of dispersion patterns. Behaviour Analysis Letters, 2, 249-257.

Goss-Custard, J. D. (1970). The responses of redshank [Tringa totanus (L.)] to spatial variations in their prey density. Journal of Animal Ecology, 39, 91-113.

Goss-Custard, J. D. (1977). Optional foraging and the size selection of worms by redshank, Tringa totanus, in the field. Animal Behavior, 25, 10-29.

Graft, E. Lea, S. & Whitworth, T. (1977). The matching law in and within groups of rats. Journal of the Experimental Analysis of Behavior, 27, 183-194.

Grott, R. & Neuringer, A. (1974). Group behavior of rats under schedules of reinforcement. Journal of the Experimental Analysis of Behavior, 22, 311-321.

Green, L. Rachlin, H. & Hanson, H. (1983). Matching and maximizing with concurrent ratio-interval schedules. Journal of the Experimental Analysis of Behavior, 40, 387-403.

Hassel, M. P. (1971). Mutual interference between searching insect parasites. Journal of Animal Ecology, 40, 472-486.

Hassel, M. P. & May, R. M. (1974). Aggregation in predators and insect parasites and its effects on stability. Journal of Animal Ecology, 43, 567-594.

Herrnstein, R. (1961). Relative and absolute strength of response as a function of frequency of reinforcement. Journal of the Experimental Analysis of Behavior, 4, 267-272.

Herrnstein, R. (1970). On the law of effect. Journal of the Experimental Analysis of Behavior, 13, 243-266.

Herrnstein, R. & Loveland, D. (1975). Maximization and matching on concurrent ratio schedules. Journal of the Experimental Analysis of Behavior, 24, 107-116.

Husted, J. F. & McKenna, F. S. (1966). The use of rats as discriminitive stimuli. Journal of the Experimental Analysis of Behavior, 9, 677-679.

Johnson, R. F. (1961). Population movement of birds. Condor, 63, 386-388.

Killeen, P. R. Smith, J. P. & Hanson, S. H. (1981). Central place foraging in Rattus norvegicus. Animal Behaviour, 29, 64-70.

Krebs, J. & Davies, N. (1978). Behavioural Ecology. Oxford: Blackwell Scientific Publications.

Krebs, J. & Davies, N. (1981). An Introduction to Behavioural Ecology. London: Sinauer Associates.

Krebs, J. R. Erichsen, J. T. Webber, M. I. & Charnov, E. (1977). Optional prey selection in the great tit (Parus major). Animal Behaviour, 25, 30-38.

Krebs, J. R. Kacelnik, A. and Taylor, P. (1978). Test of optimal sampling by foraging great tits. Nature, 275, 27-31.

Lack, D. (1954). The Natural Regulation of Animal Numbers. Oxford: Clarendon.

Lea, S. (1979). Foraging and reinforcement schedules in the pigeon: Optional and non-optional aspects of choice. Animal Behaviour, 27, 875-886.

Levy, D. Moermond, T. & Denslow, J. (1984). Fruit choice in neotropical birds: The effect of distance between fruits on preference patterns. Ecology, 65, 844-850.

Lima, S. (1984). Downy woodpecker foraging behavior: Efficient sampling in simple stochastic environments. Ecology, 65, 166-174.

McNair, J. (1979). A generalized model of optimal diet. Theoretical Population Biology, 15, 159-170.

McNair, J. (1980). A stochastic foraging model of optimal diet. Theoretical Population Biology, 15, 159-170.

Mellgren, R. L. (1982). Foraging in a simulated natural environment: there's a rat loose in the lab. Journal of the Experimental Analysis of Behavior, 38, 93-110.

Poole, R. W. (1974). An Introduction to Quantitative Ecology. New York: McGraw-Hill.

Puliman, H. (1974). On the theory of optimal diets. American Naturalist, 108, 54-74.

Rashotte, M. E. O'Connell, J. M. & Baidler, D. L. (1982). Associative influence on the foraging behavior of pigeons (Columbia livia). Journal of Experimental Psychology: Animal Behavior Processes, 8, 142-153.

Royama, T. (1970). Factors governing the selection of food by the Great Tit. Journal of Animal Ecology, 39, 619-668.

Skinner, B. F. (1984). The evolution of behavior. Journal of the Experimental Analysis of Behavior, 41, 217-222.

Smith, R. W. (1985). Fixed interval control of dispersion patterns in a patchy environment. Lakehead University Honours Thesis.

Smith, J. N. & Dawkins, R. (1971). The hunting behavior of individual great tits in relation to spatial variations in their food density. Animal Behaviour, 19, 695-706.

Smith, J. & Sweatman, P. (1974). Food selection in Titmice. Ecology,55, 1216-1232.

Snyderman, M. (1983). Optimal prey selection: The effects of food deprivation. Behaviour Analysis Letters, 3, 359-369.

Taylor, L. Woiwood, I. & Perry, J. (1978). The density dependence and the rarity of randomness. Journal of Animal Ecology, 47, 383-406.

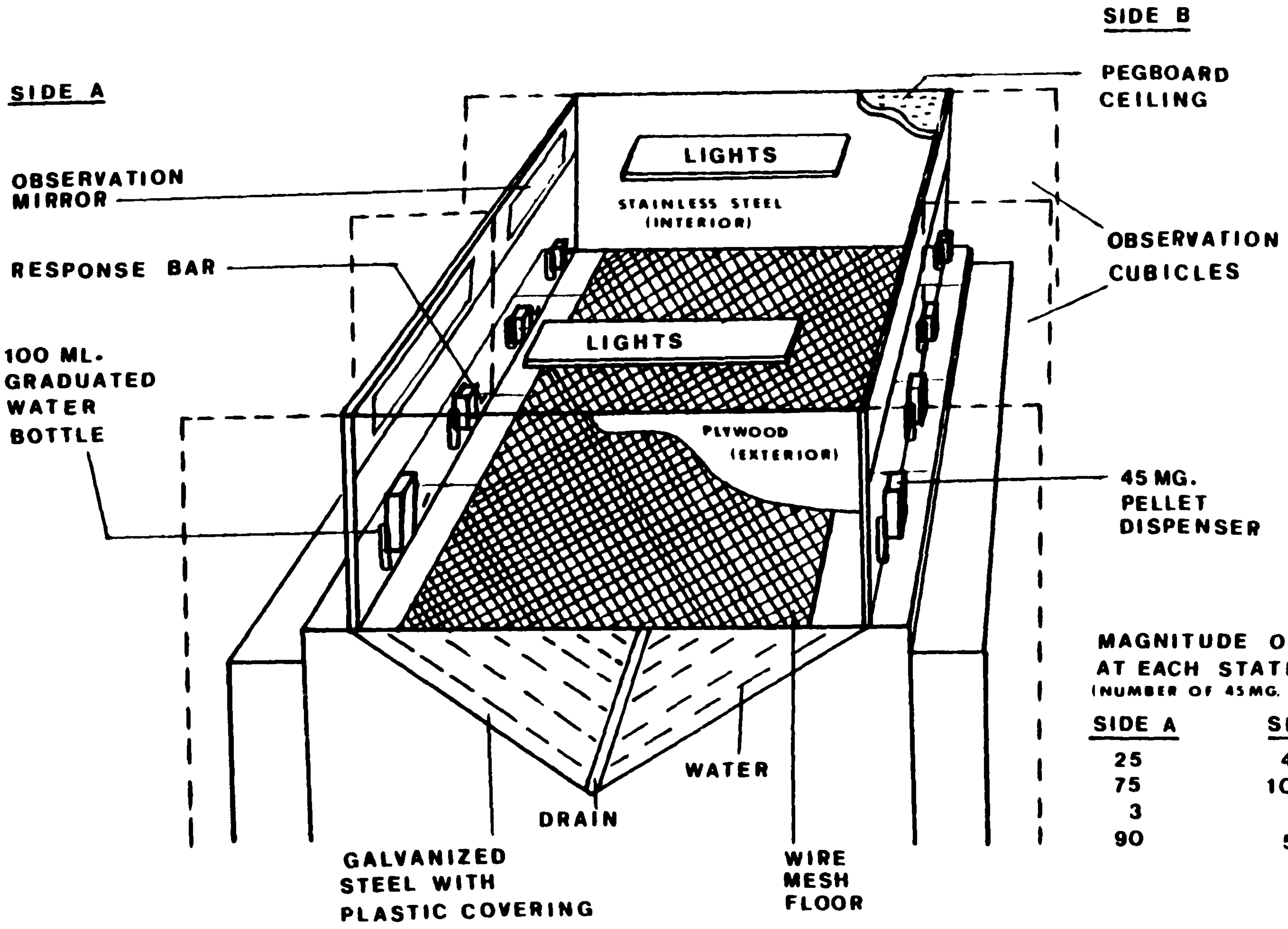
Ward, P. (1964). Feeding ecology of the black-faced Kioch Quelea in Nigeria. The Canadian Entomologist, 96, 173-374.

Watson, A. & Moss, R. (1970). Dominance, spacing behavior, and aggression in relation to population limitations in vertebrates. In A. Watson (ed.) Animal Populations in Relation to Their Food Resources. Oxford: Blackwell.

Wiens, J. (1976). Population responses to patchy environments. Annual Review of Ecology and Systematics, 7, 81-120.

Wynne-Edwards, V. C. (1962). Animal Dispersion in Relation to Social Behaviour. Edinburgh: Oliver & Boyd.

FIGURE 1. The 8 Station Operant Arena



MAGNITUDE OF REWARD AT EACH STATION
(NUMBER OF 45MG. PELLETS)

SIDE A	SIDE B
25	40
75	105
3	6
90	55

FIGURE 1a. The Adjustable Multiple Pellet Dispenser

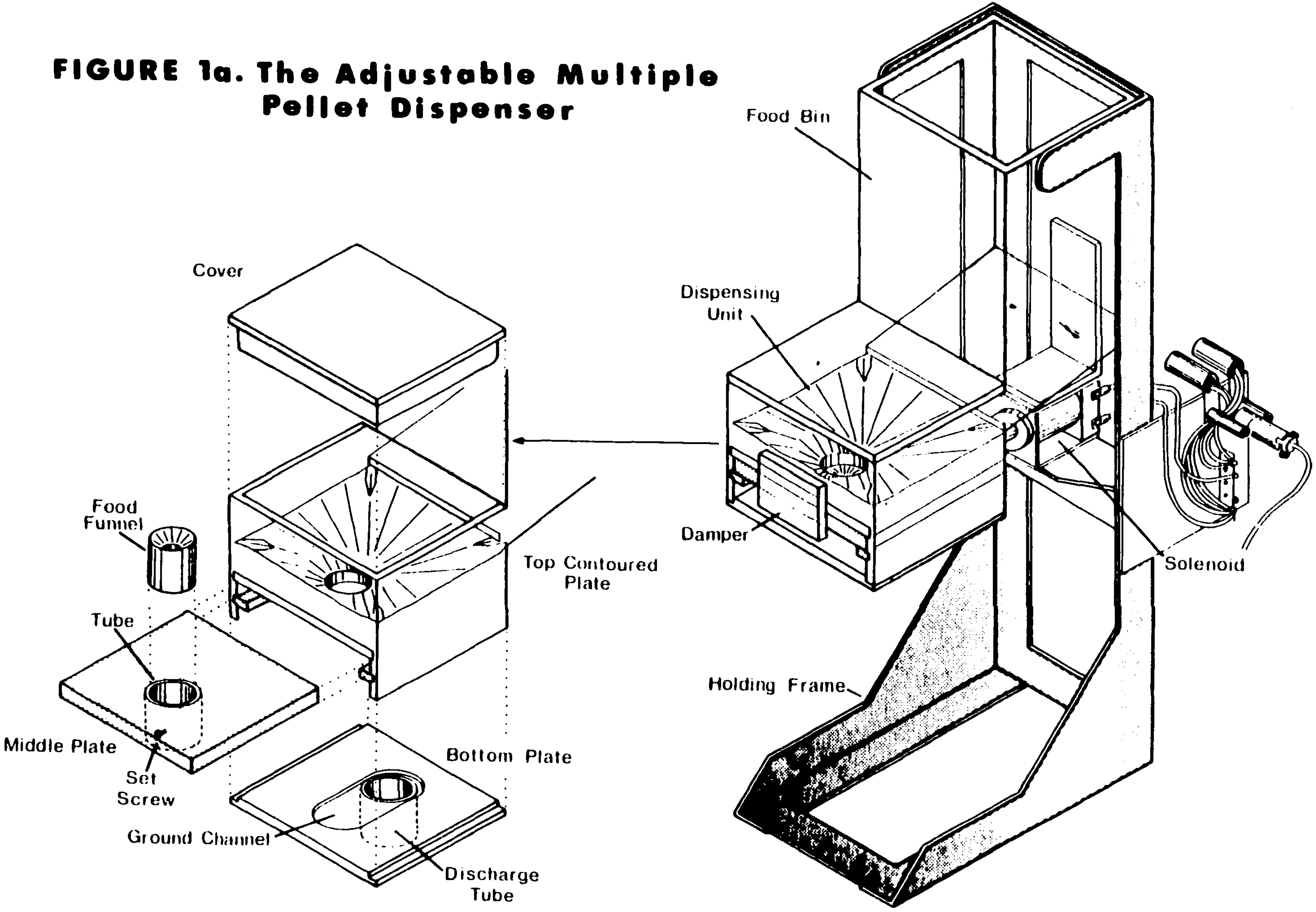


FIGURE 2. The Percent of Occasions When All 8 Rats Were Working During Each Schedule

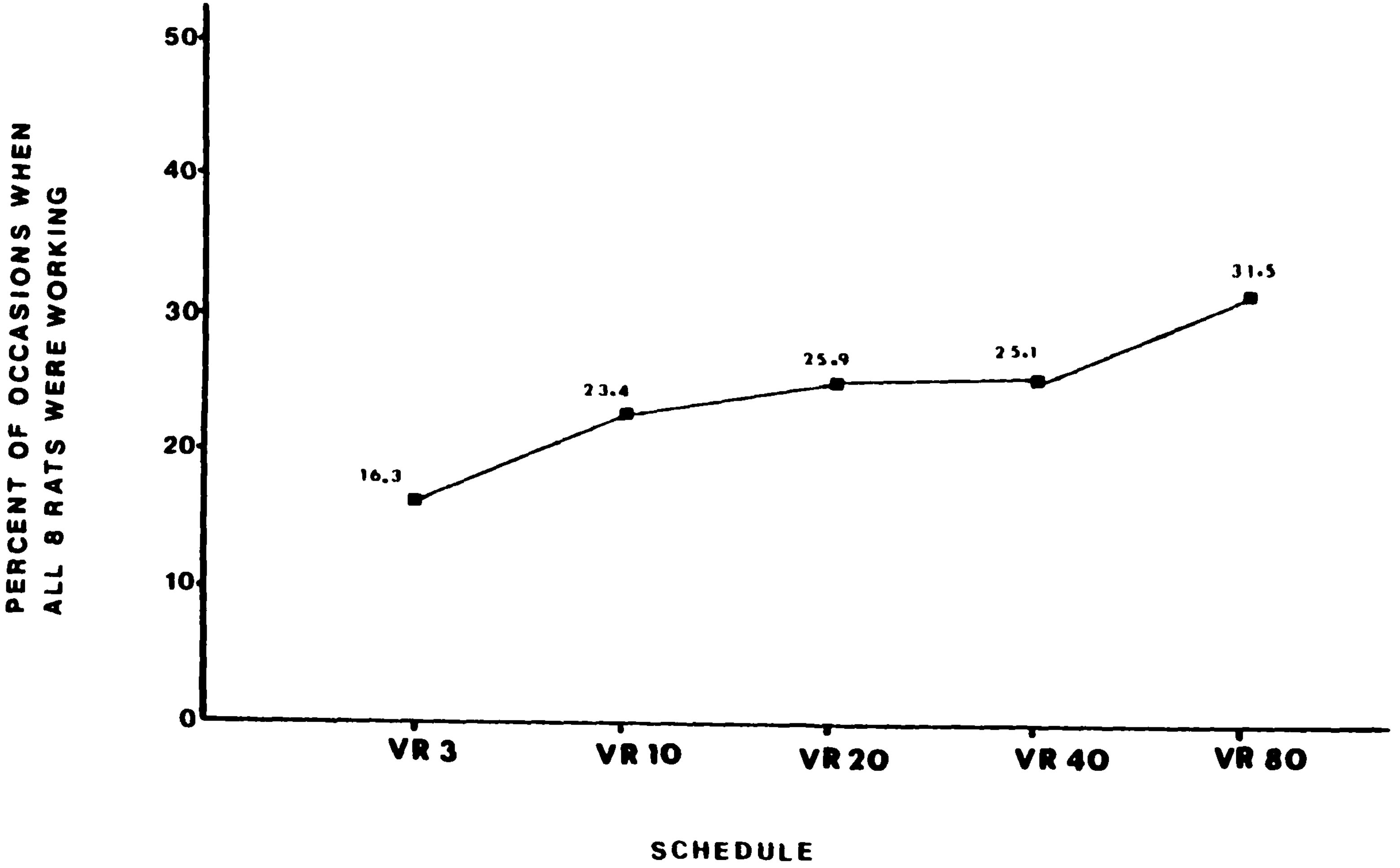


FIGURE 3. Dispersion Patterns for Each Schedule With All 8 Rats Working

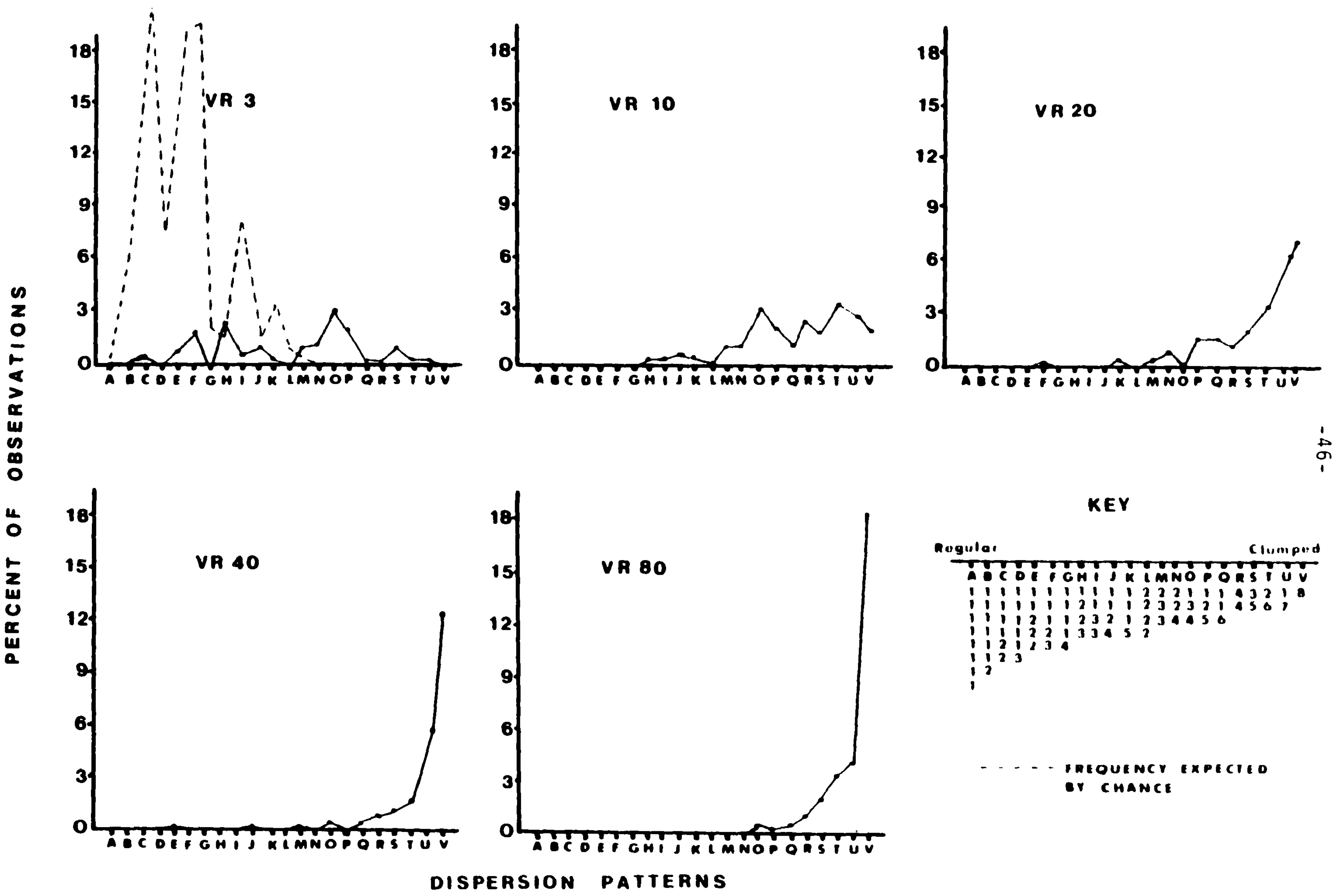


FIGURE 4. The Percent of Occasions With All 8 Rats Working at 1 Station During Each Schedule

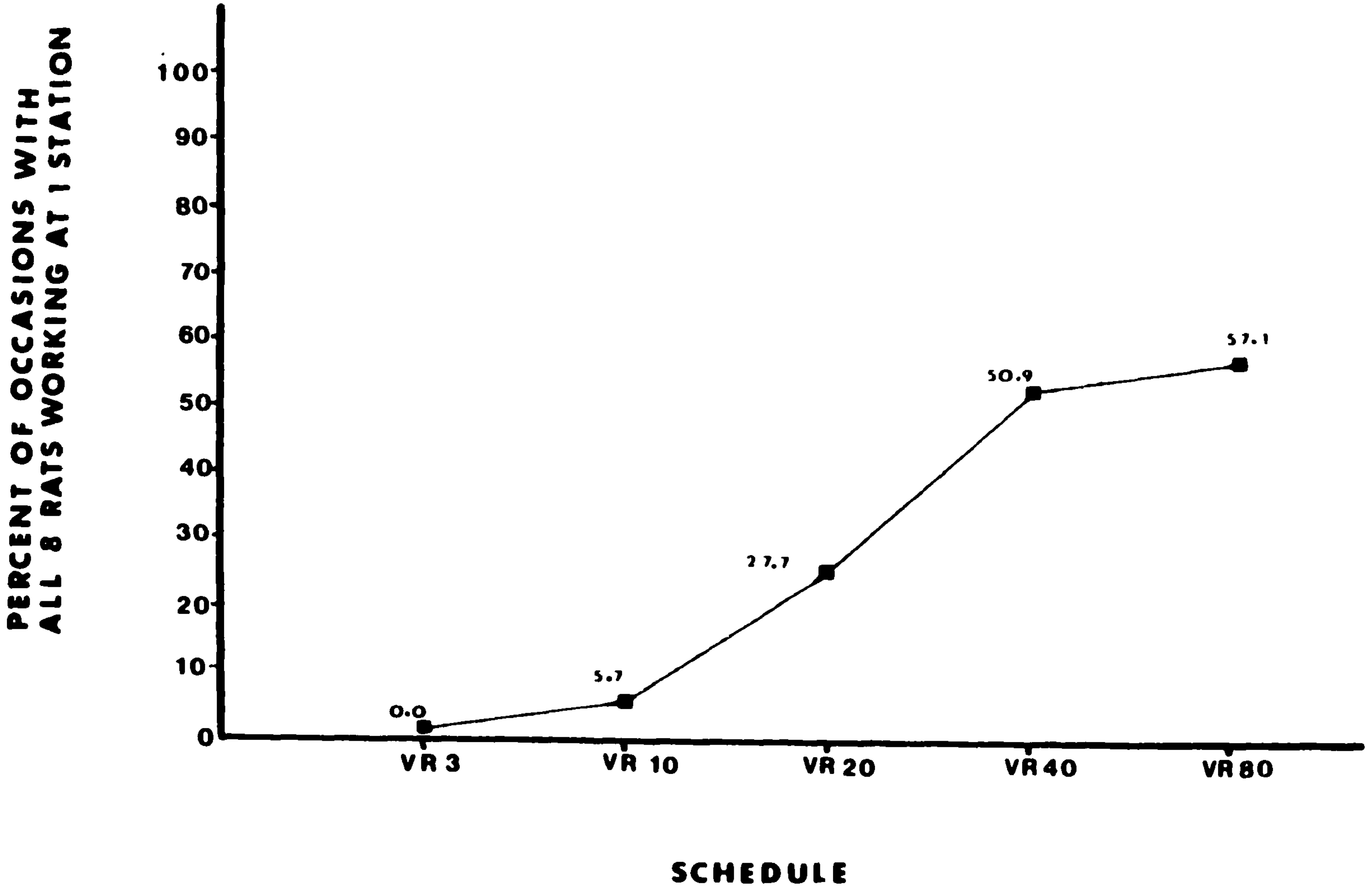


FIGURE 5. Variance / Mean Ratio By Schedule

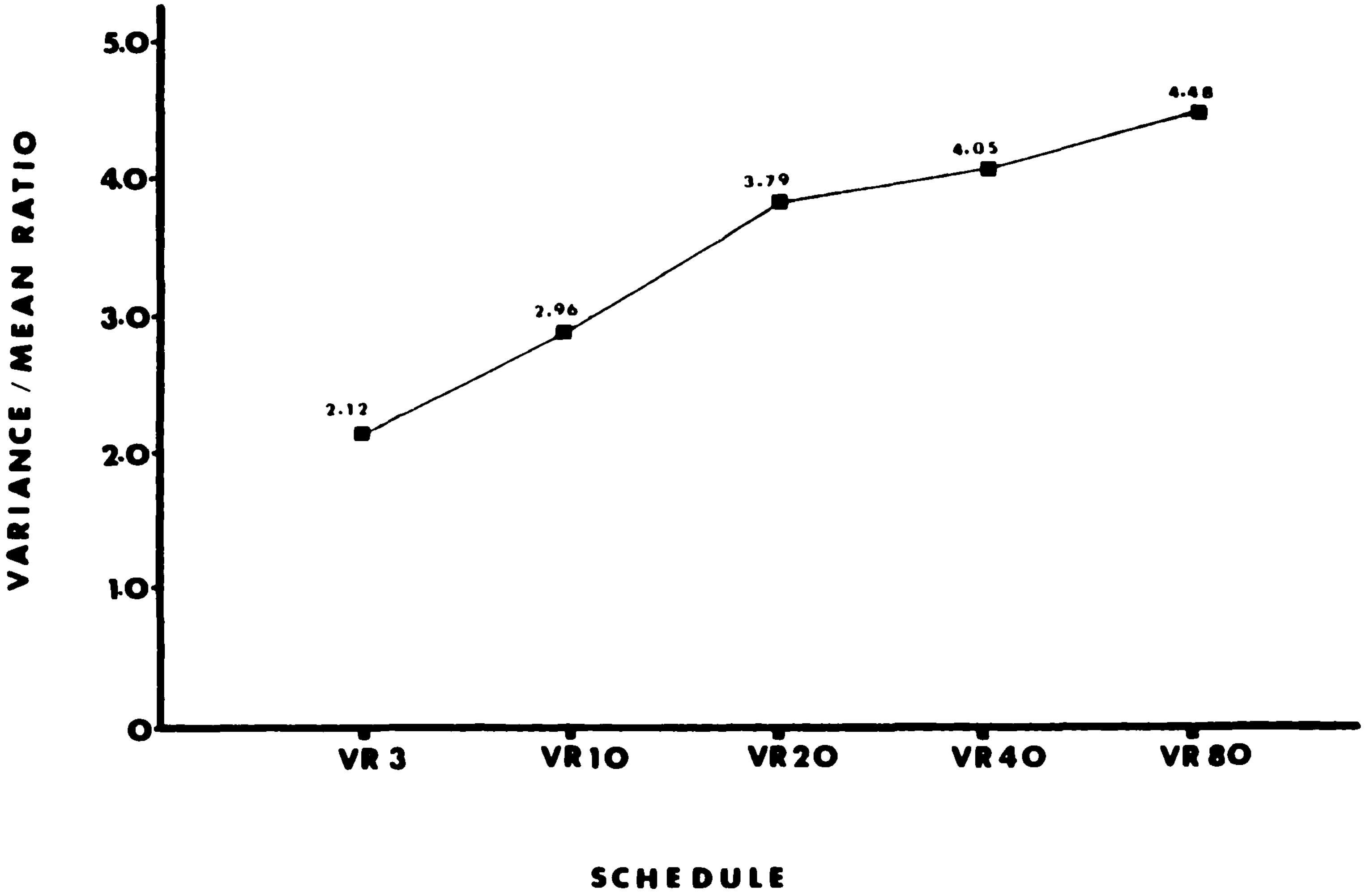


FIGURE 7a. Mean Rat Density at Each of the 8 Work Stations

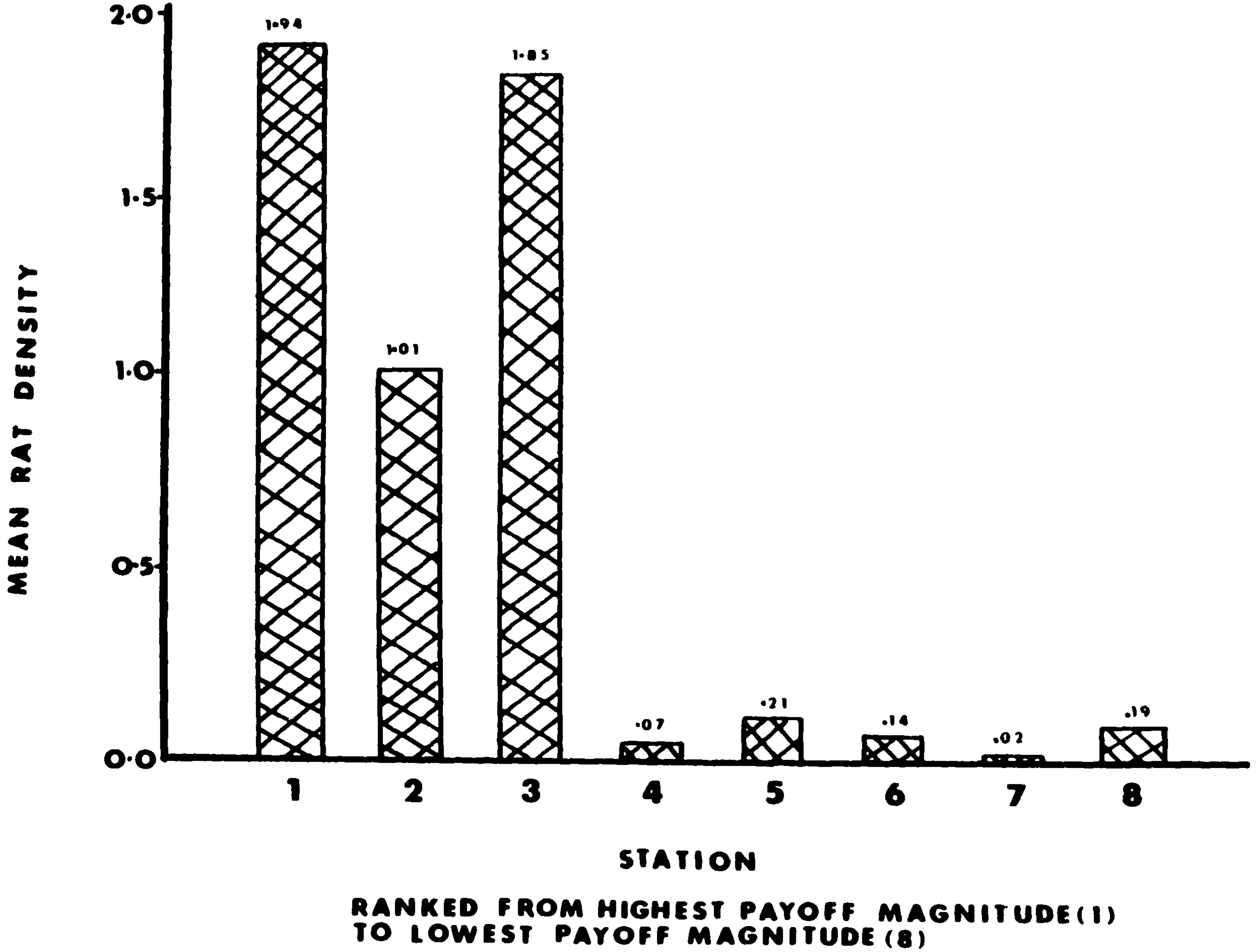


FIGURE 7b. Mean Rat Density at Each of the 8 Work Stations During Each of the 5 Variable Ratio Schedules

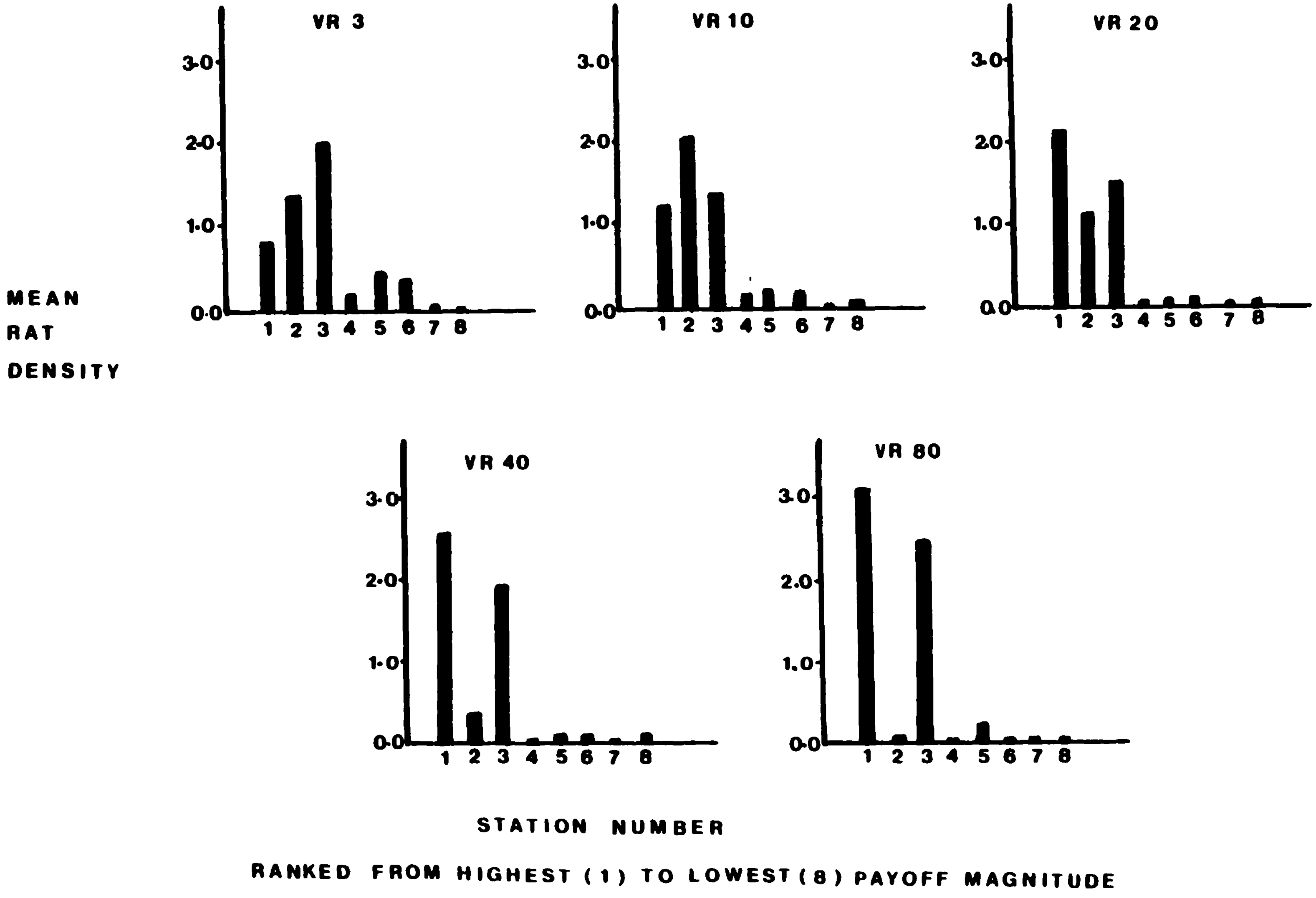


FIGURE 7c. Mean Rat Density by Programed Magnitude of Reward

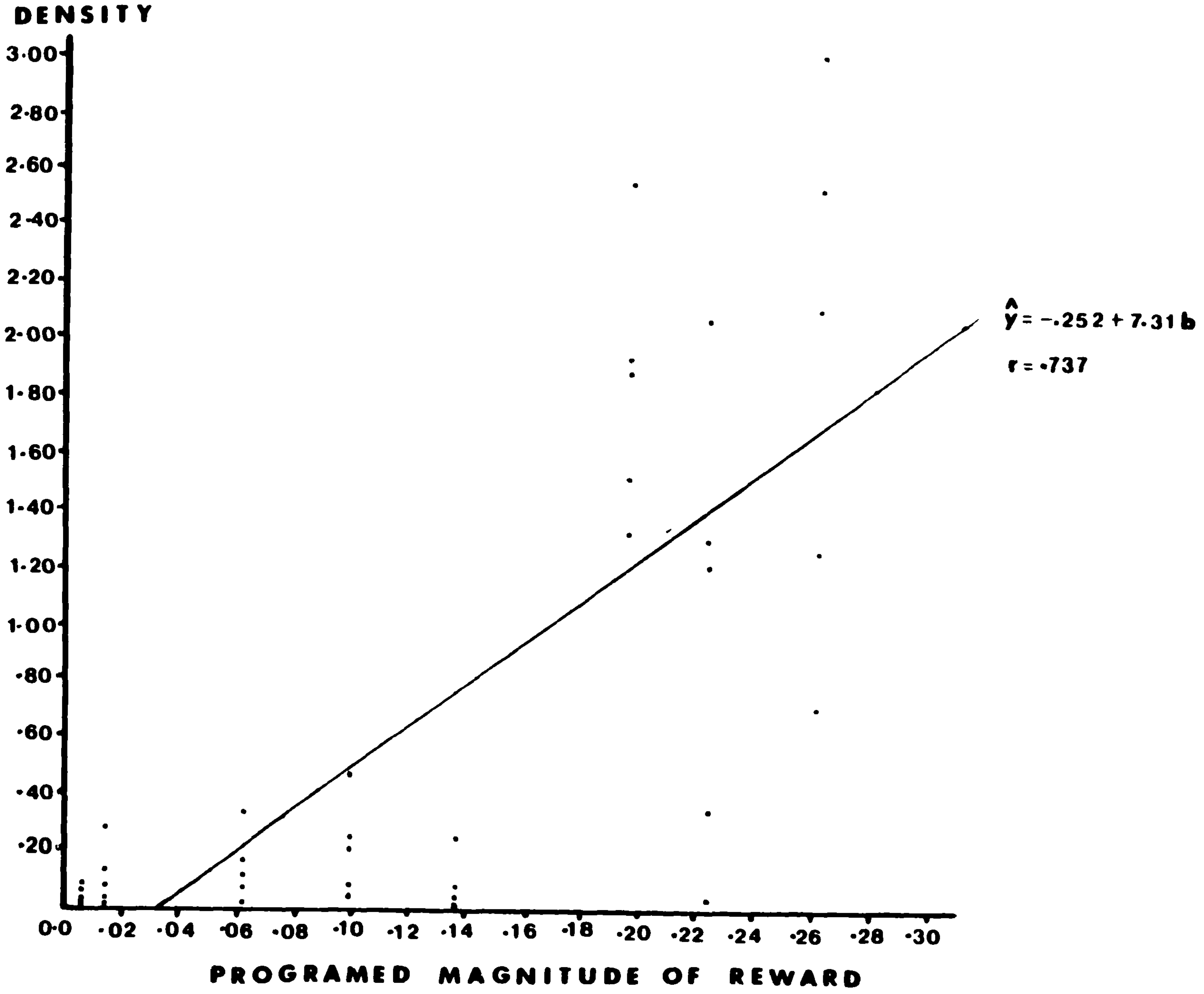


FIGURE 7d. Mean Rat Density by Programed Magnitude of Reward During Each Schedule

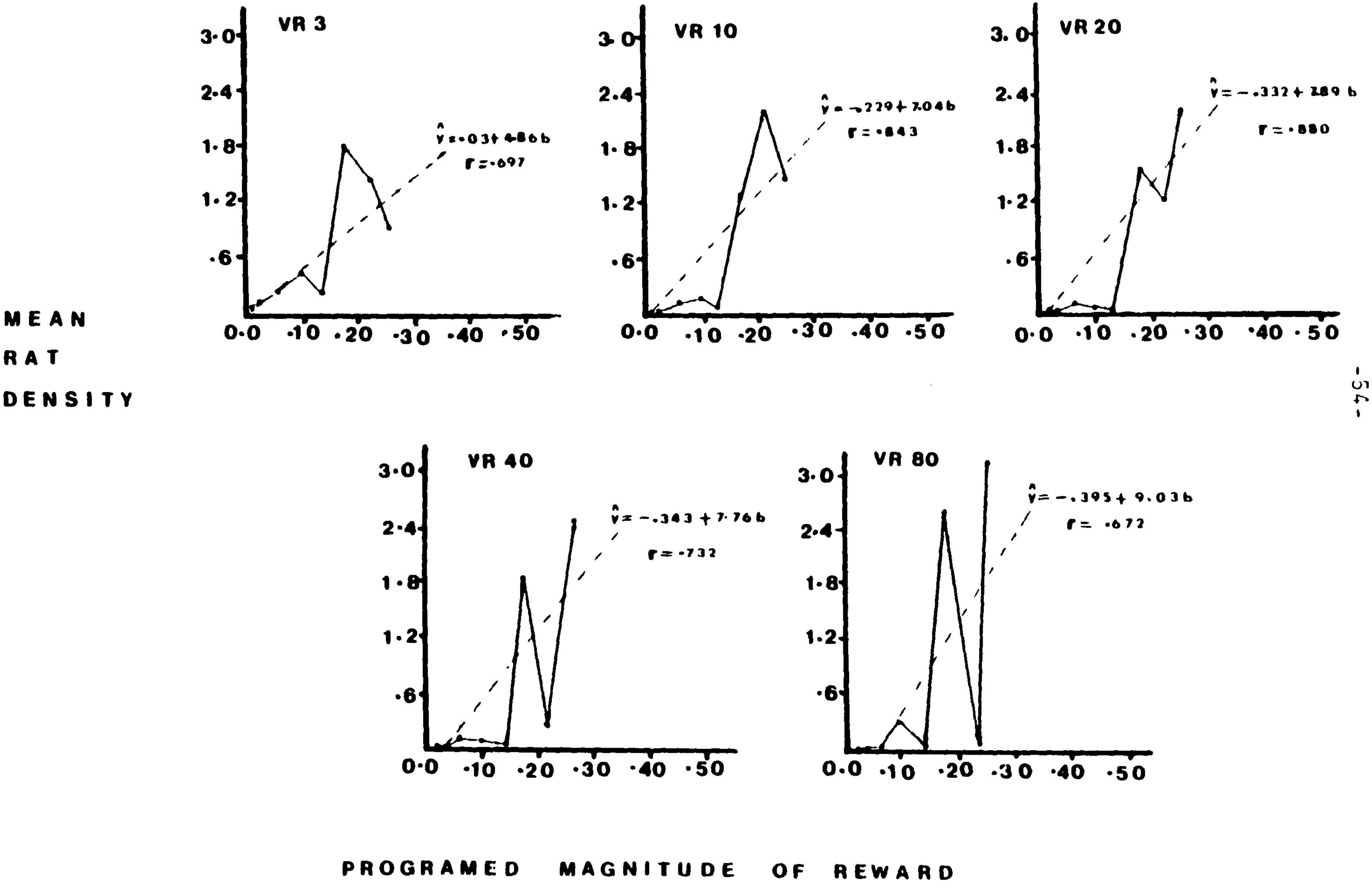


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FIGURE 8. Mean R[redacted] Density by Mean Obtained Magnit[redacted]e of Reward

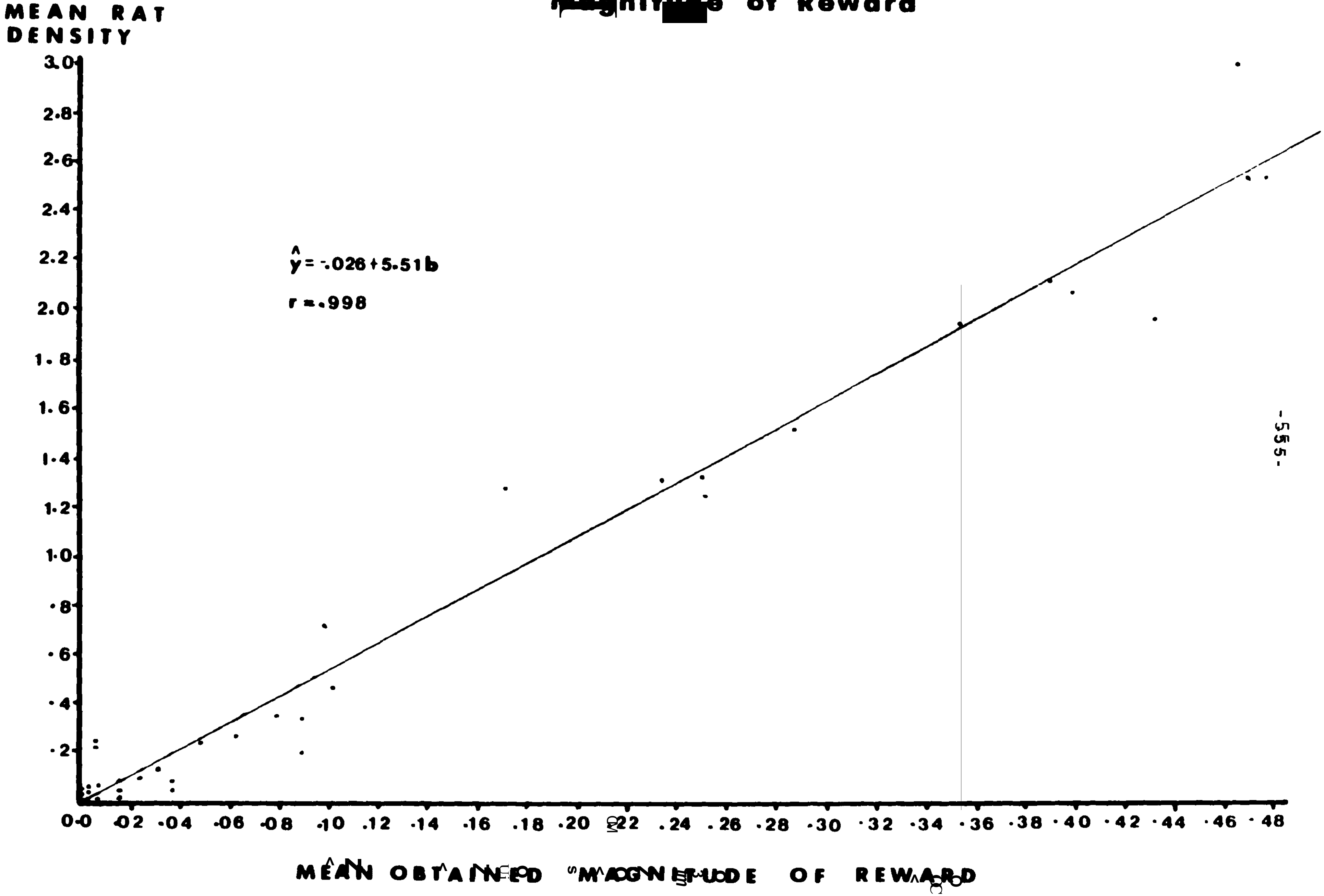

FIGURE 8a. Mean Rat Density by Mean Obtained Magnitude of Reward During Each Schedule

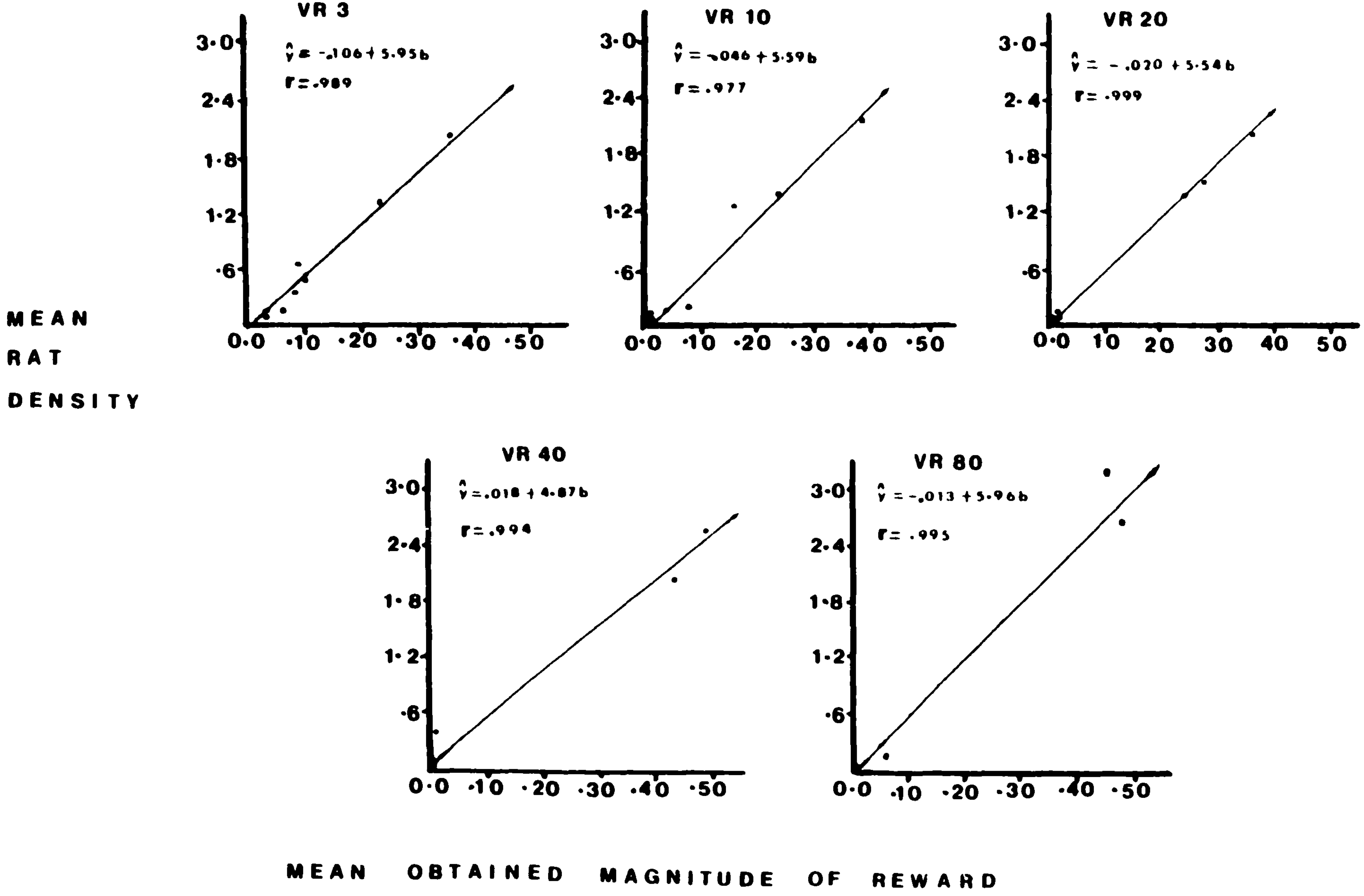

FIGURE 9. Mean Probability of a Rat by Programed Magnitude of Reward

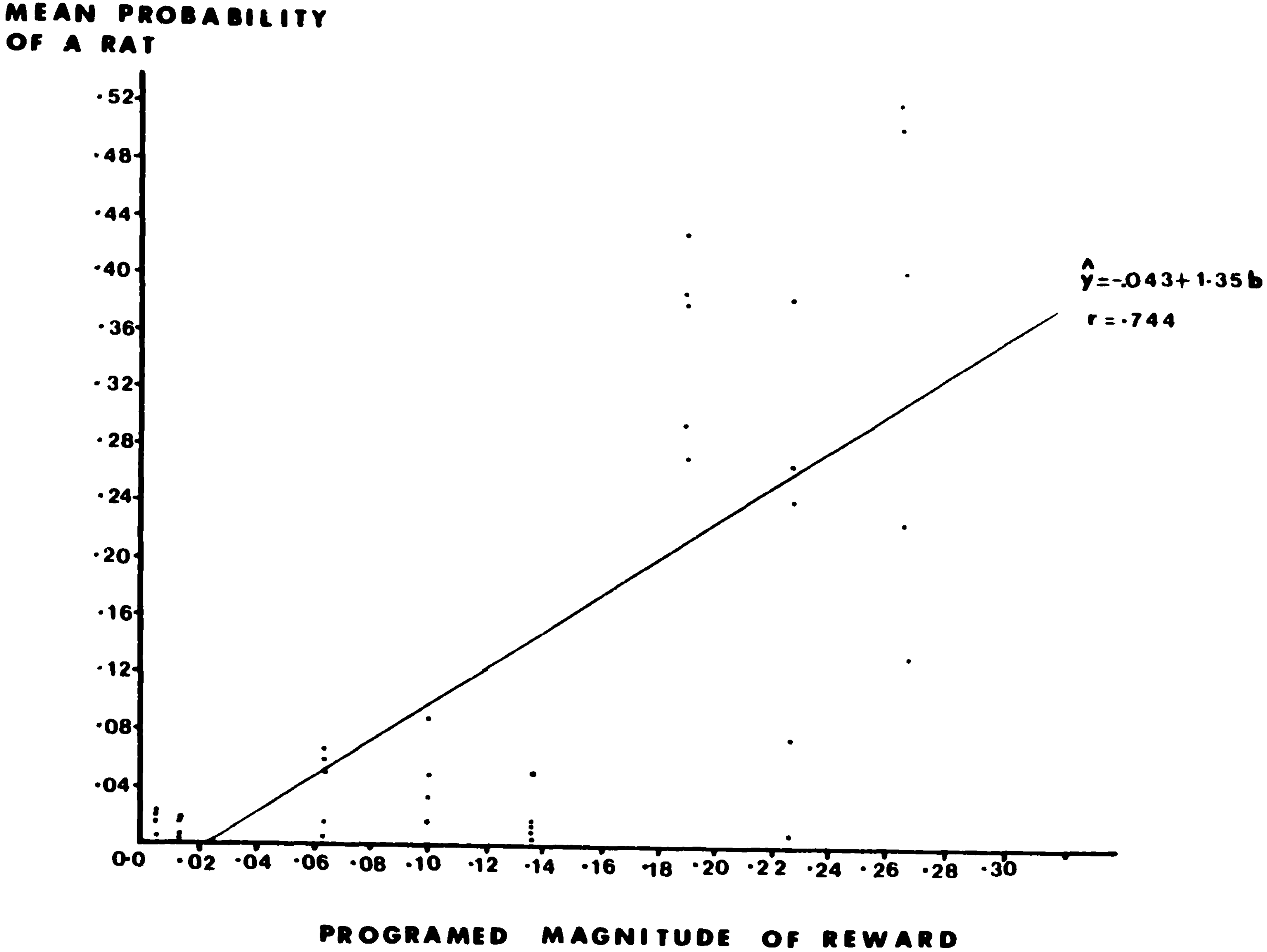

FIGURE 9a. Mean Probability of a Rat by Programed Magnitude of Reward During Each Schedule

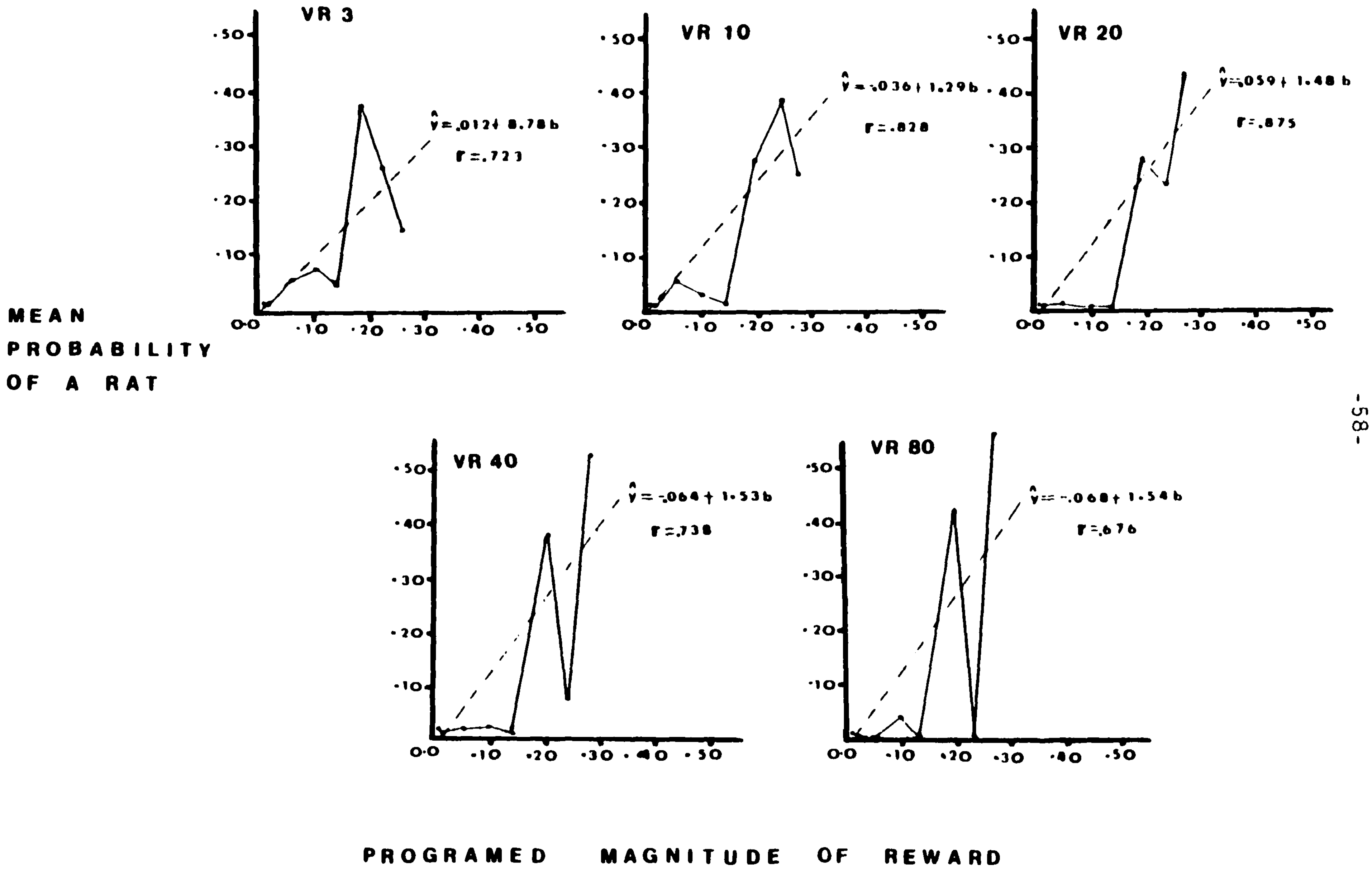

FIGURE 10. Mean Probability of a Rat by Mean Obtained Magnitude of Reward

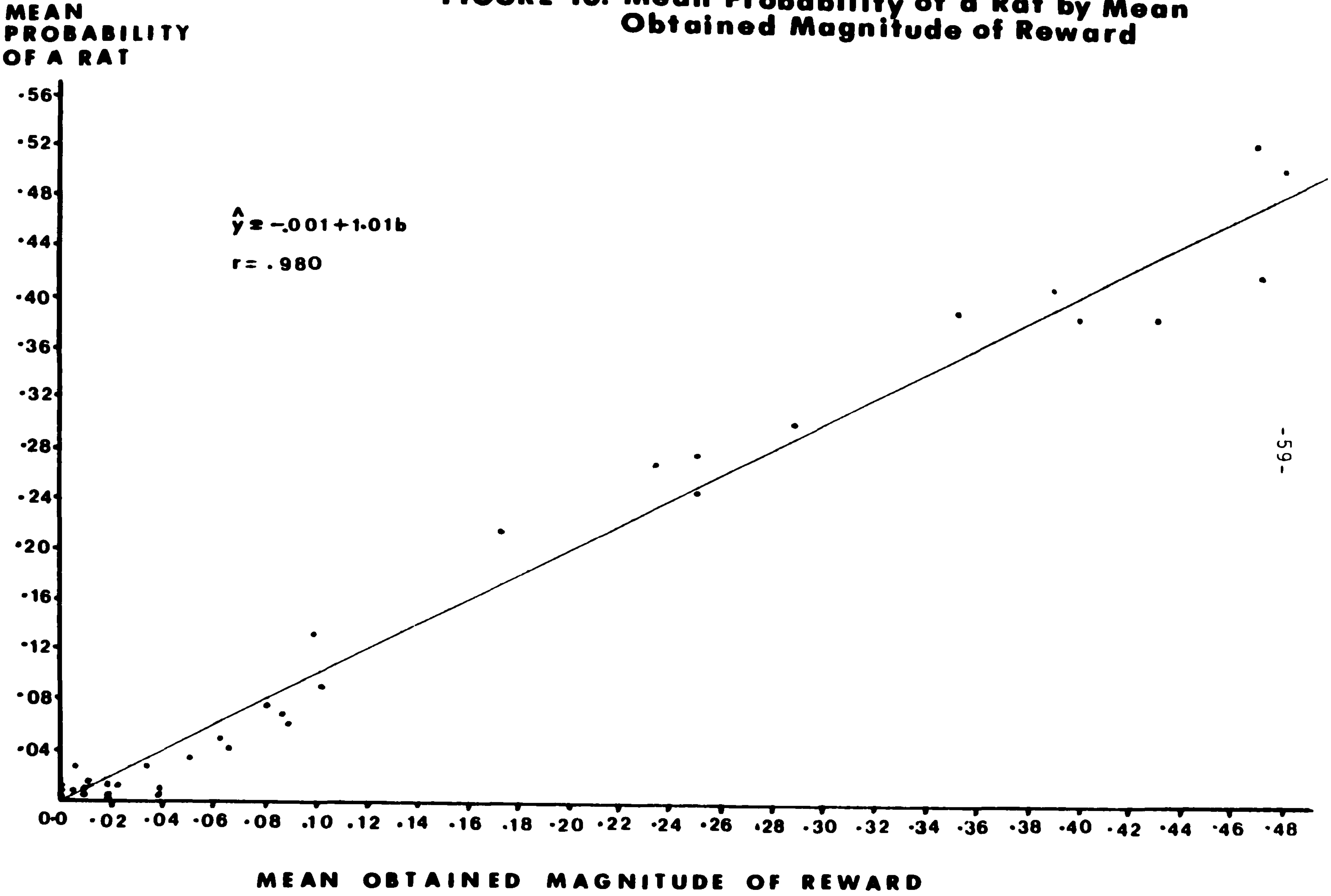

FIGURE 10a. Mean Probability of a Rat by Mean Obtained Magnitude of Reward During Each Schedule

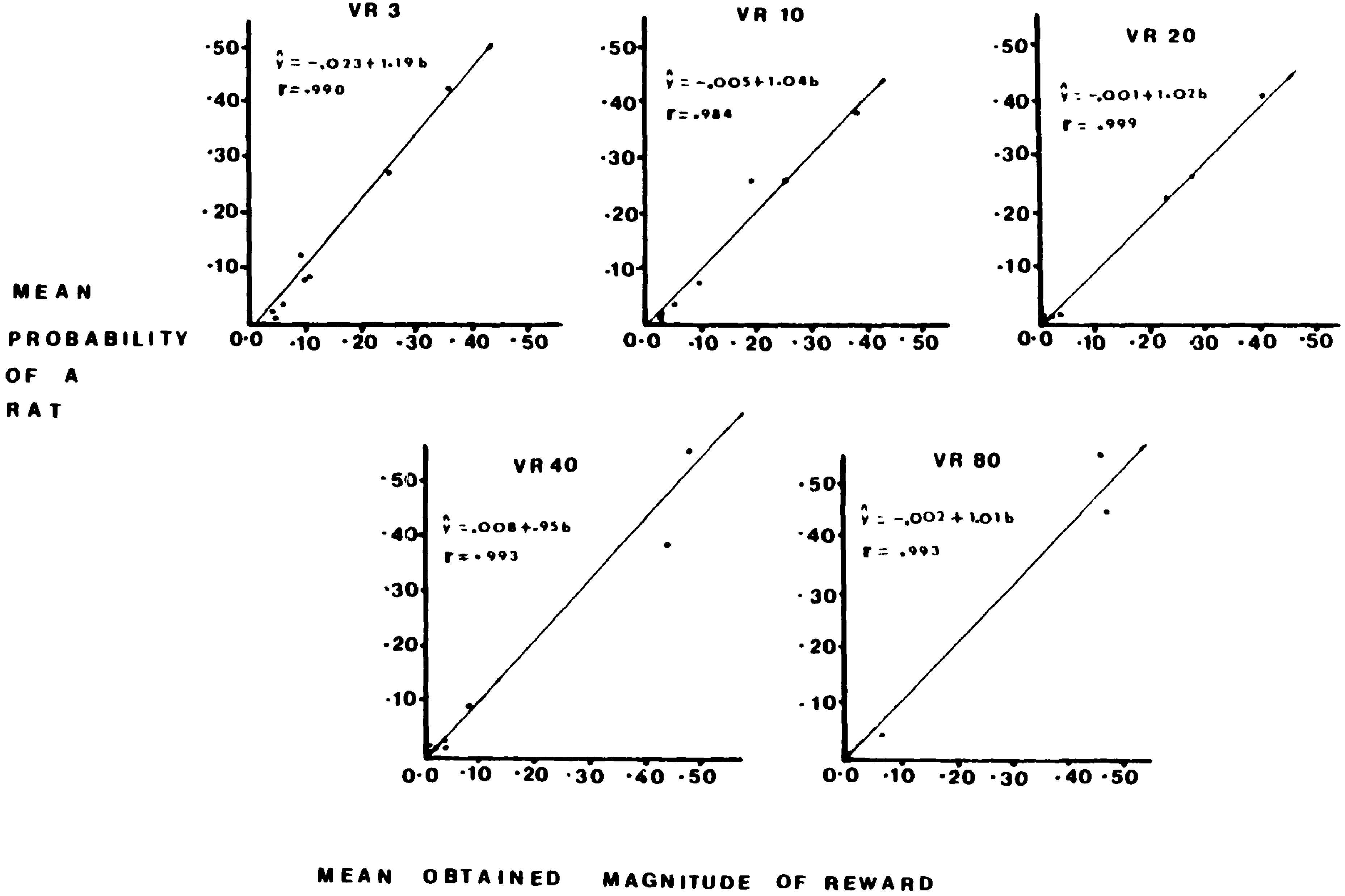

FIGURE 11. Mean Probability of a Response by Programed Magnitude of Reward

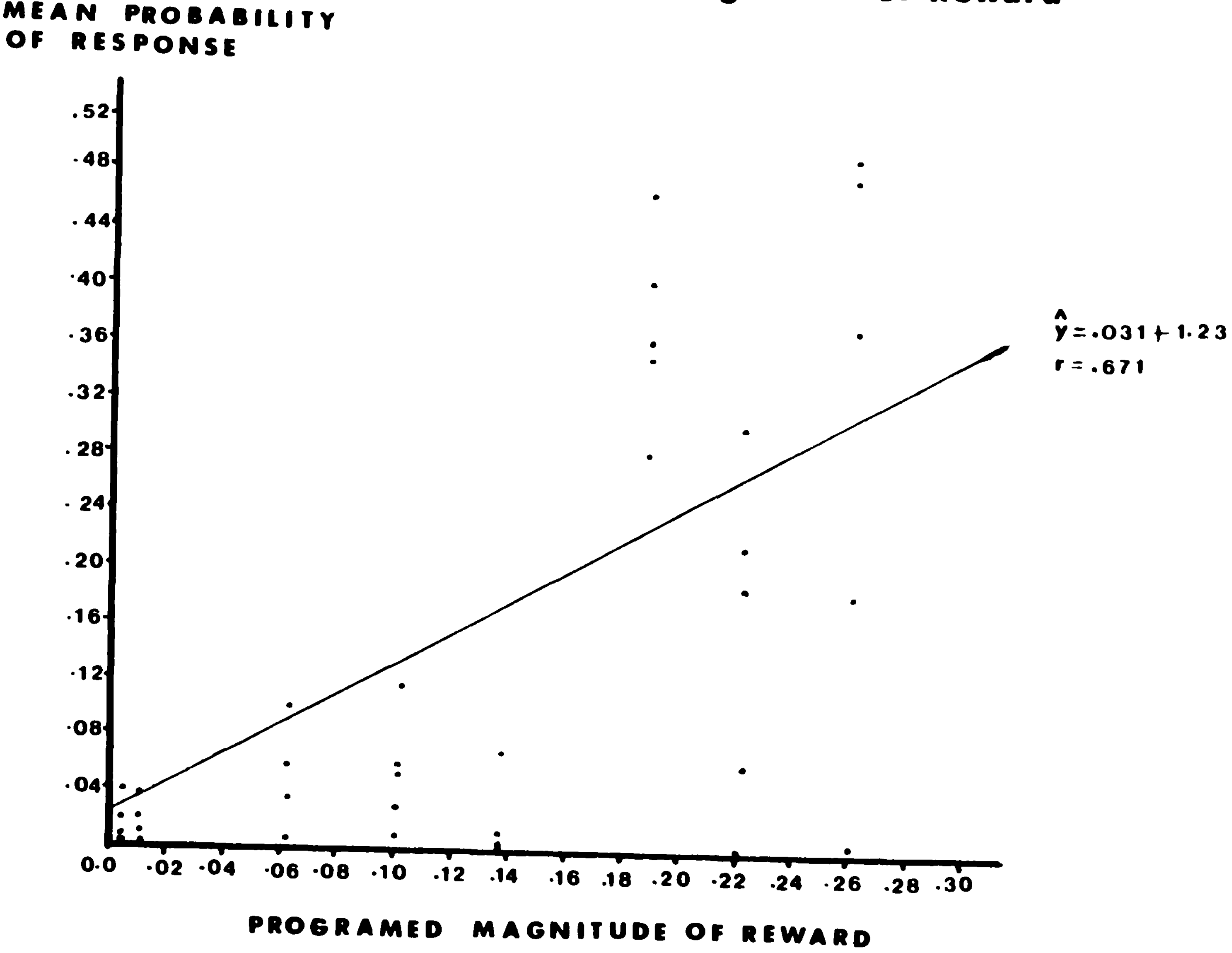

FIGURE 11a. Mean Probability of a Response by Programed Magnitude of Reward During Each Schedule

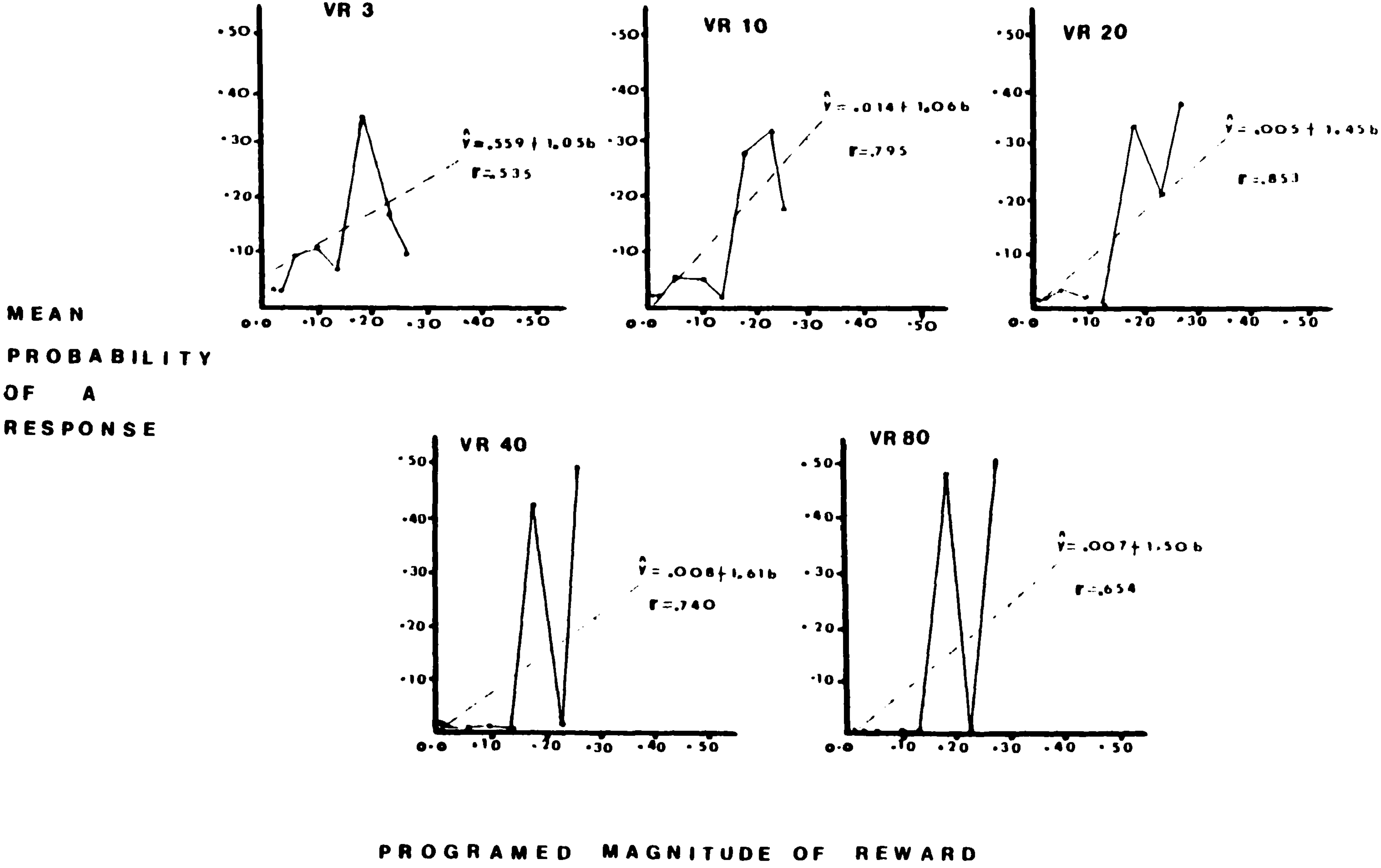

FIGURE 12. Mean Probability of a Response by Mean Obtained Magnitude of Reward

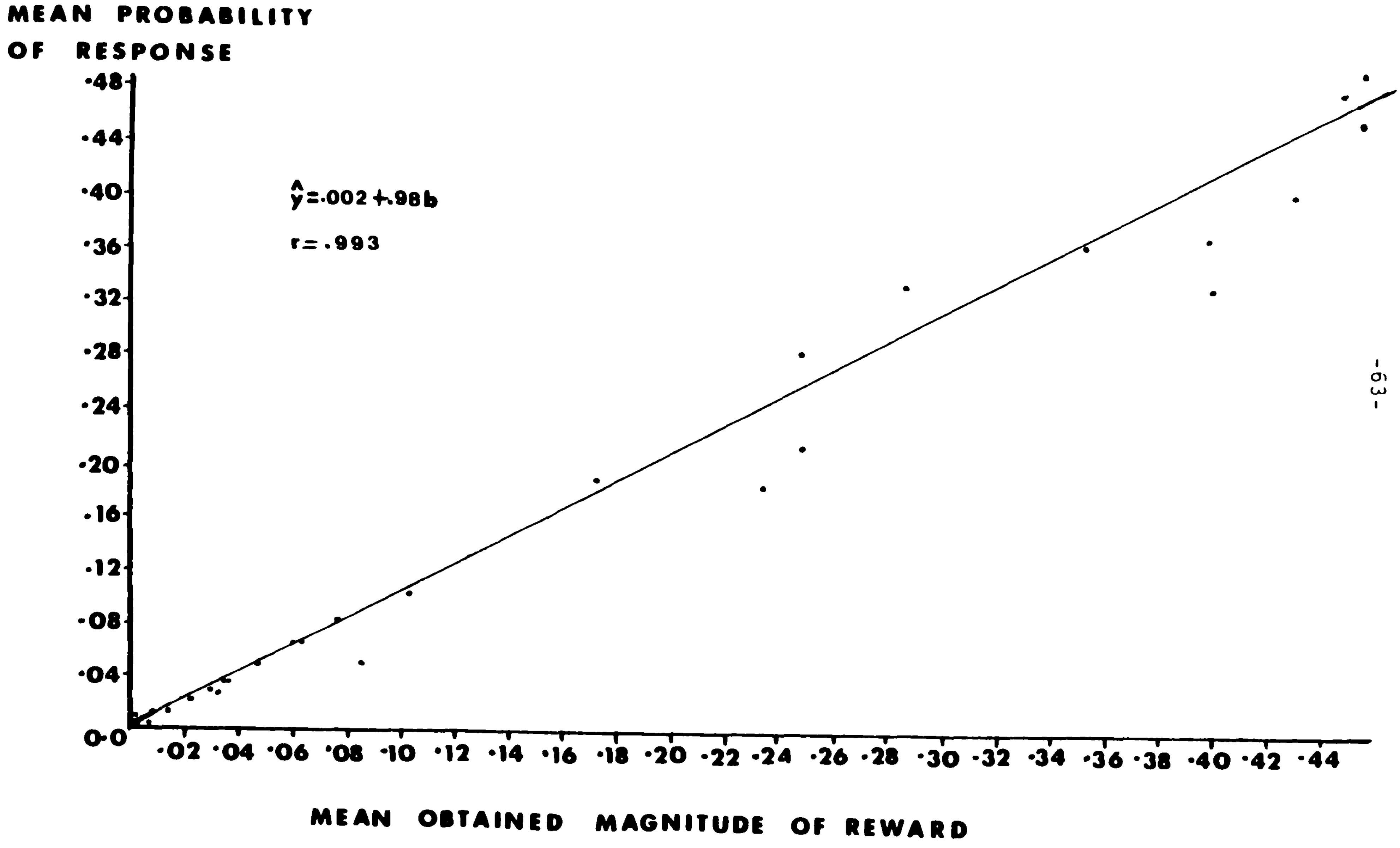

FIGURE 12a. Mean Probability of a Response by Mean Obtained Magnitude of Reward During Each Schedule

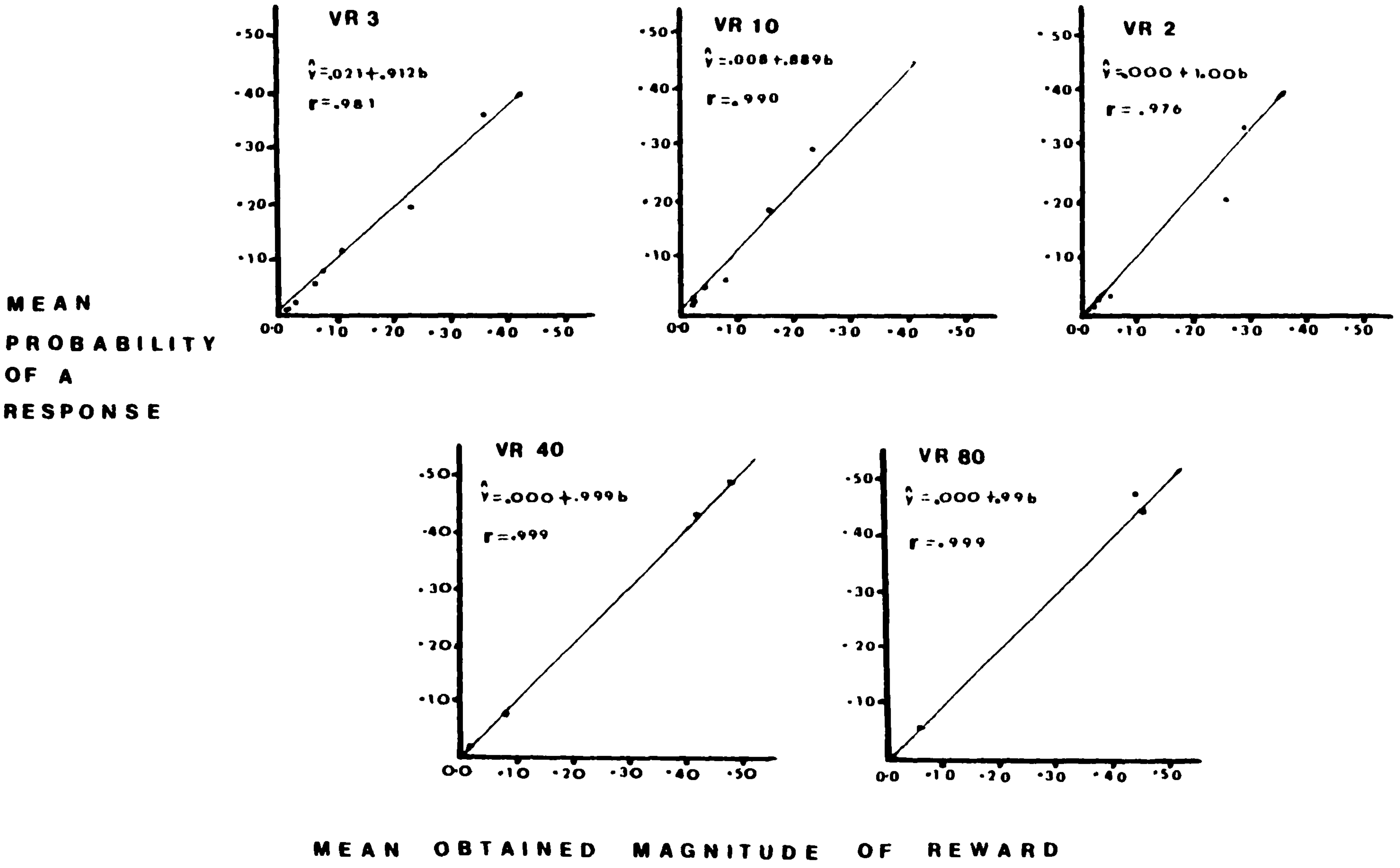

FIGURE 13.Number of Pellets Consumed During Each of the 5 Schedules

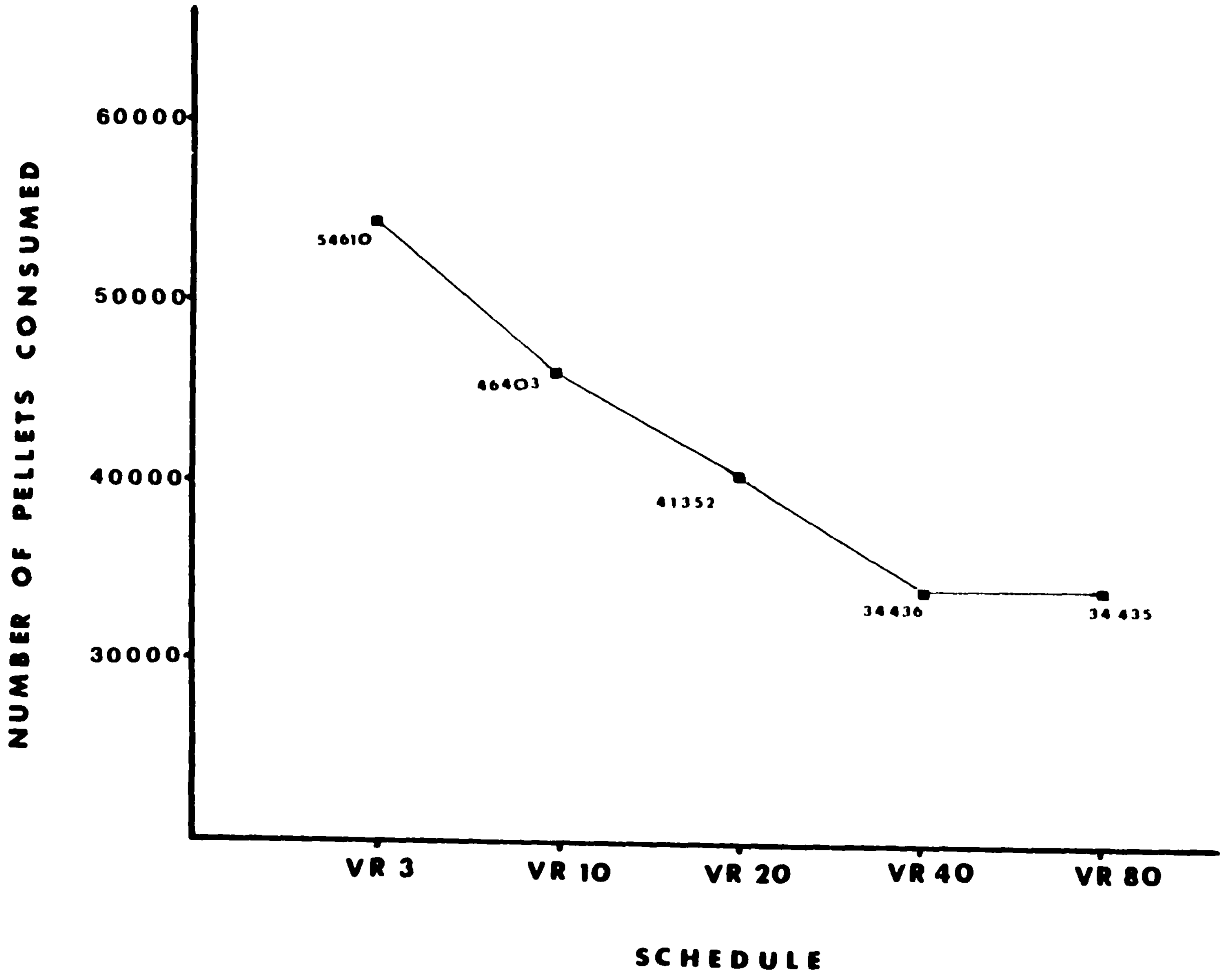

FIGURE 14. Work Performed During Each of the 5 Schedules

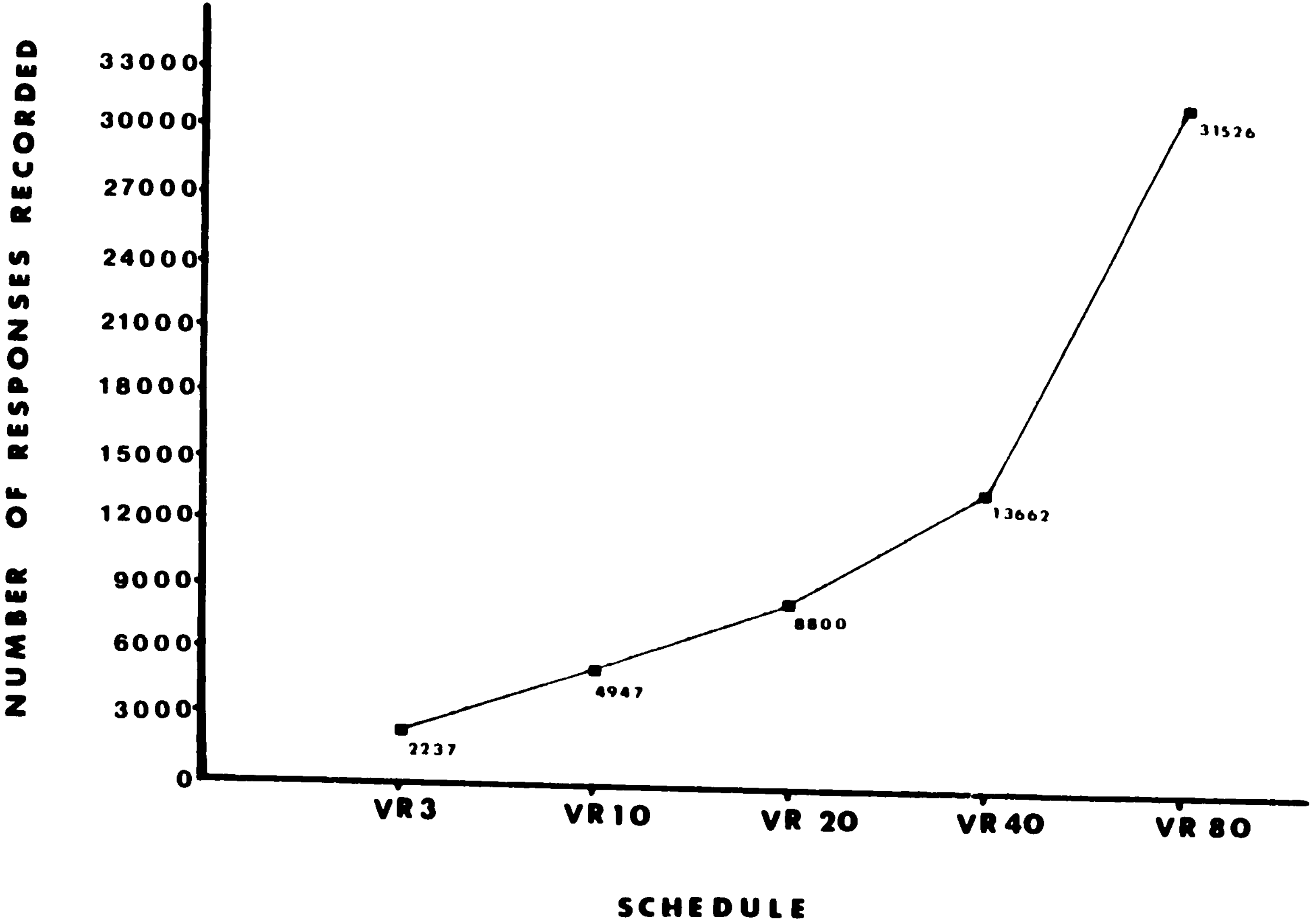

FIGURE 15. Mean Number of Pellets Obtained per Response During Each Schedule Condition

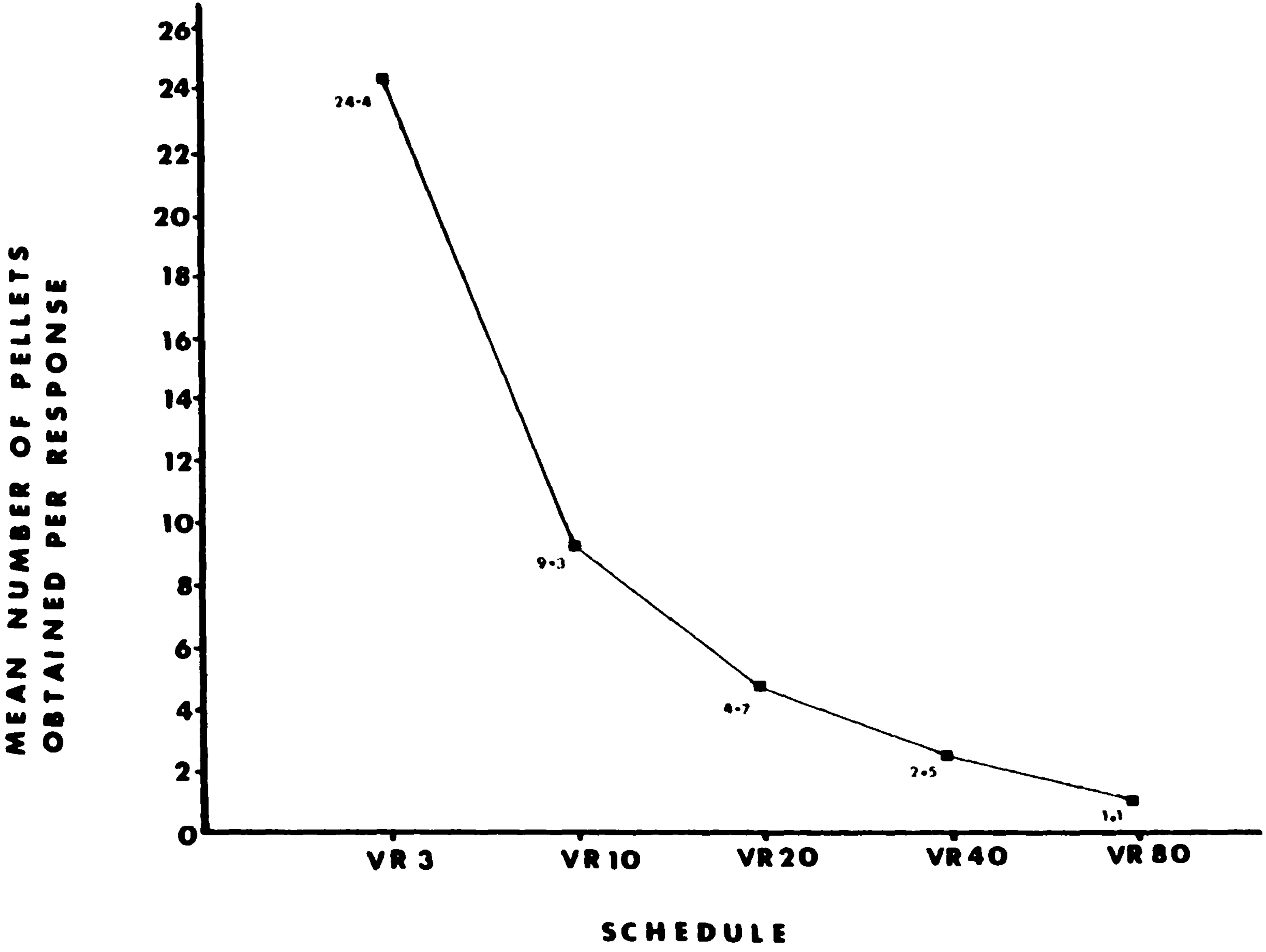

TABLE 1.

CHI-SQUARE analysis between observed dispersion pattern frequency and expected (chance) dispersion pattern frequency for each schedule.

VARIABLE RATIO SCHEDULE	CHI - SQUARE VALUE	SIGNIFICANCE LEVEL
VR 3	804.06	$p. < .01$
VR 10	1401.00	$p. < .01$
VR 20	1084.84	$p. < .01$
VR 48	2388.51	$p. < .01$
VR 80	3254.98	$p. < .01$