VARIABLE INTERVAL SCHEDULE CONTROL OF DISPERSION AND DENSITY

BY

© PAUL A. JOHNSON

A THESIS
SUBMITTED TO THE FACULTY OF ARTS
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF MASTER OF ARTS

DEPARTMENT OF PSYCHOLOGY
LAKEHEAD UNIVERSITY
THUNDER BAY, ONTARIO, CANADA
NOVEMBER 1984

ACKNOWLEDGEMENTS

The thesis research was supported by a grant from the National Science and Engineering Research Council (NSERC) of Canada and by the President's NSERC fund presented to Dr. Stephen R. Goldstein, Lakehead University, Thunder Bay, Ontario, Canada.

I thank Dr. S. R. Goldstein for his excellent advice in preparing this thesis.

ABSTRACT

The effects of Variable Interval (VI) schedules of reinforcement on the dispersion patterns and aggregate densities of a small population of rats was studied. Eight male rats were permanently housed in an arena in which food pellets were delivered to eight food troughs when a bar press response followed a scheduled period of time. Once every minute for each 30 minute session the dispersion and density of the rats in the arena was recorded. There were 20 sessions in which the rats were exposed to each of the following VI values: 5, 10, 20, 40 and 80. Gradual changes in dispersion and density over ascending VI values were observed and formed curvilinear U-shaped relationships. This supports the contention that VI schedules of reinforcement influence the spatial and temporal dispersion and density of rat colony members. It is suggested that ecological data can be studied in terms of operant behavioural principles.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

The density and dispersion of animal populations has been traditionally studied under the rubric of population ecology (Hanski, 1982). This involves an understanding of the interrelationship of organisms and their environment (Emmel, 1973; Odum, 1965). An essential starting point in the investigation of population density and dispersion includes a description of the research format used (Caswell, Koenig, Resh, and Quentin, 1972). In order to analyse population movement two conceptual guidelines are used. One describes the key ecological factors that have been found to be related to changes in population and the other describes a method that is used in analysing the effects that the key controlling factors exert on density and dispersion. The former area falls into the traditional domain of ecology and the latter has been studied under the auspices of operant research as described more fully later on.

Ecological variables in population dispersion

Dispersion is commonly described as a change in the relative spatial and temporal position of the members of a population that exist within a prescribed area (Pimental, 1966). Dispersion is observed and measured as being either statistically regular, random, or aggregated (Brown and Orians, 1970; Lewis and Taylor, 1967).

Major variables that have a significant effect on dispersion at the ecological level of analysis include: physical barriers (geographic space, terrain and habitat), weather, density and dispersion of food, predators, conspecifics, parasites, and other species (Fretwell,1972; Krebs, 1978).

A population's members live in open space which contains nonpermeable barriers that are relatively unchanging and/or uninhabitable. These geographic constraints have played a minor role in ecological research (Terborsh, 1971). By the same token they are of major importance because these physical barriers dictate where the animal can not go (Emmel,1973; Mac Arthur, 1972; Terborsh, 1971). Open space, on the other hand, is distance that has to be covered thereby requiring an expenditure of energy and time and acts to suppress dispersion (Baum, 1982; Berryman, 1981; Murdoch and Oaten, 1975). Both open space and the barriers within help to regulate competitive and predatory interaction (Covich, 1976; Huffaker, 1958). Pertinent to this thesis it should be noted that change in population dispersion for spatial advantage is common in rodent species (Grant, 1972; Wiens, 1976).

Weather is another major variable that is related to the dispersion of species (Berryman, 1981; Birch, 1965; Giesel,1974; Krebs, 1978; Lewis and Taylor, 1967; Mac Arthur, 1972). Its effect is direct when survival can only be maintained within specific temperature, humidity and pressure ranges. Its effect is indirect when it limits the abundance of predators, prey and other food supplies thereby altering patterns of survival of a species.

Fretwell (1972) has suggested that the dispersion of a predator population is partially controlled by the density of its members. In a study by Fraser and Thomas (1980) it was observed that the adult and young *R. atratulus* and young *S. atromacutatus* aggregated at low population densities, yet became more regularly dispersed at high population densities. They suggested that increases in the density of populations of certain species of minnows increases the spatial regularity of that population. Predation and food search is believed to slow down at high prey densities because the population has a limited rate of consumption (Holling, 1959) and consequently this slows the rate of dispersion.

The food supply of a species has been given much attention in dispersion analysis (Stueck and Barrett, 1978). It is common for animal populations to aggregate in areas where there are abundant resources (Wynne-Edwards, 1962). Stueck and Barrett (1978) studied the effect of food-outlet location on the dispersion patterns of Feral house mice *Mus musculus* in a natural setting. They found that central food outlets created different aggregations of mice from decentralized food outlets. Huffaker (1958) studied the dispersion of predator and prey interaction using a predator mite _Typhlodronus accidentalis_ and a phytophagus mite species _Eotetranychus sexmacculatus_ as prey. Both mite species were placed in an enclosed environment in which the prey mite's food (oranges) was arranged in random sequence with rubber balls and vaseline barriers. The dispersion of the oranges was found to exert control over the dispersion of the prey mite population and in turn controlled the dispersion of the predator population. Curio (1976) made observations of blackbirds _Merula turdus_ in the wild and reported that the dispersion of the blackbirds was a function of the dispersion of its prey and other food sources. It was concluded that the blackbirds' searching pattern was a function of both prey type and arrangement. All of these studies show that the dispersion of food supply has control of the dispersion of the foragers.

Some animal populations have small hunting territories in which they search for relatively small prey of great abundance (high density) while other populations have large territories in which they search for large prey of low density (Giesel, 1974; Soloman,1969). Giesel (1974) observed that some animals, wolves for instance, hunt in packs (aggregated dispersion) while other animals, eagles for example, hunt alone (regular dispersion). These usual foraging strategies may, however, be altered under certain conditions. Density can alter the eating behaviour of the members of a population when the availability of food, or its prey, changes. If the density of a favoured food decreases there is an increase in the consumption of a less favoured food even though the total caloric value of food intake remains relatively constant (Currio, 1976). When food is readily available a population can reduce gross energy expenditure by selecting foods that take less effort to consume. For example, seed eaters will choose seeds that are easy to crack over seeds that have very hard shells (Giesel, 1974). The size of the food source also affects comsumption efficiency (Elton, 1971). Consumption efficiency is centered around an optimal size gradient of food (Mac Arthur, 1972). For example, a house cat will stalk and capture more birds the size of a robin than a goose. In addition to caloric value food must also be palatable (Covich, 1976). As the food type changes so does dispersion in order to search for alternate food sources.

Behavioural analysis of animal populations

Changes in the above variables: geography, weather, predators, prey, food quality and density, have been observed to be correlated with changes in the dispersion of animal populations. How these variables interact in predictable ways is still in question. Several authors have been investigating this question in terms of operant conditioning. It has been suggested that methods of behavioural research may provide a methodology in which ecological phenomena may be objectively and systematically investigated (Baum, 1982, 1974; Goldstein, 1981a; Goldstein and Mazurski, 1982; Goldstein, Johnson, and Ward, 1984; Fretwell, 1972; Krebs, Kacelnik and Taylor, 1978; Staddon, 1981; Wilson, 1975).

A major variable in ecological studies is food. Similarly in operant conditioning food is also a major variable. Because food is a major factor that is common to both disciplines, ecological phenomena may be discussed in operant terminology. The resulting formulation would be one in which major ecological variables (geography, weather, predators, prey, food quality and density) would be considered discriminative stimuli (SD) which, depending on the species, may act as positive or negative reinforcers and punishers for controlling dispersion patterns (Rachlin, 1980). A discriminative stimulus is a stimulus which is present when a response is reinforced and when absent a response goes unreinforced. The relationship between foraging effort and food procurement would determine the schedule of reinforcement.

Individual organisms produce predictable behaviour that corresponds to contingencies of reinforcement (Skinner, 1969). Environmental contingencies not only affect individual responding; they also have been shown to exert control over the collective responding of groups of organisms. In an experiment involving choice behaviour in free-ranging pigeons Baum (1974) found that a constant ratio between responses and reinforcements (behavioural matching) was encountered when the pigeons had access to pecking keys that delivered food on various schedules of reinforcement. Graft, Lea and Whitworth (1977) made observations of groups of rats in a complex running maze that contained four small single-lever operant chambers. In two of those chambers food was available on successively higher Variable Interval (VI) schedules of reinforcement. In VI schedules a randomly generated amount of time must pass before a bar press will be reinforced with food and the average time is the VI value. These authors found that the response rates match the rates of reinforcement. Grott and Neuringer (1974) studied groups of rats in a chamber containing only one response lever and analysed the collective response rates under VI schedules of reinforcement. They also found systematic relationships between rates of response and reinforcement. All of these studies demonstrate two things. firstly, that under experimental conditions global group responses can be shown to come under operant control. Secondly, they show that group response to reinforcement ratios conform to the Matching Law. The Matching Law states that under conditions of concurrent schedules of reinforcement (two or more schedules of differing values that an animal has access to) the relative rates of responding to reinforcement are equivalent under each schedule (Herrnstein, 1974). In general terms, the frequency of an activity relative to all others, matches its reward value relative to all others (Baum, 1981).

Goldstein (1981a) conducted experiments that took into consideration dispersion and abundance within a circumscribed terrain called an operant arena. The dispersion patterns of the colony were considered the behaviours to be modified in relation to various schedules of reinforcement. He observed that rats adjust dispersion patterns to the constraints imposed by reinforcement schedules, such that dispersion was more regular under some Fixed Ratio (FR) schedules than under others. In FR schedules a constant number of predetermined responses (bar presses) must be made before a reinforcement (food) can be delivered for consumption by the animal. In another study using the operant arena Goldstein and Mazurski (1982) found that the dispersion of rats became more regular in a direct relation to increases in FR values. In both cases schedules of reinforcement were shown to exert control over collective response rates and over the dispersion of a population of the same species.

Variable Interval schedules and population dispersion

This thesis investigates the effect of Variable Interval (VI) schedules of reinforcement on population dispersion and economy. Under an experimentally imposed VI schedule food (reinforcement) was delivered to a food trough only after an appropriate response was made following a scheduled period of time. The effect of VI scheduling on dispersion, carried out under controlled experimental conditions, was to be representative of the food procurement strategies of many animals in the wild. For instance, in a natural setting prey-capture strategies emulate VI schedules when an animal's prey or food are available only at certain times of the day, season or year and can then only be captured when appropriate behaviours are performed. When no food is available no response of an animal can be reinforced with food. The prey-capture style of the ant lion is an example of a naturally occurring VI schedule of food reinforcement. The ant lion builds a pit and then hides in it waiting for an unsuspecting prey to come within range before it attacks (Wilson, 1975). In this example the prey is available at unequal intervals (e.g., variable intervals) in time. The ant lion has an opportunity to capture food only when that food is within a specific range. Thus it has to make an appropriate response after a variable interval of time in order to obtain food. An attack response that is made before food is present will go unrewarded.

In order to draw parallels between nature and the laboratory the most conspicuous variable (food) that affects behaviour in both settings was considered. The effect of VI scheduling on population dispersion was observed by studying the movement of eight food-deprived rats in an operant arena as they bar pressed for food at eight food delivery stations. The utility of the operant arena in studying dispersion would be increased by showing that Interval schedules exert systematic effects on the dispersion behaviour of populations. The results are discussed in terms of operant control and optimal foraging theory.

METHOD

Subjects:

Eight 50 day old, male, black-hooded rats were used. The rats were experienced at bar pressing for food pellets under various ratio and interval schedules.

Apparatus:

The animals' habitat was a 3.7m x 3.4m x 1.2m operant arena containing eight food magazines each with a response bar, food trough and 100ml graduated water bottle (Goldstein, 1981b) (Figure 1). The feeding stations were arranged symmetrically with four on each side of the arena. The edible reinforcers consisted of 45mg Noyes food pellets that were released into the food trough whenever a bar press was made after a computer-scheduled period of time passed. The reinforcement schedules, data acquisition, and analysis were controlled by a preprogrammed PET series 2001 micro processor (Blekkenhorst and Goldstein, 1983; Goldstein, Blekkenhorst, and Mayes, 1982). Bar presses and reinforcements were

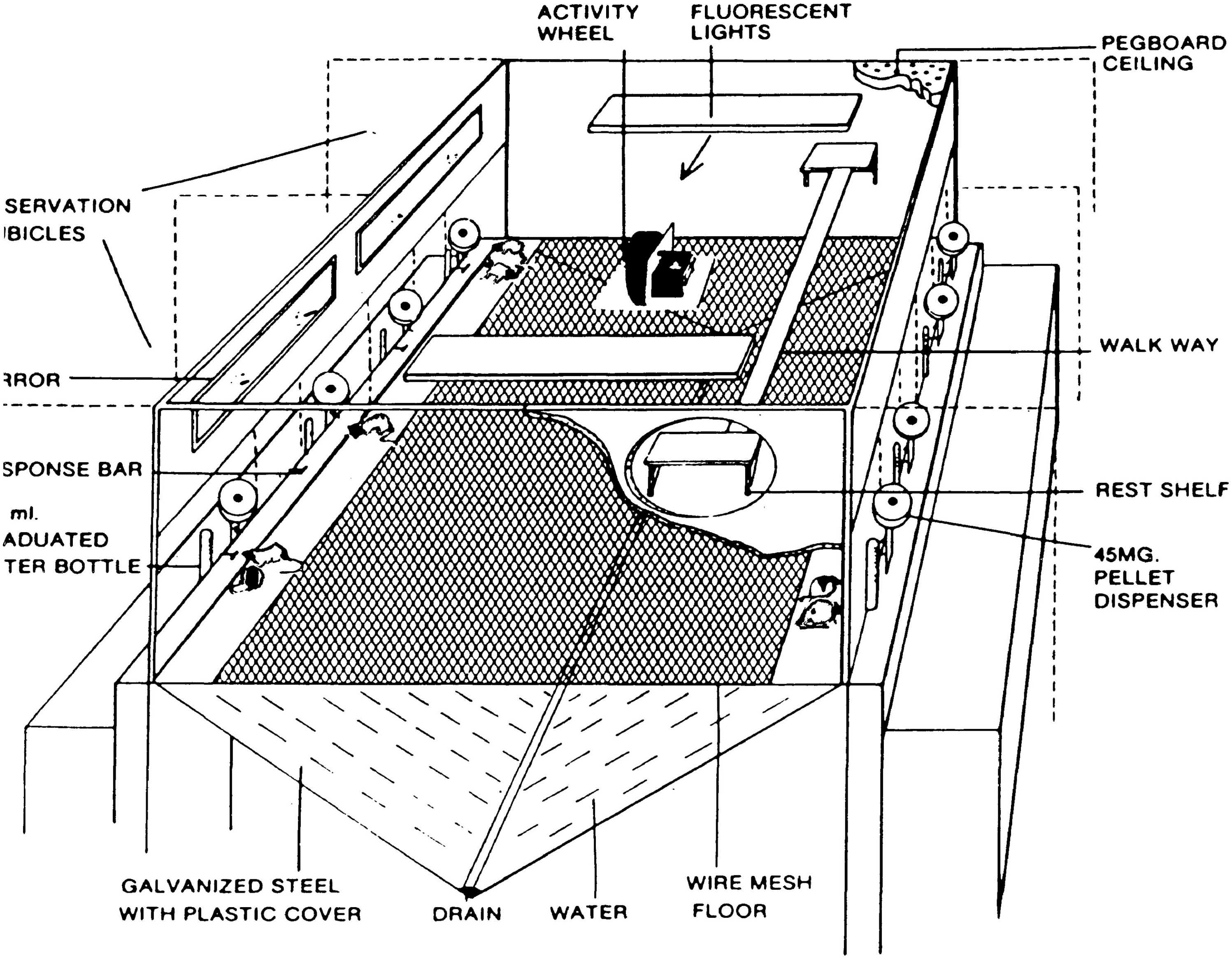


Figure 1. Diagramatic representation of the eight-rat eight-station operant arena.

also graphically recorded on a standard cumulative recorder.

Procedure:

The animals were exposed to five VI schedules of 5, 10, 20, 40, and 80 seconds sequentially. Each schedule was in effect for ten consecutive days and each station was programmed to deliver food reinforcement at the same VI value. Once each day there was a morning (10:30) and an afternoon (4:30) session of one half hour duration providing the population with 20 exposures to each VI value. A session commenced with the placement of the eight bars into position in the arena and terminated one half hour later with the withdrawl of the bars from the arena. The rats lived in the arena and were never removed and never handled.

Responses, reinforcements, post-reinforcement pauses and response/reinforcement matching were logged by the computor for each station during each session along with a cumulative numerical recording of collective responses and reinforcements. Dispersion was determined by recording the number of rats within an approximate 54cm x 22cm perimeter around each feeding station at the beginning of each minute of the 30 minute sessions. A graphic cumulative recording of the response and reinforcement rates was also obtained. A food supplement was provided daily at the conclusion of the 4:30 session of the VI 20, 40 and 80 schedules.

Data analysis:

Spatial dispersion was represented by: dispersion (number of rats per station at each of the eight stations in the arena), frequency of regular spatial dispersion (one rat per station), the local density (number of animals per food station), and attrition (number of rats not present at any food station). In order to analyse regular spatial dispersion, regularity, and all other spatial dispersion patterns a frequency count was made. If the identity of both the individual rats and the bars is ignored, a possible 67 different spatial dispersion patterns (Table 1) can be observed each minute per session. Six hundred observations per schedule were made. The frequency totals for each of the spatial dispersion patterns were analysed in terms of AM, PM, and daily totals per schedule. The frequency totals were then averaged to show AM, PM, and daily spatial dispersion means for each VI schedule.

```
    T O   D A T E
CLASS0   ENTRIES (          0)  %-( 0.000000000      )
    CATEGORY           HITS     LOCAL%              GLOBAL%
           0              0   0.000000000     %   0.000000000     %
CLASS1   ENTRIES (          0)  %-( 0.000000000      )
    CATEGORY           HITS     LOCAL%              GLOBAL%
           1              0   0.000000000     %   0.000000000     %
CLASS2   ENTRIES (          0)  %-( 0.000000000      )
    CATEGORY           HITS     LOCAL%              GLOBAL%
           2              0   0.000000000     %   0.000000000     %
          11              0   0.000000000     %   0.000000000     %
CLASS3   ENTRIES (          0)  %-( 0.000000000      )
    CATEGORY           HITS     LOCAL%              GLOBAL%
           3              0   0.000000000     %   0.000000000     %
          12              0   0.000000000     %   0.000000000     %
         111              0   0.000000000     %   0.000000000     %
CLASS4   ENTRIES (          0)  %-( 0.000000000      )
    CATEGORY           HITS     LOCAL%              GLOBAL%
           4              0   0.000000000     %   0.000000000     %
          13              0   0.000000000     %   0.000000000     %
          22              0   0.000000000     %   0.000000000     %
         112              0   0.000000000     %   0.000000000     %
        1111              0   0.000000000     %   0.000000000     %
CLASS5   ENTRIES (          0)  %-( 0.000000000      )
    CATEGORY           HITS     LOCAL%              GLOBAL%
           5              0   0.000000000     %   0.000000000     %
          14              0   0.000000000     %   0.000000000     %
          23              0   0.000000000     %   0.000000000     %
         113              0   0.000000000     %   0.000000000     %
         122              0   0.000000000     %   0.000000000     %
        1112              0   0.000000000     %   0.000000000     %
       11111              0   0.000000000     %   0.000000000     %
CLASS6   ENTRIES (          0)  %-( 0.000000000      )
    CATEGORY           HITS     LOCAL%              GLOBAL%
           6              0   0.000000000     %   0.000000000     %
          15              0   0.000000000     %   0.000000000     %
          24              0   0.000000000     %   0.000000000     %
          33              0   0.000000000     %   0.000000000     %
         114              0   0.000000000     %   0.000000000     %
         123              0   0.000000000     %   0.000000000     %
         222              0   0.000000000     %   0.000000000     %
        1113              0   0.000000000     %   0.000000000     %
        1122              0   0.000000000     %   0.000000000     %
       11112              0   0.000000000     %   0.000000000     %
      111111              0   0.000000000     %   0.000000000     %



CLASS7   ENTRIES (          3)  %-( 8.333333253E-01)
    CATEGORY           HITS     LOCAL%              GLOBAL%
           7              0   0.000000000     %   0.000000000     %
          16              0   0.000000000     %   0.000000000     %
          25              0   0.000000000     %   0.000000000     %
          34              0   0.000000000     %   0.000000000     %
         115              0   0.000000000     %   0.000000000     %
         124              0   0.000000000     %   0.000000000     %
         133              0   0.000000000     %   0.000000000     %
         223              0   0.000000000     %   0.000000000     %
        1114              0   0.000000000     %   0.000000000     %
        1123              0   0.000000000     %   0.000000000     %
        1222              0   0.000000000     %   0.000000000     %
       11113              0   0.000000000     %   0.000000000     %
       11122              0   0.000000000     %   0.000000000     %
      111112              0   0.000000000     %   0.000000000     %
     1111111              3   1.000000000E+02%   8.333333253E-01%
CLASS8   ENTRIES (        357)  %-( 9.916666746E+01)
    CATEGORY           HITS     LOCAL%              GLOBAL%
           8              0   0.000000000     %   0.000000000     %
          17              0   0.000000000     %   0.000000000     %
          26              0   0.000000000     %   0.000000000     %
          35              0   0.000000000     %   0.000000000     %
          44              0   0.000000000     %   0.000000000     %
         116              0   0.000000000     %   0.000000000     %
         125              0   0.000000000     %   0.000000000     %
         134              0   0.000000000     %   0.000000000     %
         224              0   0.000000000     %   0.000000000     %
         233              0   0.000000000     %   0.000000000     %
        2222              0   0.000000000     %   0.000000000     %
        1115              0   0.000000000     %   0.000000000     %
        1124              0   0.000000000     %   0.000000000     %
        1133              0   0.000000000     %   0.000000000     %
        1223              0   0.000000000     %   0.000000000     %
       11114              0   0.000000000     %   0.000000000     %
       11123              0   0.000000000     %   0.000000000     %
       11222              0   0.000000000     %   0.000000000     %
      111113              0   0.000000000     %   0.000000000     %
      111122              1   2.801120460E-01%   2.777777791E-01%
     1111112             20   5.602240860     %   5.555555522     %
    11111111            336   9.411764740E+01%   9.333333253E+01%

    T O   D A T E


              ITRAN           PTRAN          MITRAN         MBTRAN          MATRAN
ITRAN          293               2               0              3              13              311
   8.419540166E+01% 5.747126400E-01% 0.000000000      % 8.620689630E-01% 3.735632181      %
PTRAN            1               1               0              0               2                4
   2.873563200E-01% 2.873563200E-01% 0.000000000      % 0.000000000     % 5.747126400E-01%
MITRAN           0               0               0              0               0                0
   0.000000000     % 0.000000000     % 0.000000000      % 0.000000000     % 0.000000000      %
MBTRAN           2               0               0              3               0                5
   5.747126400E-01% 0.000000000     % 0.000000000      % 8.620689630E-01% 0.000000000      %
MATRAN          14               1               0              0              13               28
   4.022988498     % 2.873563200E-01% 0.000000000      % 0.000000000     % 3.735632181      %
```

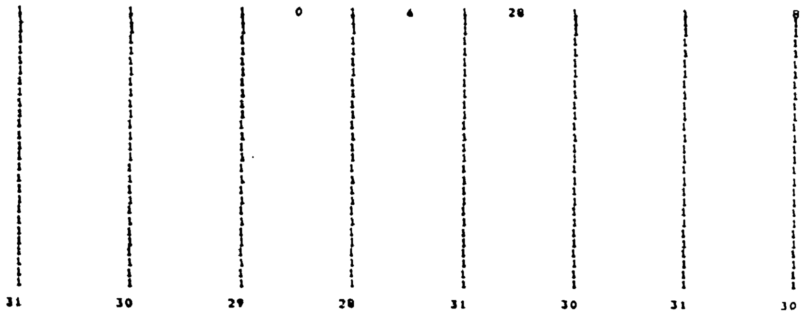


Table 1. Dispersion and density analysis.

A local density measure was obtained by developing percentages based on observations made minute by minute at each food station thirty times a session over 20 sessions per schedule. The local density percentages were based on 4800 observations per schedule for each VI schedule. In addition a frequency count of the occurrence of each possible density per station (zero through eight) was made for a total of 300 observations per session. These data were then analysed in terms of AM, PM, and daily totals for each schedule. Following this the frequency totals of each density (zero through eight) that was obtained within each session per schedule were averaged together to produce AM ,PM, and daily local density means.

The attrition levels per schedule were derived from a frequency count of the number of rats absent from any of the eight stations on a minute by minute basis for each session per schedule. Attrition occurred when less than eight rats were observed working during an observation frame. Frequency totals of missing rats were made from 4800 observations per schedule.

Temporal changes in the dispersion patterns were analysed in terms of several transitions from minute to minute (Goldstein, 1981a). An Identical Transition (ITRAN) is one in which the dispersion is unchanged from one minute to the next and it is considered herein as a statistical measure of temporal stability. In a Position Transition (PTRAN) the spatially aggregated dispersions are the same as in the previous recording while the position of aggregations has changed. For instance, there may be a dispersion where two rats are at station one and none at station two (20111111) and then in the next minute there may be no rats at station one and two at station two (02111111). This signifies that the spatial aggregations are the same but have changed position. A Microstate Transition (MITRAN) is one in which the same number of feeding stations were occupied while the number of rats at each occupied station changed from minute to minute. For example at one minute the dispersion may have included the colonization of the first four stations each with two rats (22220000). Then in the next minute the dispersion at those occupied stations changed by one rat moving from station one to four (12230000) so that the same bars were occupied but the aggregation at them changed. Type A Macrostate Transition (MATRAN) changes are those in which the number of bars colonized from one minute to the next changes, e.g., the first seven food stations are occupied (11111120) and then two rats migrate from station seven to station six (11111300) leaving two food stations open rather than one as before. Type B Macrostate Transition (MBTRANS) changes are those in which the sum total of the number of rats within the parimeter of all food stations changes from minute to minute. In this type of transition there may have been one rat at each food station (11111111) for a total of eight but then one goes into the centre of the arena from station one and is therefore excluded from the tally which would then be seven (01111111).

A frequency count of the temporal transitions observed minute by minute for each session was made. AM, PM, and daily measures were calculated from the frequency totals for each schedule. These totals were then averaged to show AM, PM, and daily transition means for the schedules.

The total number of responses made during each session was automatically recorded by computer. These session response frequency totals for each schedule were analysed in terms of AM, PM, and daily totals. Means were determined for each schedule from the AM, PM and daily response frequency totals. This procedure was repeated in analysing the reinforcement totals obtained during each session per schedule.

Two measures were made of the economy of the reinforcement and response rates in relation to VI values. Firstly, economy was viewed as a measure of work and has been described in terms of a ratio between reinforcement and responding (Goldstein, 1982; Phillipson, 1967). The cost of pellets (COP) (Goldstein, 1982) was calculated by dividing the number of reinforcements obtained by the number of bar pressing responses emitted to produce them. A second measure of economy provides a mathematical description of the amount of food obtained divided by the estimated amount of food that was available based on the schedule in effect and its duration. This latter measure, Percentage of Food Obtained (POFO) is a general description of efficiency.

RESULTS

Figure 2 and Table 2 show the obtained spatial dispersion frequencies for each VI value. The highest number of different dispersion patterns was obtained under VI5. Under VI10 there was a decrease in the number of possible dispersion patterns and the narrowest range of patterns was observed under VI20 and 40. The range again was wider under VI80. The sum of the aggregated dispersion means was highest under VI5 and decreased under VI10, 20 and 40 respectively and then increased under VI80. Generally, spatial dispersion was more regular under the mid-values VI10, 20 and 40 as opposed to the extreme values VI5 and 80 which produced more aggregated patterns.

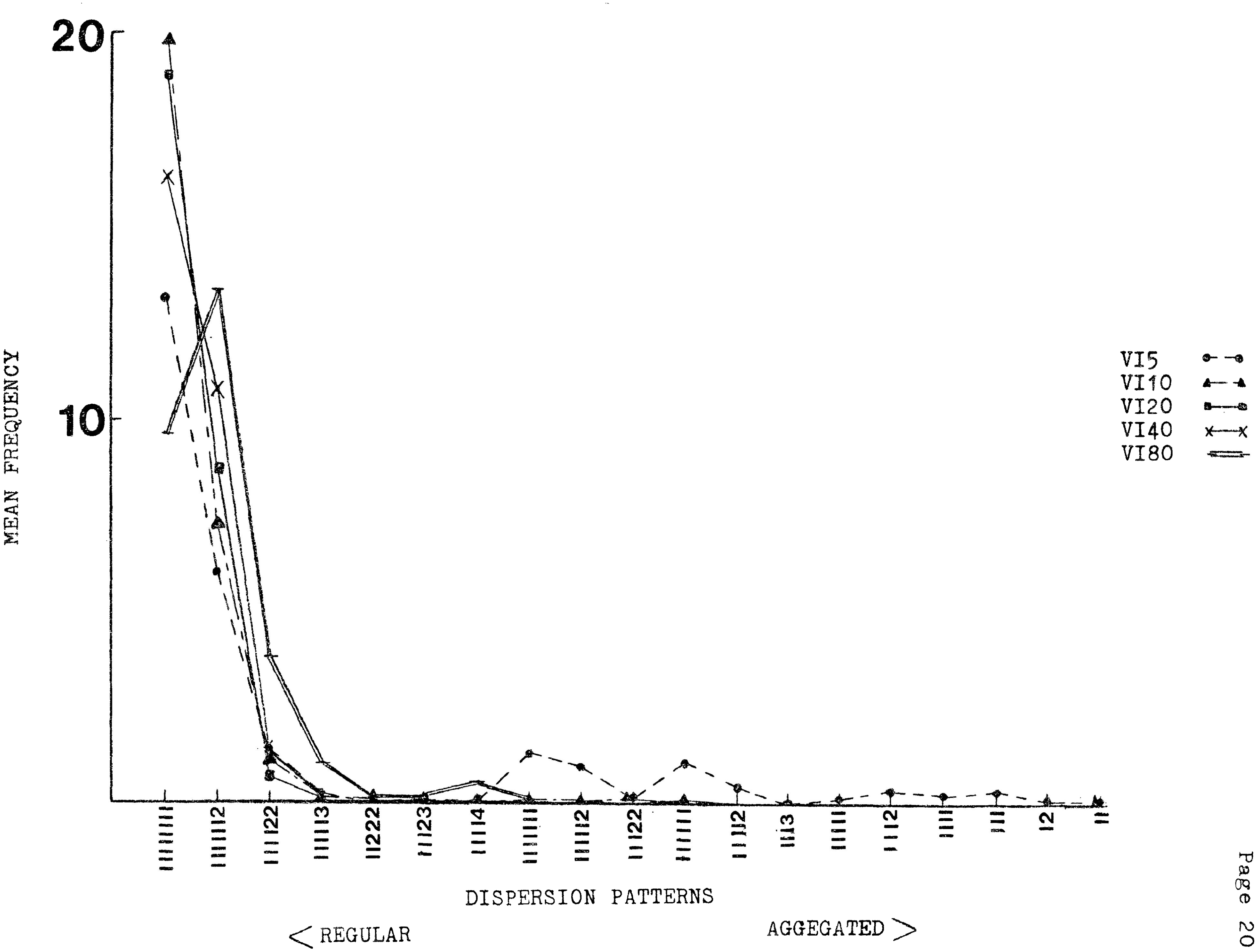


Figure 2. Mean number of occasions on which each observed spatial dispersion occurred during each VI schedule.

Table 2

Mean number of occasions on which each spatial dispersion pattern was observed during each Variable Interval schedule.

Dispersion pattern	Mean occurrences per schedule				
	VI5	VI10	VI20	VI40	VI80
11111111	13.85	20.85	19.90	17.10	10.15
11111120	9.35	7.45	9.15	11.30	14.00
11112200	1.45	1.20	0.80	1.35	4.00
11111300	0.20	0.10	0.10	0.20	0.95
11222000	— — —	0.10	0.10	— — —	0.15
11123000	0.05	— — —	0.05	0.05	0.15
11114000	0.05	— — —	— — —	— — —	— — —
11111110	1.35	0.05	— — —	— — —	0.45
11111200	0.95	0.05	— — —	— — —	0.10
11122000	0.10	— — —	— — —	— — —	— — —
11111100	1.10	0.10	— — —	— — —	— — —
11112000	0.35	0.05	— — —	— — —	— — —
11130000	0.10	— — —	— — —	— — —	— — —
11111000	0.35	— — —	— — —	— — —	— — —
11120000	0.25	— — —	— — —	— — —	— — —
11110000	0.35	— — —	— — —	— — —	— — —
11100000	0.05	— — —	— — —	— — —	— — —
12000000	0.05	— — —	— — —	— — —	— — —
11000000	0.05	0.05	— — —	— — —	— — —
Total number of dispersion patterns	18	10	6	5	8

The second method of viewing dispersion was in terms of regular spatial dispersion (11111111). Figure 3 and Table 3 depict the frequency with which each of eight rats concurrently worke at a separate food station per session. The greatest amount of regularity was seen under the mid-VI values. AM and PM means were derived from the session frequency totals (Figure 4) and showed a decrease in regularity between VI5 and 80 during the AM sessions while a U-shaped relationship was obtained over schedules VI5 to 80 in the PM sessions. Daily mean frequency totals of regular spatial dispersion were found to be low under VI5, but increased maximally under VI10. These frequency totals decreased slightly under VI20 and 40 until reaching the minimum level of regularity under VI80. Means for each session per schedule are shown in Figure 5. This created an inverted U-shaped curve of spatial regularity over ascending VI values suggesting that the most regularity occurred during the mid-VI values.

The third measure of spatial dispersion provides a description of the percent frequency of each observed density per schedule. The possible densities per station could have ranged between zero and eight but the observed range was between zero and four over all of the VI schedules. Figure 6 and Tables 4, 5, 6 and 7 show the percent frequency of each density per VI value. Zero density produced a U-shaped curve over ascending

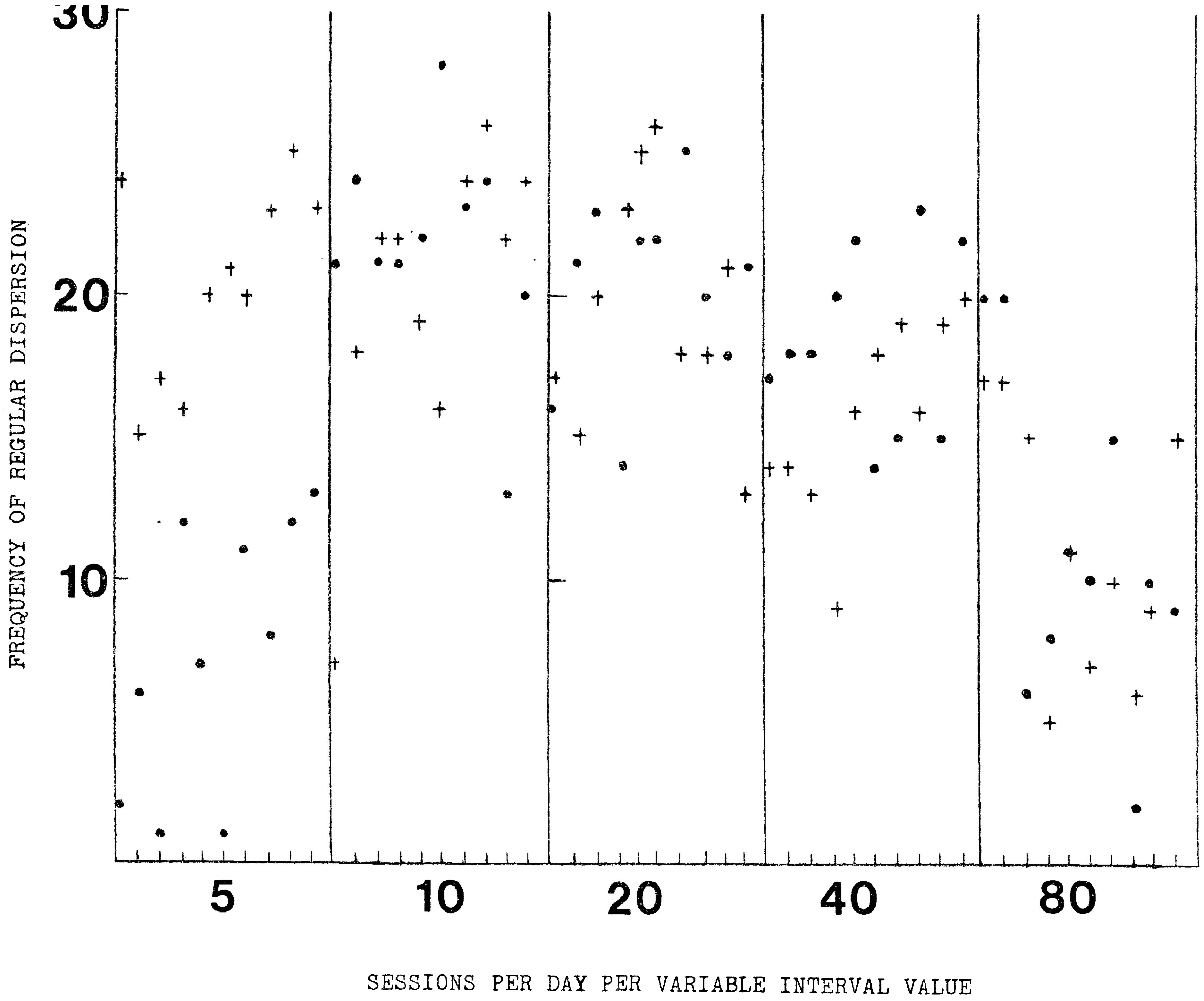


Figure 3. Total occasions on which each of eight rats concurrently worked at a separate station during each AM (+) and PM (•) session.

Table 3

Total and mean number of occasions on which each of eight rats concurrently worked at a separate food station per AM and PM session and per Variable Interval schedule.

Day	Frequency per session									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	24	2	7	21	17	16	14	17	17	10
2	15	6	18	24	15	21	14	18	17	11
3	17	1	22	21	20	23	13	18	15	6
4	16	12	22	21	23	14	9	20	5	8
5	20	7	19	22	25	22	16	22	11	11
6	21	1	16	28	26	22	18	14	7	10
7	20	11	24	23	18	25	19	15	10	15
8	23	8	26	24	18	20	16	23	6	2
9	25	12	22	13	21	18	19	15	9	10
10	23	13	24	20	13	21	20	22	15	9
AM Mean	20.40		20.00		19.60		15.80		11.20	
AM SD	3.47		5.48		4.22		3.39		4.54	
PM Mean		7.30		21.70		20.20		18.40		9.10
PM SD		4.72		3.83		3.33		3.24		3.38
Total Mean	13.85		20.85		19.90		17.10		10.15	
SD	7.84		4.68		3.71		3.49		4.04	

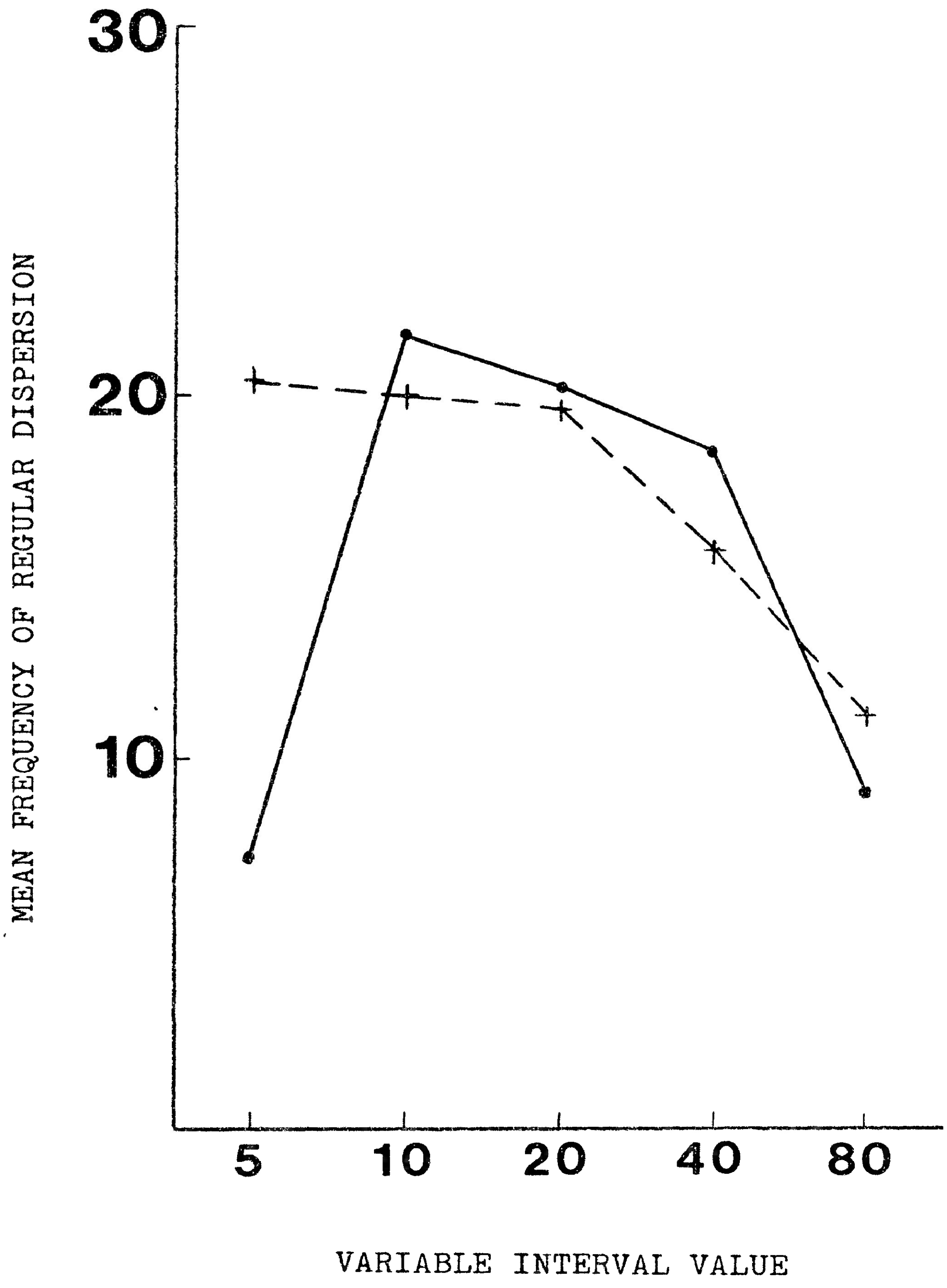


Figure 4. Mean number of occasions on which a regular spatial dispersion occurred during the AM (+) and PM (•) sessions.

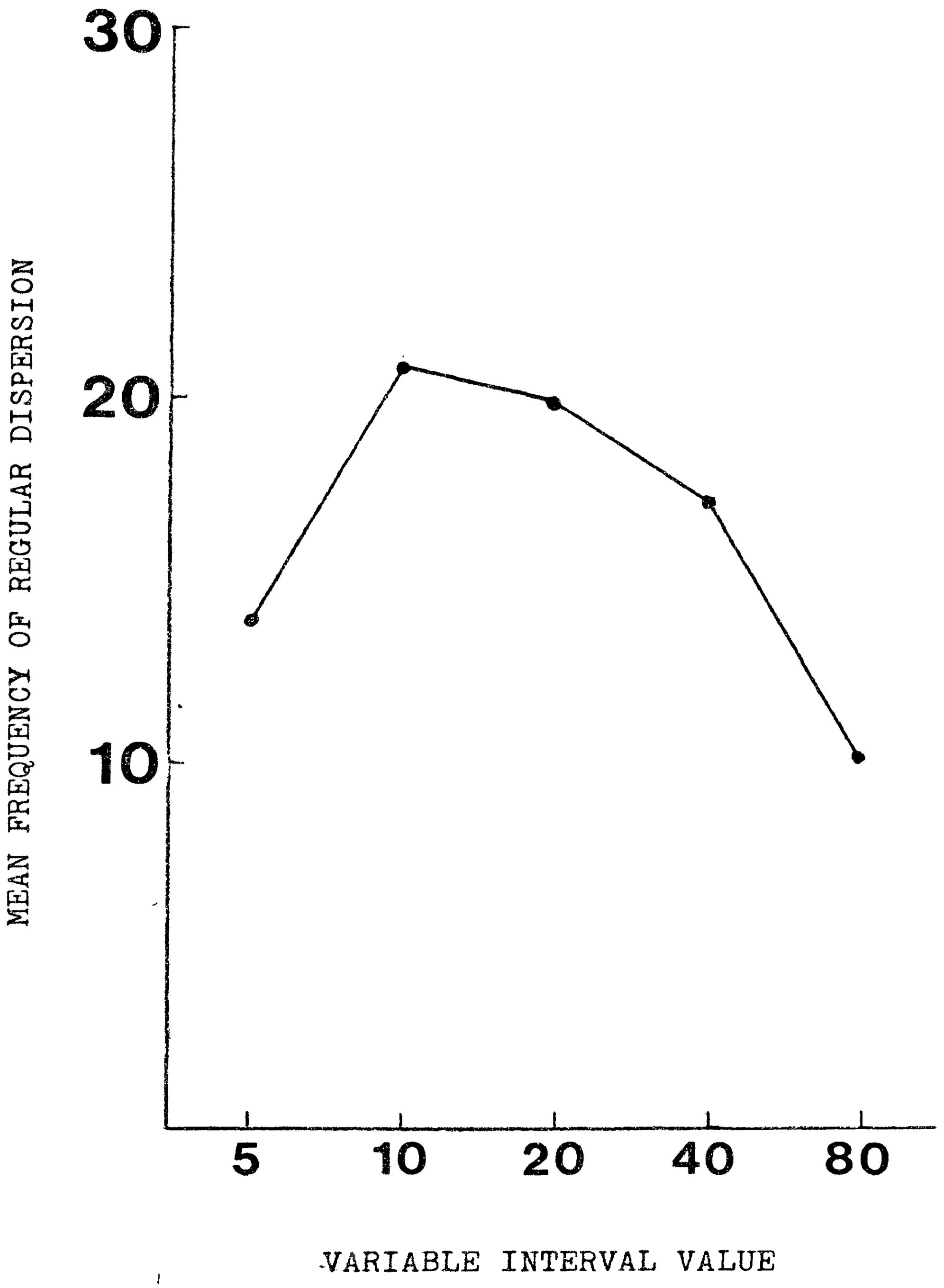


Figure 5. Mean number of occasions on which a regular spatial dispersion occurred during each VI schedule.

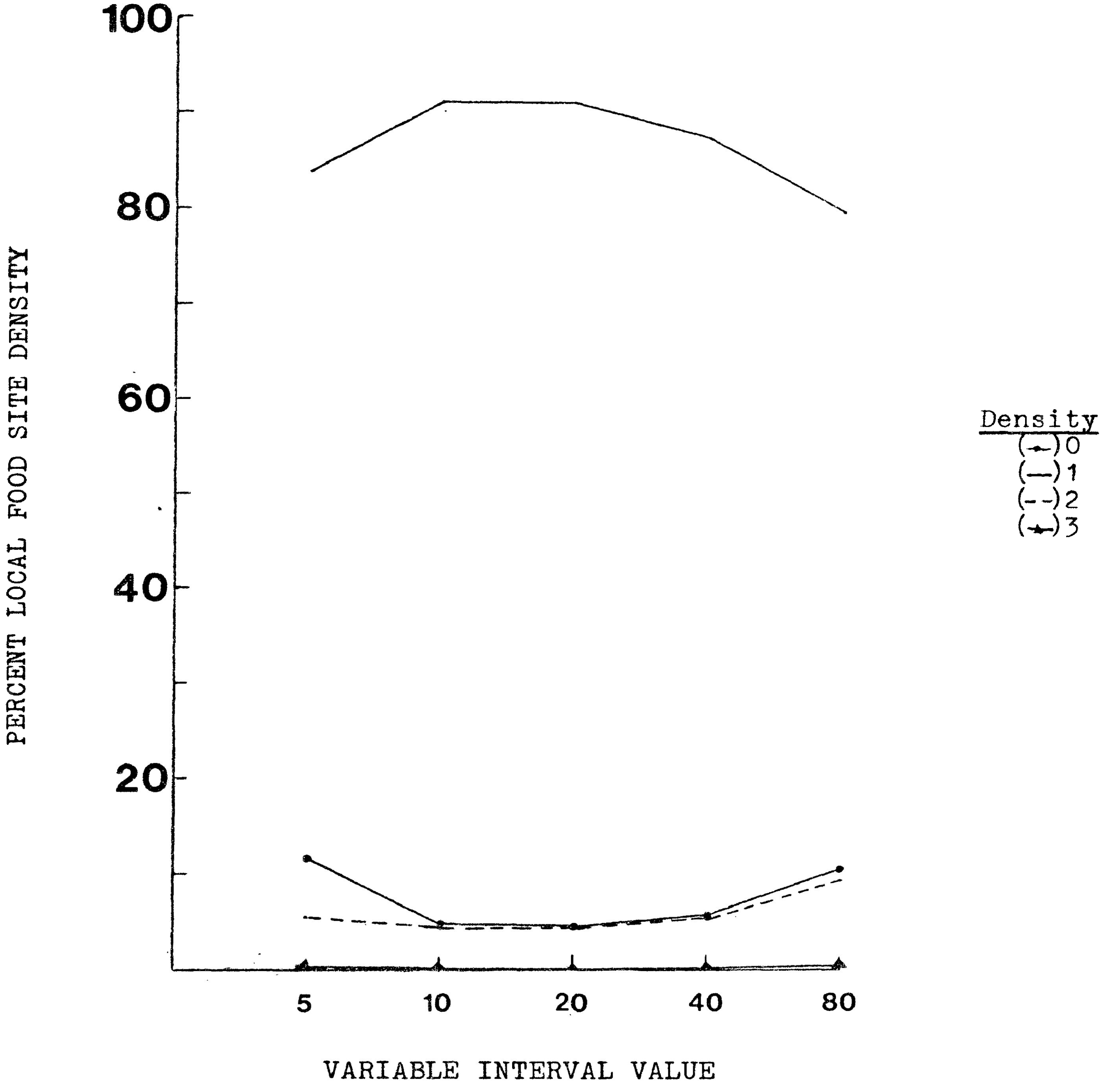


Figure 6. Mean frequency percentage of each local food site density per VI schedule.

Table 4

Total and mean number of occasions on which no rats worked at a food station per AM and PM session and per Variable Interval schedule.

Day	Frequency per session									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	7	30	30	10	15	16	18	18	14	28
2	15	28	15	6	16	11	22	14	18	25
3	14	84	8	11	12	7	19	13	20	33
4	18	23	10	10	7	17	22	10	34	28
5	10	43	12	8	7	8	15	8	22	25
6	10	38	19	2	4	8	13	16	27	27
7	11	32	6	8	12	5	13	16	23	18
8	11	41	4	6	13	11	15	7	36	40
9	7	26	8	24	10	14	16	16	28	25
10	7	33	7	19	19	10	10	9	18	24
AM Mean	11.00		11.90		11.50		16.30		24.00	
AM SD	3.0		8.0		5.0		4.0		7.0	
PM Mean	37.80		10.40		10.70		12.70		27.30	
PM SD	18.0		7.0		4.0		4.0		6.0	
Total	24.40		11.15		11.10		14.50		25.65	
Mean	18.44		7.01		4.19		4.25		6.59	
SD										

Table 5

Total and mean number of occasions on which one rat worked at a food station per AM and PM session and per Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	226	181	193	220	210	208	204	204	212	186
2	211	198	210	228	208	218	198	212	208	194
3	214	138	224	218	216	226	202	214	200	175
4	205	195	220	220	226	206	198	220	174	185
5	220	177	216	224	226	224	216	224	196	190
6	220	183	202	236	232	224	214	208	187	188
7	218	196	229	234	216	230	214	208	195	206
8	222	180	232	228	214	220	210	226	171	160
9	226	200	224	196	220	212	212	208	185	191
10	227	195	226	220	204	220	220	222	206	192
AM Mean	218.90		217.60		217.20		208.80		193.40	
AM SD	7.0		13.0		9.0		8.0		14.0	
PM Mean	184.30		221.40		218.80		214.60		186.70	
PM SD	18.0		10.0		8.0		8.0		12.0	
Total Mean	201.60		220.00		218.00		211.70		190.05	
SD	22.33		11.78		8.21		8.16		13.22	

Table 6

Total and mean number of occasions on which two rats worked at a food station per AM and PM session and per Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	7	29	26	10	15	16	18	18	14	24
2	14	24	15	6	16	11	20	14	14	21
3	12	16	8	11	12	7	19	13	20	31
4	16	22	10	10	7	17	20	10	30	26
5	10	18	12	8	7	8	13	8	22	25
6	10	18	19	2	4	8	13	16	25	23
7	11	10	5	8	12	5	13	16	21	14
8	7	19	4	6	13	9	15	7	30	40
9	7	14	8	19	10	14	12	16	26	23
10	6	12	7	11	17	10	10	9	14	24
AM Mean	10.00		11.40		11.30		15.30		21.60	
AM SD	3.0		7.0		4.0		4.0		6.0	
PM Mean		18.20		9.10		10.50		12.70		25.10
PM		6.0		5.0		4.0		4.0		7.0
Total Mean	14.10		10.25		10.90		14.00		23.35	
SD	6.20		5.76		4.04		3.92		6.56	

Table 7

Total number of occasions on which three rats worked at a food station per AM and PM session and per Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	0	0	0	0	0	0	0	0	0	2
2	0	0	0	0	0	0	1	0	2	2
3	0	2	0	0	0	0	0	0	0	1
4	1	0	0	0	0	0	1	0	2	1
5	0	1	0	0	0	0	1	0	0	0
6	0	1	0	0	0	0	0	0	1	2
7	0	2	0	0	0	0	0	0	1	2
8	0	0	0	0	0	1	0	0	3	0
9	0	0	0	1	0	0	2	0	1	1
10	0	0	0	0	1	1	0	0	2	0
AM Mean	0.10		0.00		0.10		0.50		1.20	
AM SD	0.3		0.0		0.3		0.7		1.0	
PM Mean	0.60		0.10		0.20		0.00		1.10	
PM SD	0.8		0.3		0.4		0.0		0.9	
Total Mean	0.35		0.05		0.15		0.25		1.15	
SD	0.7		0.2		0.4		0.6		0.93	

VI schedule values. Conversely, a density of One produced an inverted U-shaped curve over the ascending schedules. Again, U-shaped curves were obtained by both density measures Two and Three. A density of Four was observed only under VI5 and occurred 0.02% of the time.

A detailed analysis of the local food site density revealed relative consistency in frequency totals over sessions between schedules as seen in Figures 7, 8, 9 and 10. Mean AM and PM density measures for each schedule are shown in Figures 11, 12 and 13. A less pronounced curve was evident in the mean AM session density frequency totals than was found in the PM sessions for all the VI schedules. The mean frequency of a density of zero was low under VI5, 10 and 20 and gradually increased under VI40 and 80 respectively in the AM sessions. In the PM sessions, by contrast, the mean frequency of a density of zero was highest under VI5, then it went low under VI10, 20 and 40. It again increased under VI80. In the AM analysis, spatial density regularity (one rat per station) decreased continuously between VI5 and VI80 but during the PM sessions density regularity was greater only during the mid-VI schedules. A mean density of two was least prevalent under VI5 but became more frequent as the VI value increased in the AM sessions. In the PM sessions a mean density of two was most common under VI5, then decreased under VI10, 20 and 40. It again

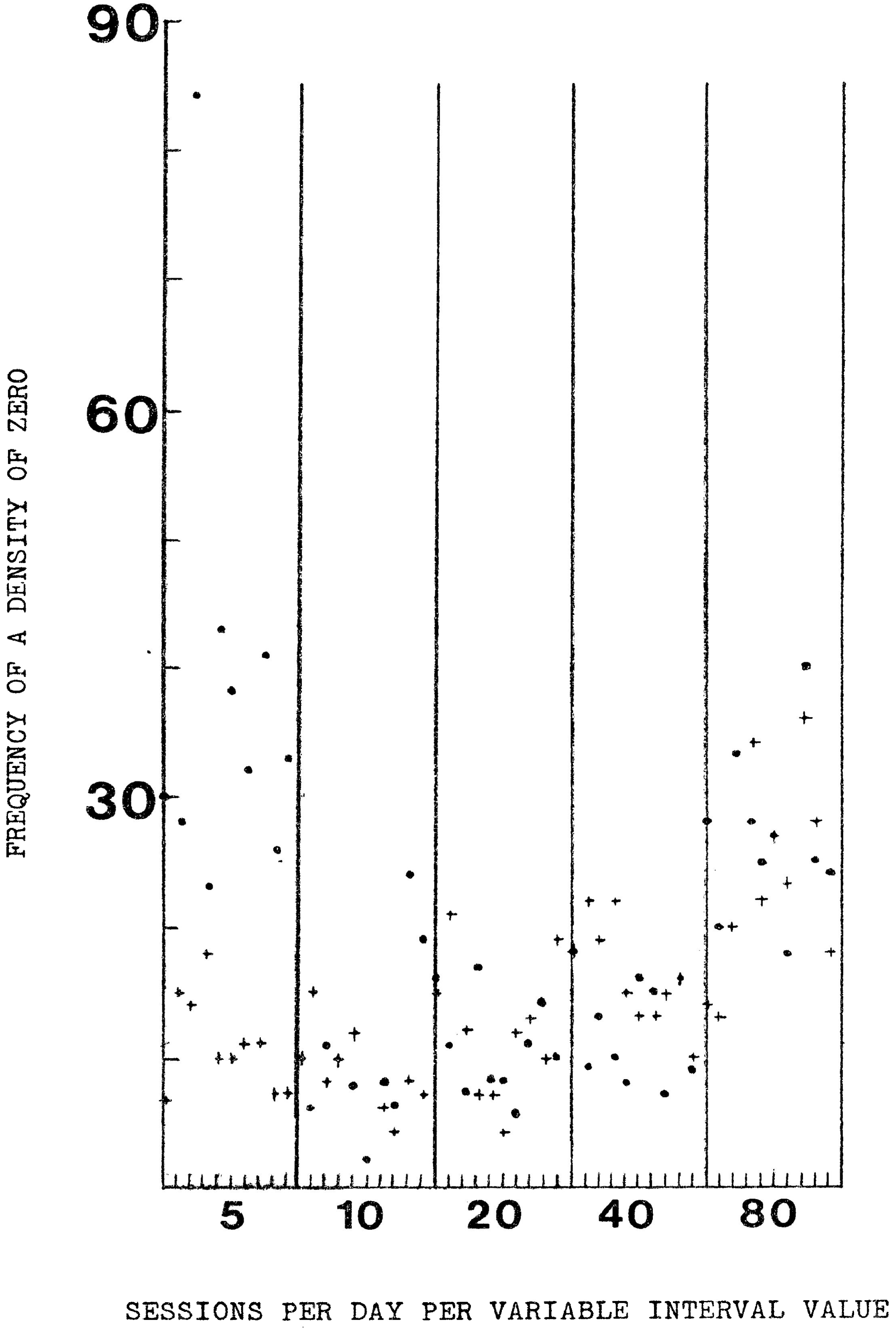


Figure 7. Total occasions on which zero density occurred during each AM (+) and PM (•) session.

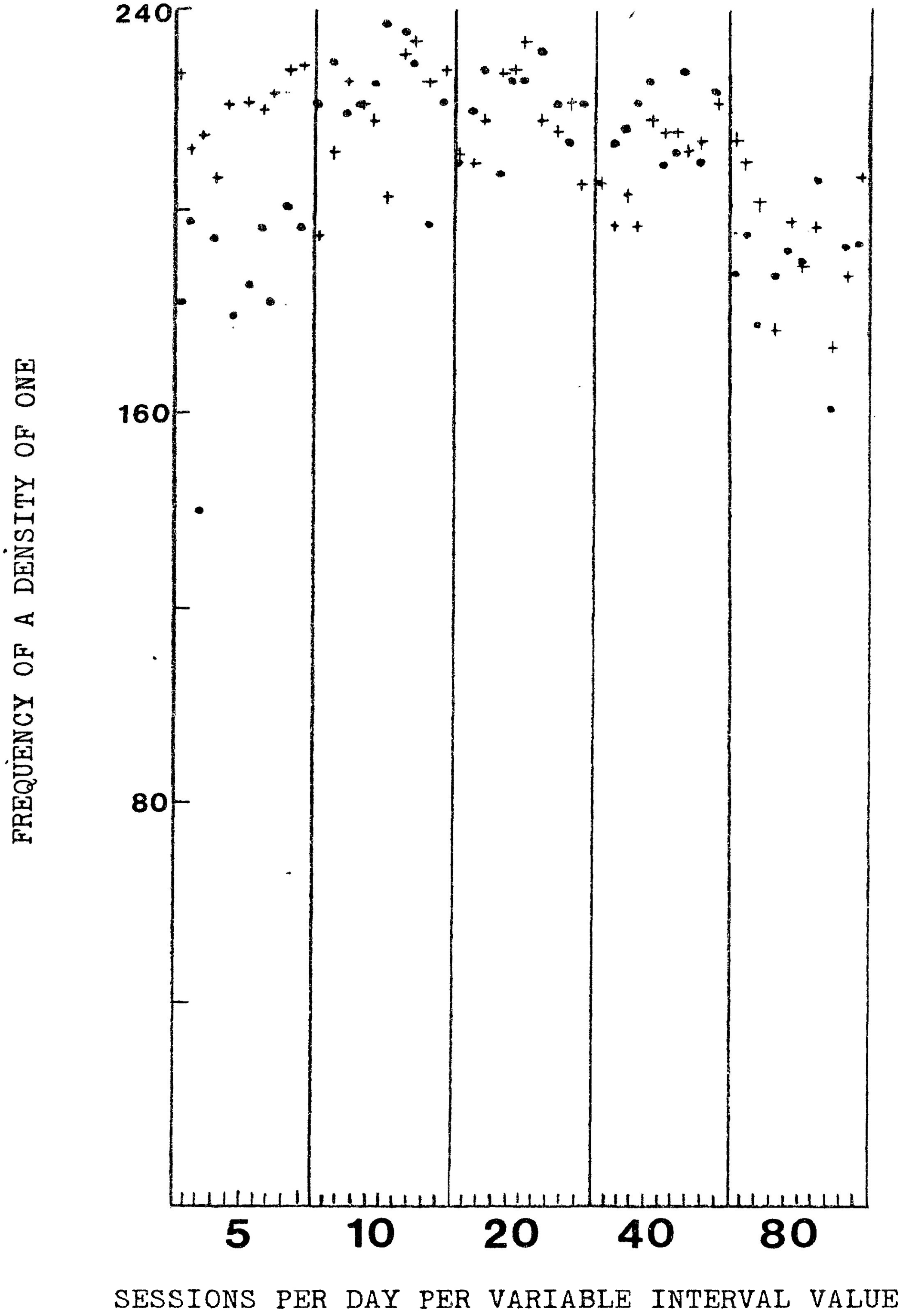
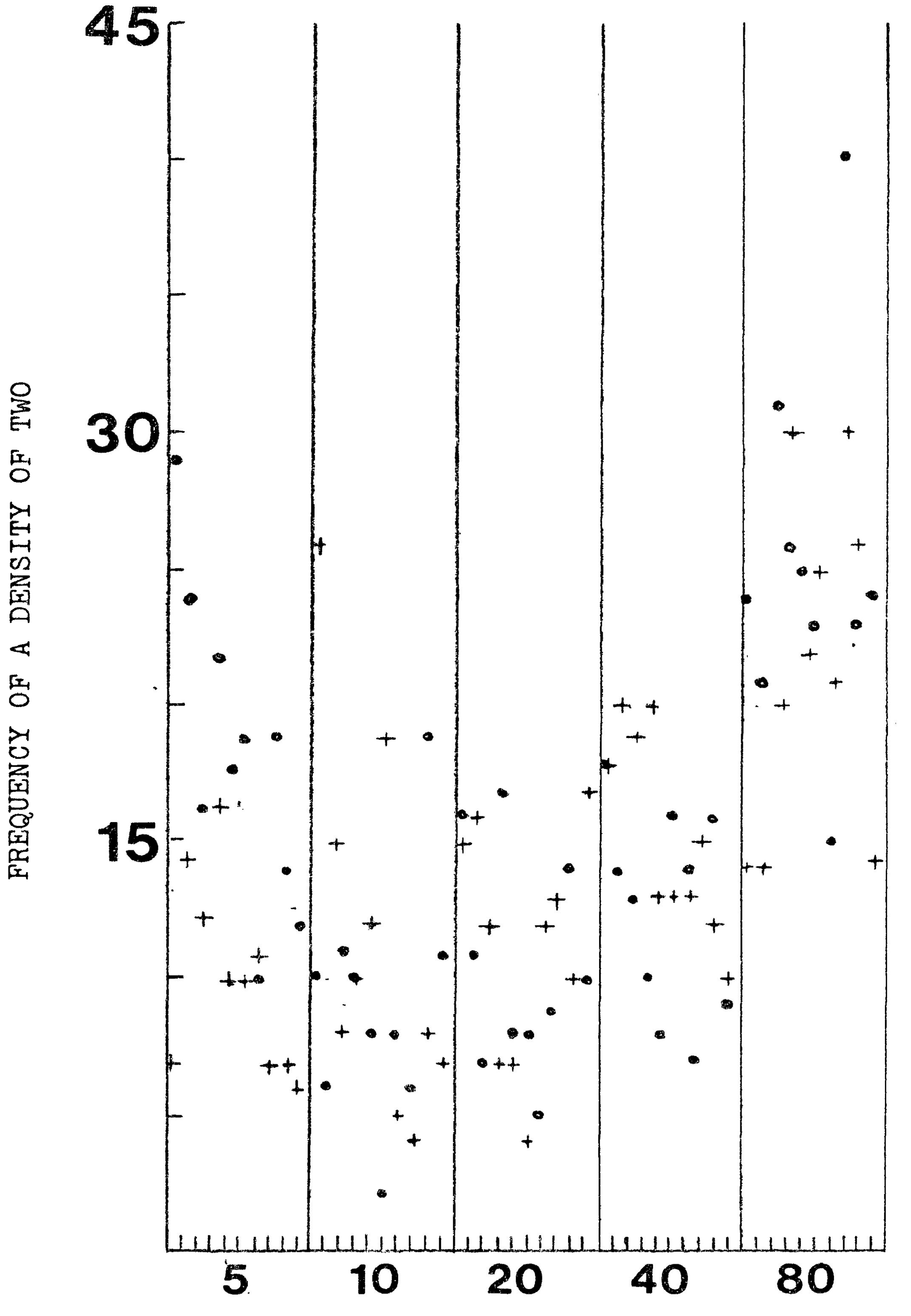


Figure 8. Total occasions on which a density of one occurred during each AM (+) and PM (•) session.



SESSIONS PER DAY PER VARIABLE INTERVAL VALUE

Figure 9. Total occasions on which a density of two occurred during each AM (+) and PM (•) session.

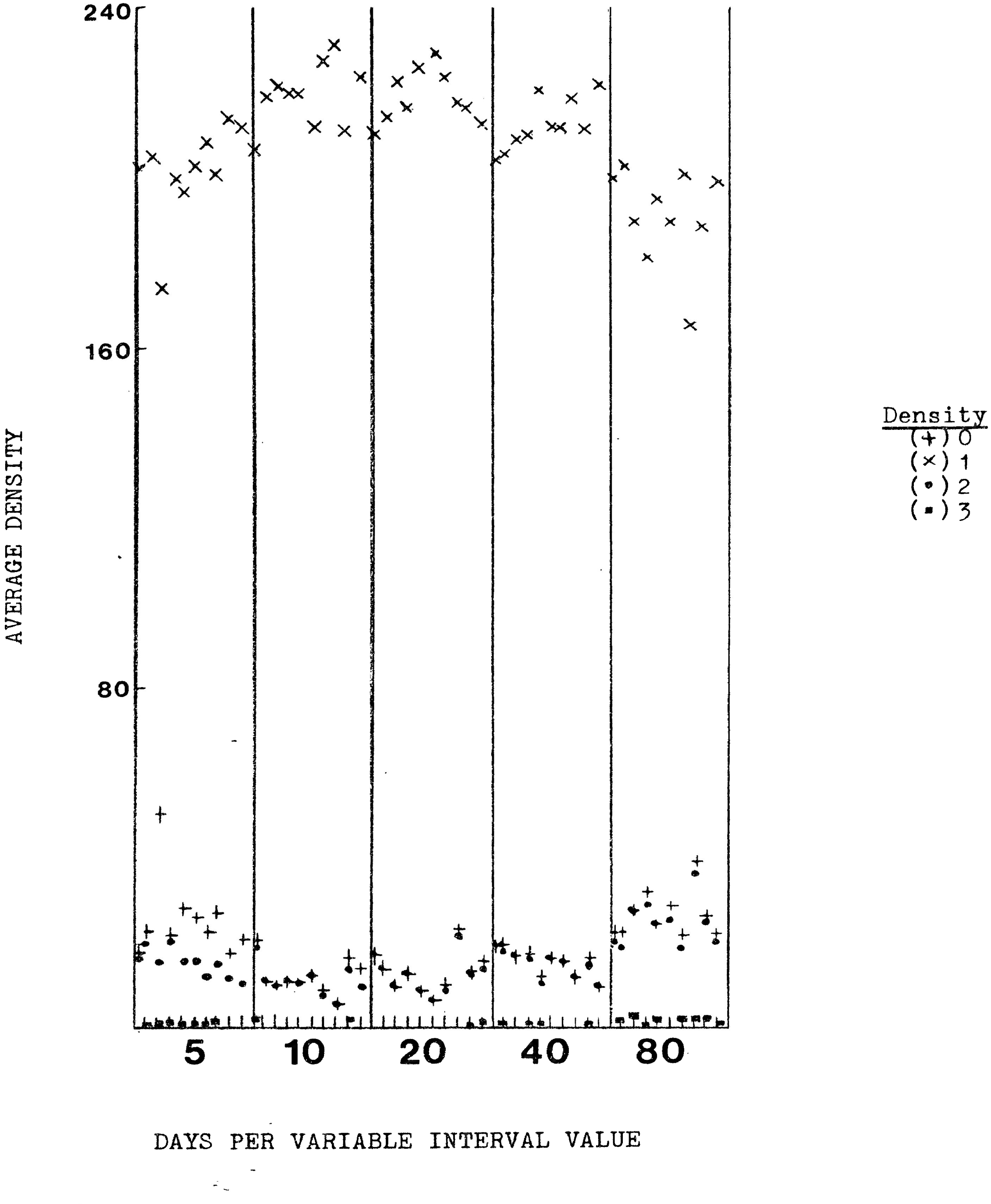


Figure 10. Average number of occasions on which each density (zero, one, two, and three) occurred each day.

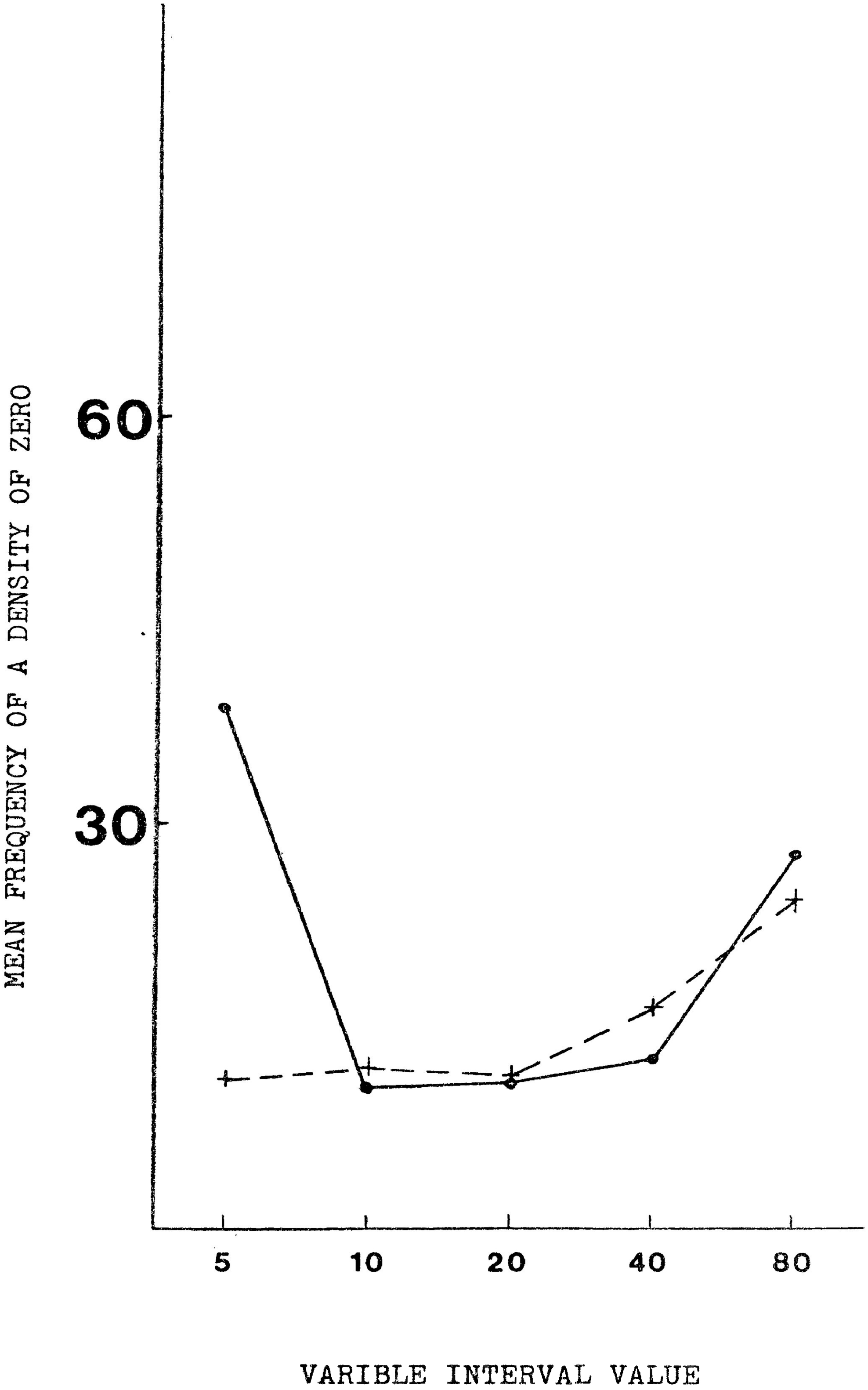


Figure 11. Mean number of occasions on which zero density occurred during the AM (+) and PM (•) sessions.

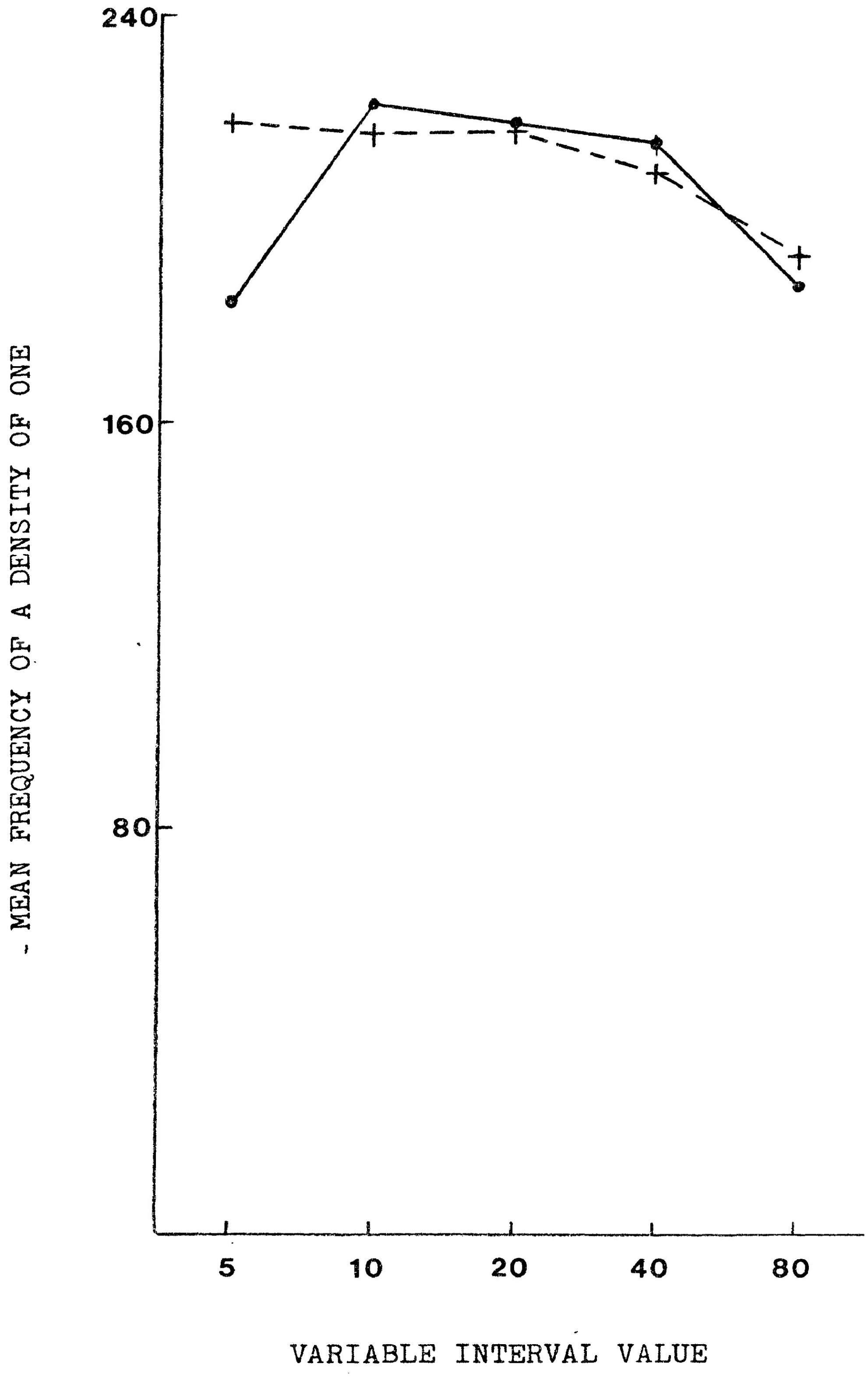


Figure 12. **Mean** number of occasions on which a density of one occurred during the AM (+) and PM (•) sessions.

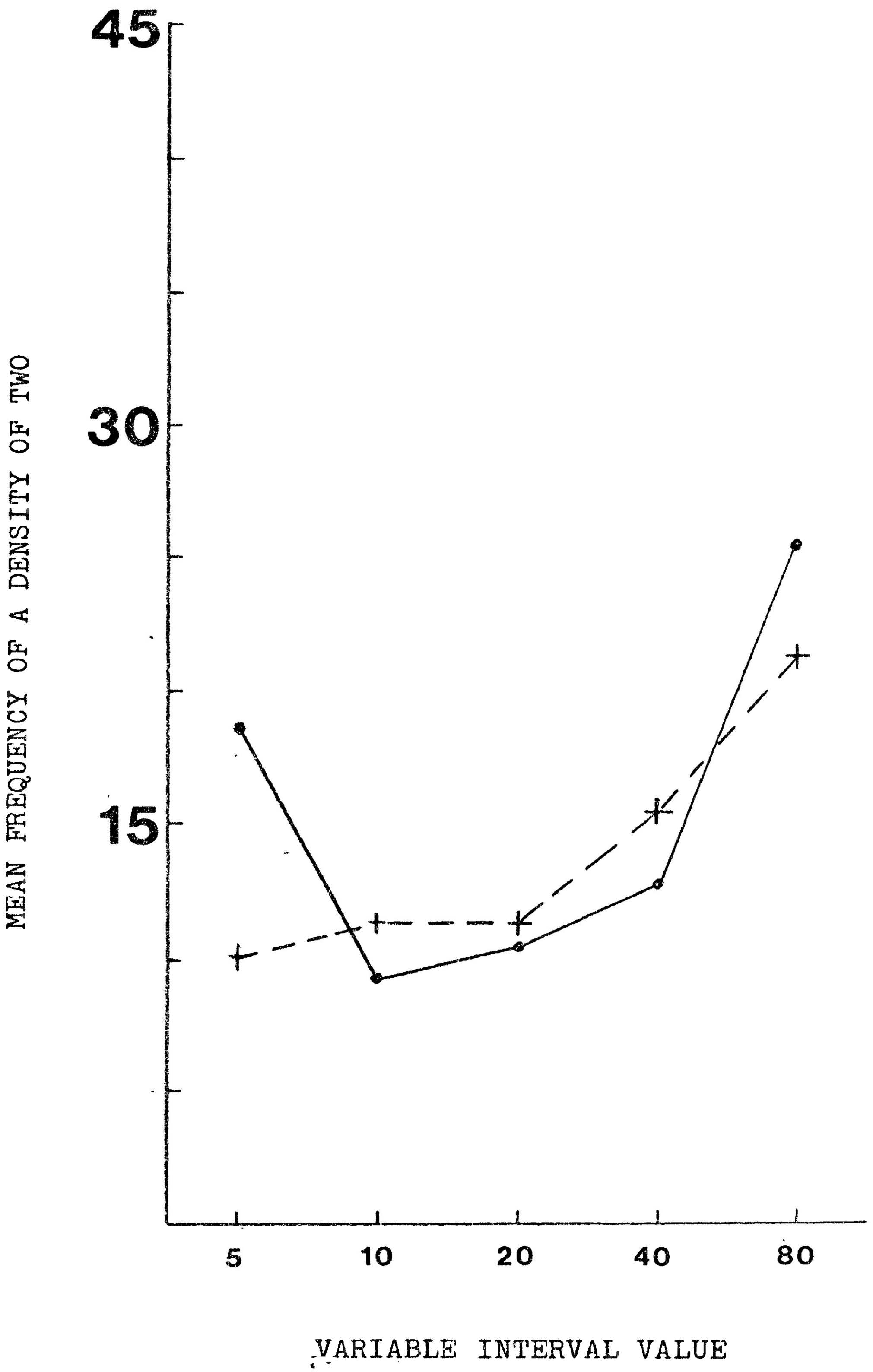


Figure 13. Mean number of occasions on which a density of two occurred during the AM (+) and PM (•) sessions.

increased under VI80. No appreciable mean AM and PM differences were found for a density of three or four. These results suggest that there are some AM and PM differences in the density totals in VI5. Figure 14 shows the mean session density frequency totals for each schedule.

A density of One was most prevalent under the mid-VI schedules 10, 20 and 40 and least prevalent under the extreme VI schedules 5 and 80. The cluster densities 0, 2, 3, and 4 were more frequent during VI5 and VI80 and less frequent during the mid-VI schedules. Generally, however, the daily totals show increased regularity in the mid-VI values and more cluster density aggregations during the extreme VI values VI5 and 80.

Figure 15 and Table 8 depict the last measure of spatial dispersion, attrition from food stations. There were more members of the colony absent from within the food station perimeters during the observation periods under VI5 than under any other schedule. Under VI10 attrition dropped dramatically. A zero level of attrition was observed under both VI20 and VI40. Attrition again increased under VI80. An attrition level of two or more was obtained only under VI5. This demonstrates that migration decreases from low to mid-VI values, levels out and then increases under a higher VI value.

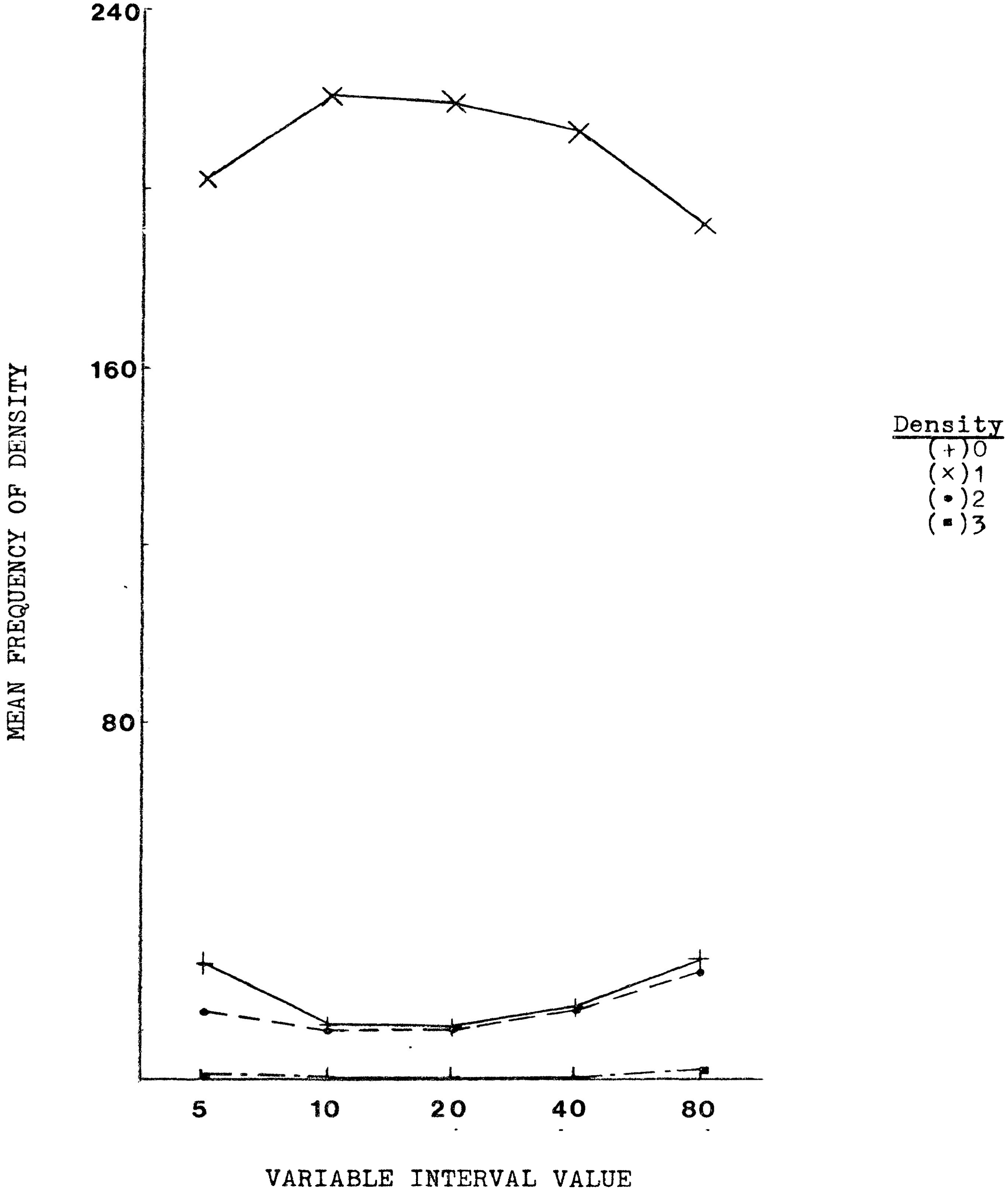


Figure 14. Mean number of occasions on which each density (zero, one, two, and three) occurred during each VI schedule.

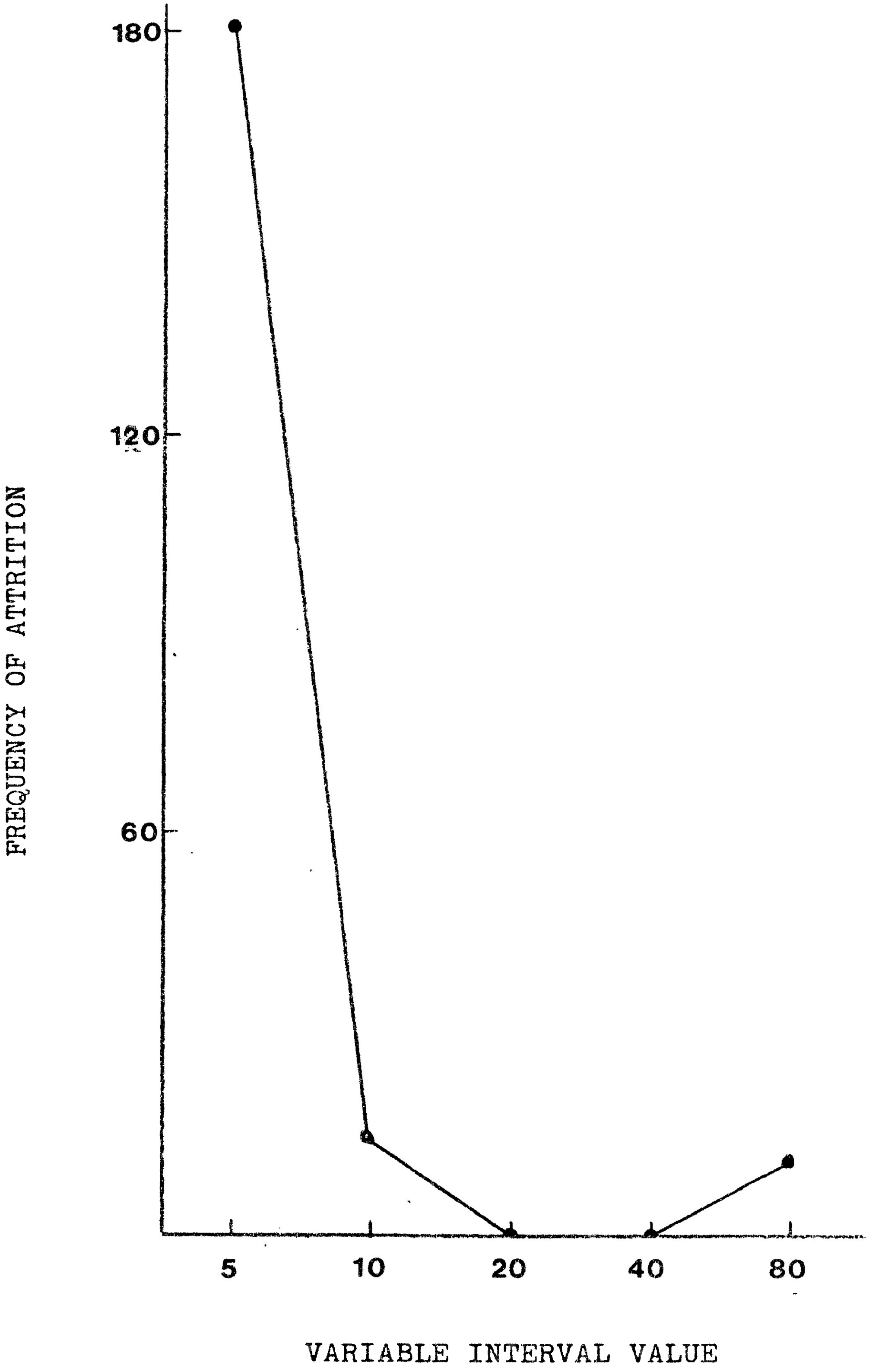


Figure 15. Total number of occasions on which a rat was not at a food station during each VI schedule.

Table 8

Total number of occasions on which there were no rats at a food station (Attrition) within each Variable Interval schedule.

Schedule	Number of absenses
VI5	181
VI10	14
VI20	0
VI40	0
VI80	11

A measure of temporal dispersion was analysed in terms of the five possible Transitions that could take place minute to minute. Figures 16, 17, 18, 19 and 20 and Tables 9, 10, 11, 12 and 13 depict in detail the AM and PM temporal changes that occurred over the five VI schedules. Figures 21, 22, 23, 24 and 25 show the average AM and PM temporal changes. The frequency of ITRANS occurring during the PM daily sessions was higher during VI10, 20 and 40 and less during VI5 and 80. During the AM session, however, there was a peak under VI5 and a steady decline in the ITRANS until VI80. The mean frequency of PTRANS occurring in the PM sessions was lowest during VI10, 20 and 40 and highest under VI5 and 80. During the AM sessions, however, there was a low level of PTRANS in VI5, 10 and 20. The number of PTRANS increased gradually to a maximum under VI80. There were no clear mean AM and PM differences in the frequency of MITRANS although a slight curvilinear U-shaped relationship was observed between the number of MITRANS and the VI value. The mean number of MATRANS in each VI schedule showed a proportional relationship over ascending VI values. The mean frequency of MBTRANS occurring in each VI schedule shows a curvilinear U-shaped relationship. The PM sessions display greater curvature than the AM sessions in the number of MBTRANS over ascending VI schedules.

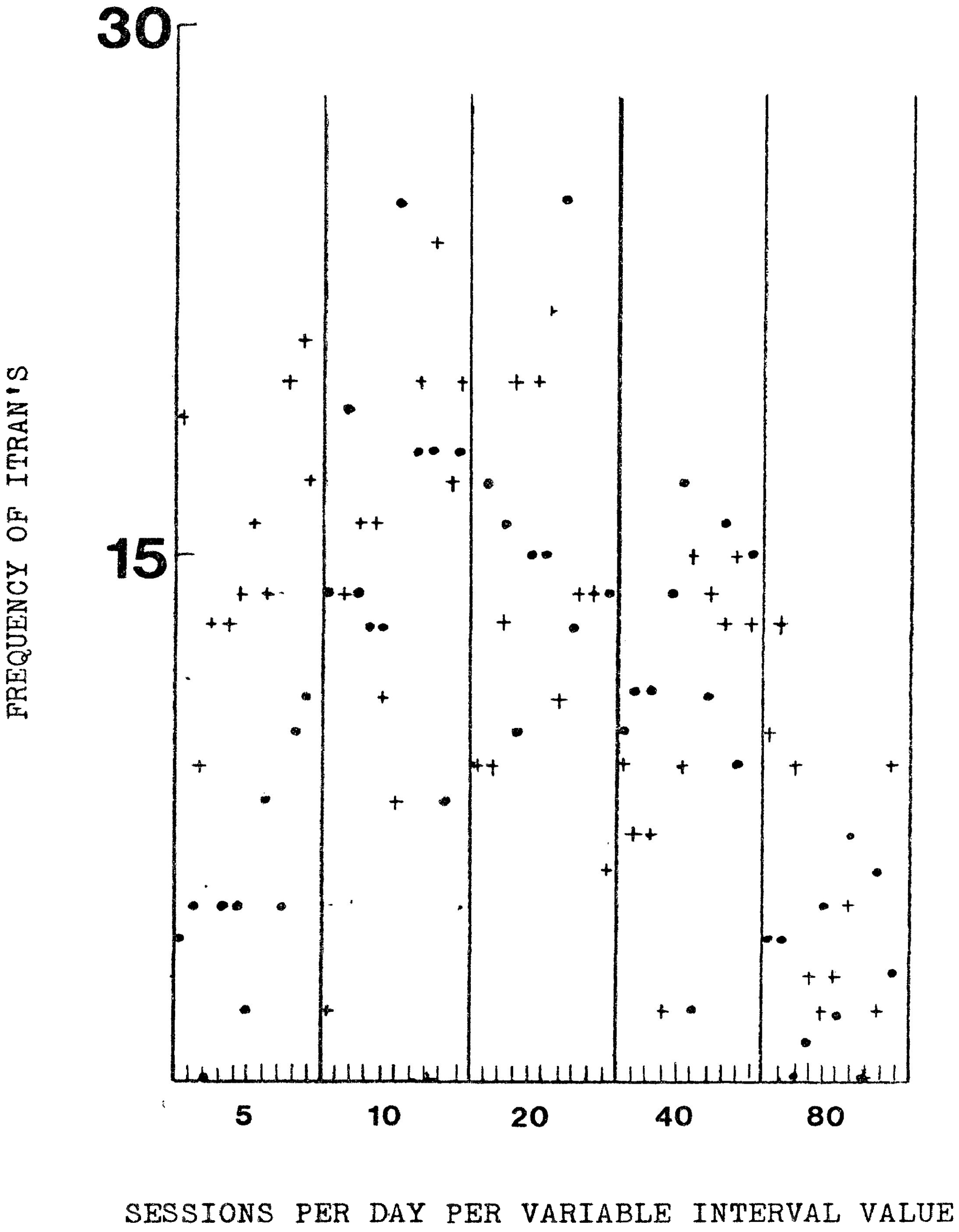


Figure 16. Total number of occasions on which an ITRAN dispersion change was observed during each AM (+) and PM (•) session.

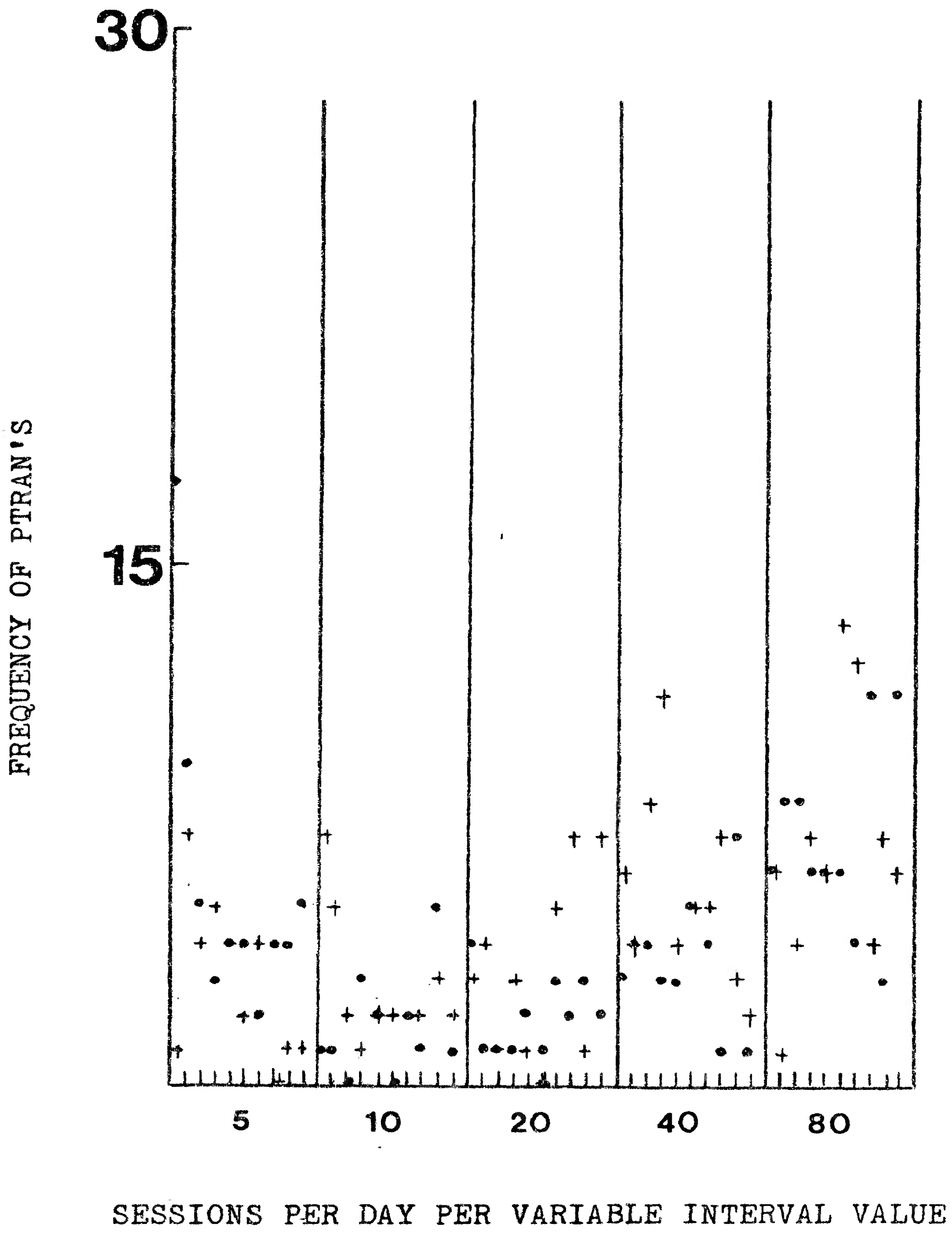


Figure 17. Total number of occasions on which a PTRAN dispersion change was observed during each AM (+) and PM (•) session.

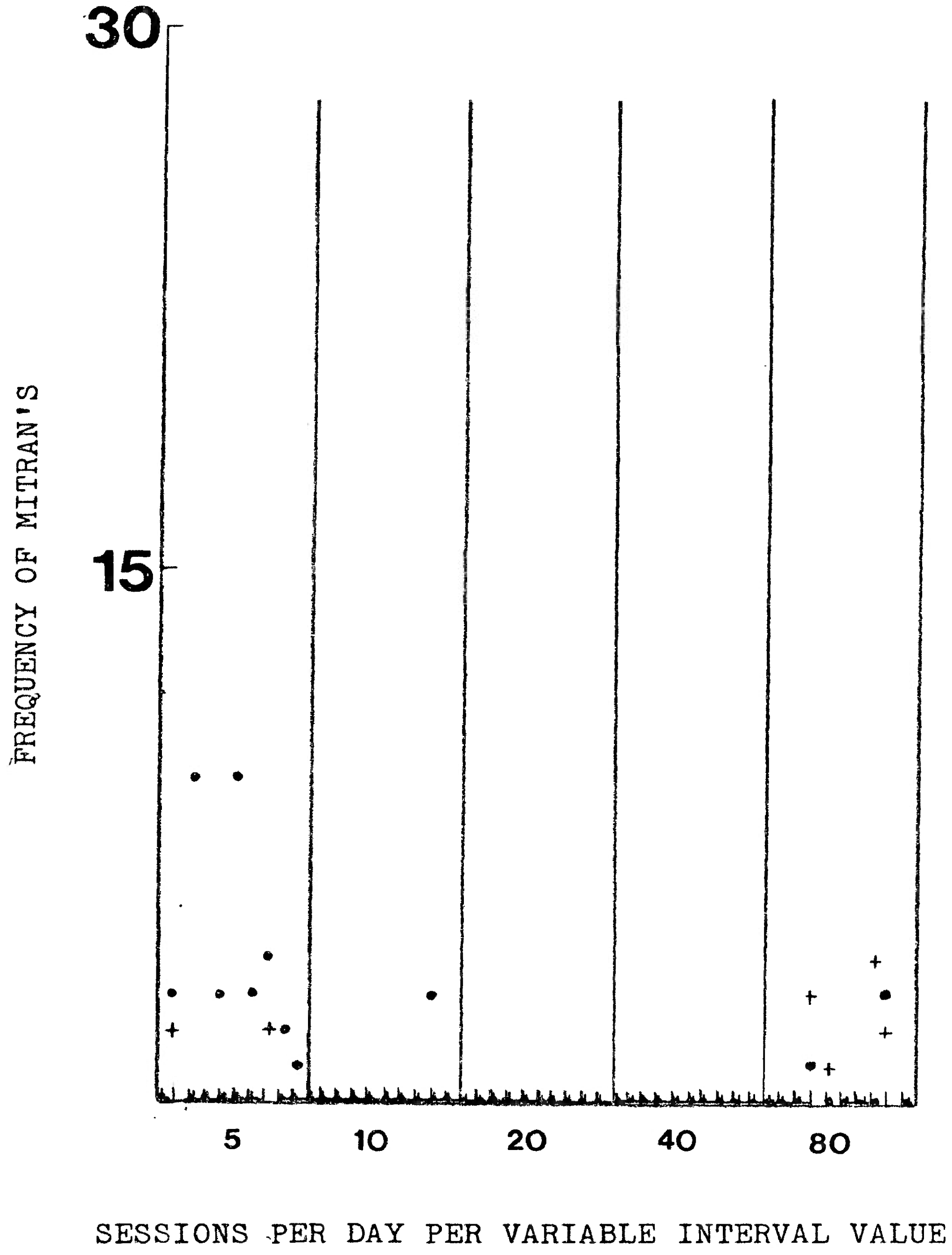


Figure 18. Total number of occasions on which a MITRAN dispersion change was observed during each AM (+) and PM (•) session.

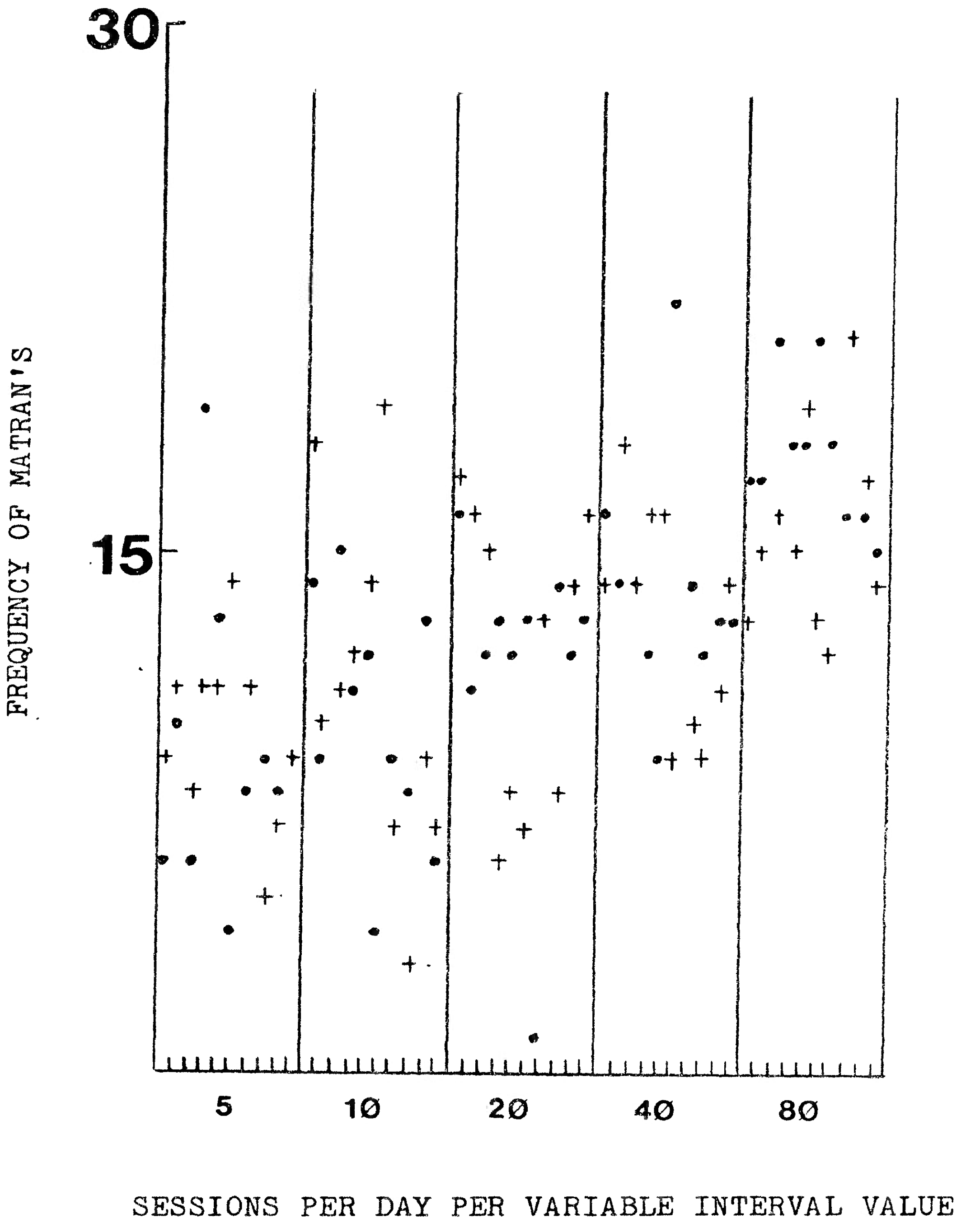


Figure 19. Total number of occasions on which a MATRAN dispersion change was observed during each AM (+) and PM (•) session.

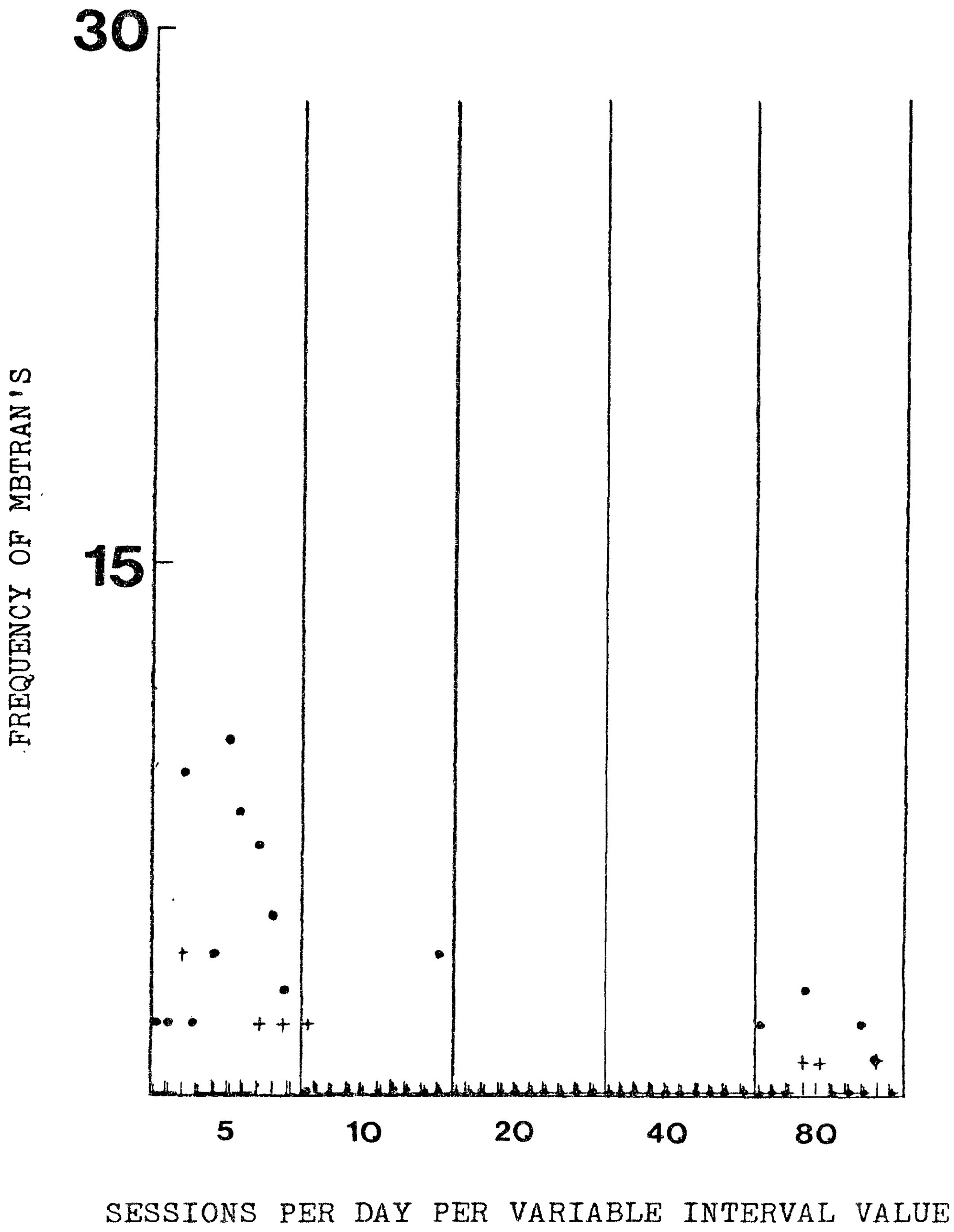


Figure 20. Total number of occasions on which a MBTRAN dispersion change was observed during each AM (+) and PM (•) session.

Table 9

Total and mean number of occasions on which an ITRAN dispersion change had taken place during each AM and PM session and each Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	19	4	2	14	9	9	9	10	10	4
2	9	5	14	19	9	17	7	11	13	4
3	13	0	16	14	13	16	7	11	9	0
4	13	5	16	15	20	10	2	14	3	1
5	14	5	13	15	20	15	9	17	2	5
6	16	2	8	25	22	15	15	2	3	2
7	14	8	20	18	11	25	14	11	5	7
8	20	5	24	18	14	13	13	16	0	0
9	21	10	17	8	14	14	15	9	2	6
10	17	11	20	18	6	14	13	15	9	3
AM Mean	15.60		15.00		13.80		10.40		5.60	
AM SD	3.72		6.33		5.37		4.30		4.33	
PM Mean		5.50		16.40		14.80		11.60		3.20
PM SD		3.38		4.40		4.37		4.33		2.40
Total Mean	10.55		15.70		14.30		11.00		4.40	
SD	6.22		5.35		4.79		4.24		3.60	

Table 10

Total and mean number of occasions on which a PTRAN dispersion change had taken place during each AM and PM session and each Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	1	17	7	1	3	4	6	3	6	6
2	7	9	5	1	4	1	4	4	1	8
3	4	5	2	0	1	1	8	4	4	8
4	5	3	1	3	3	6	11	3	7	6
5	4	4	2	2	1	2	4	3	6	6
6	1	4	2	0	0	1	5	5	13	6
7	4	2	2	2	5	3	5	4	12	4
8	0	4	2	1	7	2	7	1	4	11
9	1	4	3	5	1	3	3	7	7	3
10	1	5	2	1	7	2	2	1	6	11
AM Mean	2.80		2.80		3.20		5.50		6.60	
AM SD	2.30		1.81		2.53		2.60		3.60	
PM Mean	5.70		1.60		2.50		3.50		6.90	
PM SD	4.37		1.51		1.58		1.78		2.60	
Total Mean	4.25		2.20		2.85		4.50		6.75	
SD	3.70		1.74		2.08		2.42		3.08	

Table 11

Total and mean number of occasions on which a MITRAN dispersion change had taken place during each AM and PM session and each Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	0	0	0	0	0	0	0	0	0	0
2	2	3	0	0	0	0	0	0	0	0
3	0	9	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	3	1
5	0	3	0	0	0	0	0	0	1	0
6	0	9	0	0	0	0	0	0	0	0
7	0	3	0	0	0	0	0	0	0	0
8	2	4	0	0	0	0	0	0	4	0
9	0	2	0	3	0	0	0	0	2	3
10	0	1	0	0	0	0	0	0	0	0
AM Mean	0.40		0.00		0.00		0.00		1.00	
AM SD	0.84		0.00		0.00		0.00		1.49	
PM Mean	3.40		0.30		0.00		0.00		0.80	
PM SD	3.24		0.95		0.00		0.00		1.32	
Total Mean	1.90		0.15		0.00		0.00		0.90	
SD	2.80		0.67		0.00		0.00		1.37	

Table 12

Total and mean number of occasions on which a MATRAN dispersion change had taken place during each AM and PM session and each Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	9	6	18	14	17	16	14	16	13	17
2	11	10	10	9	16	11	18	14	15	17
3	8	6	11	15	15	12	14	14	16	21
4	11	19	12	11	6	13	16	12	15	18
5	11	13	14	12	8	12	16	9	19	18
6	12	4	19	4	7	13	9	22	13	21
7	11	8	7	9	13	1	10	14	12	18
8	5	9	3	8	8	14	9	12	21	16
9	7	8	9	13	14	12	11	13	17	16
10	9	9	7	6	16	13	14	13	14	15
AM Mean	9.40		11.00		12.00		13.10		15.50	
AM SD	2.22		4.99		4.27		3.18		2.84	
PM Mean	9.20		10.10		11.70		13.90		17.70	
PM SD	4.24		3.50		4.00		3.38		2.00	
Total										
Mean	9.30		10.55		11.85		13.50		16.60	
SD	3.29		4.24		4.30		3.22		2.64	

Table 13

Total and mean number of occasions on which a MBTRAN dispersion change had taken place during each AM and PM session and each Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	0	2	2	0	0	0	0	0	0	2
2	0	2	0	0	0	0	0	0	0	0
3	2	9	0	0	0	0	0	0	0	0
4	0	2	0	0	0	0	0	0	1	3
5	0	4	0	0	0	0	0	0	1	0
6	0	10	0	0	0	0	0	0	0	0
7	0	8	0	0	0	0	0	0	0	0
8	4	7	0	2	0	0	0	0	0	2
9	0	5	0	0	0	0	0	0	1	1
10	0	3	0	4	0	0	0	0	0	0
AM Mean	0.80		0.20		0.00		0.00		0.30	
AM SD	1.40		0.63		0.00		0.00		0.48	
PM Mean	5.20		0.60		0.00		0.00		0.80	
PM SD	3.08		1.35		0.00		0.00		1.14	
Total Mean	3.00		0.40		0.00		0.00		0.55	
SD	3.24		1.05		0.00		0.00		0.89	

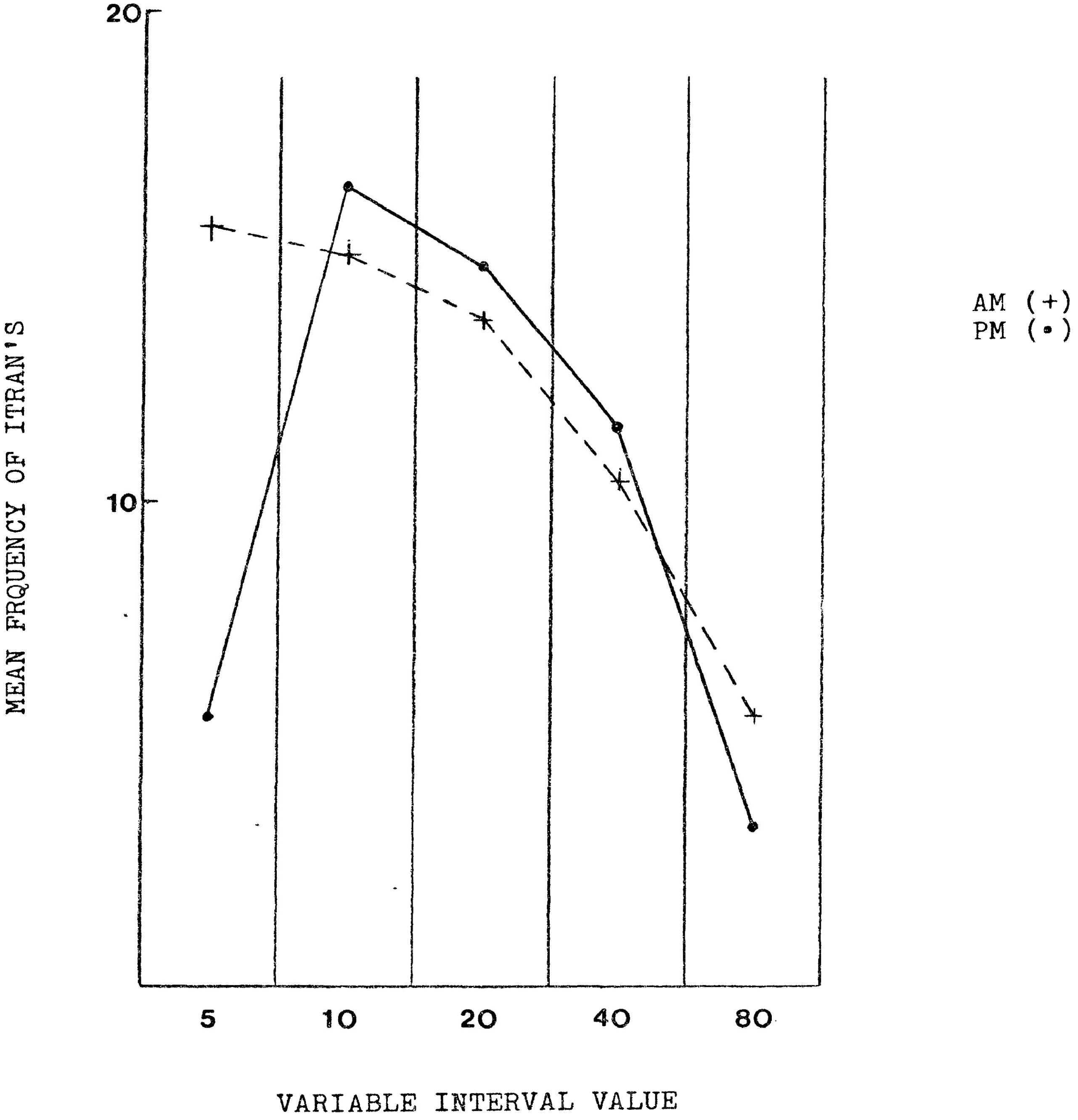


Figure 21. Mean number of occasions on which an ITRAN dispersion change occurred during each VI schedule.

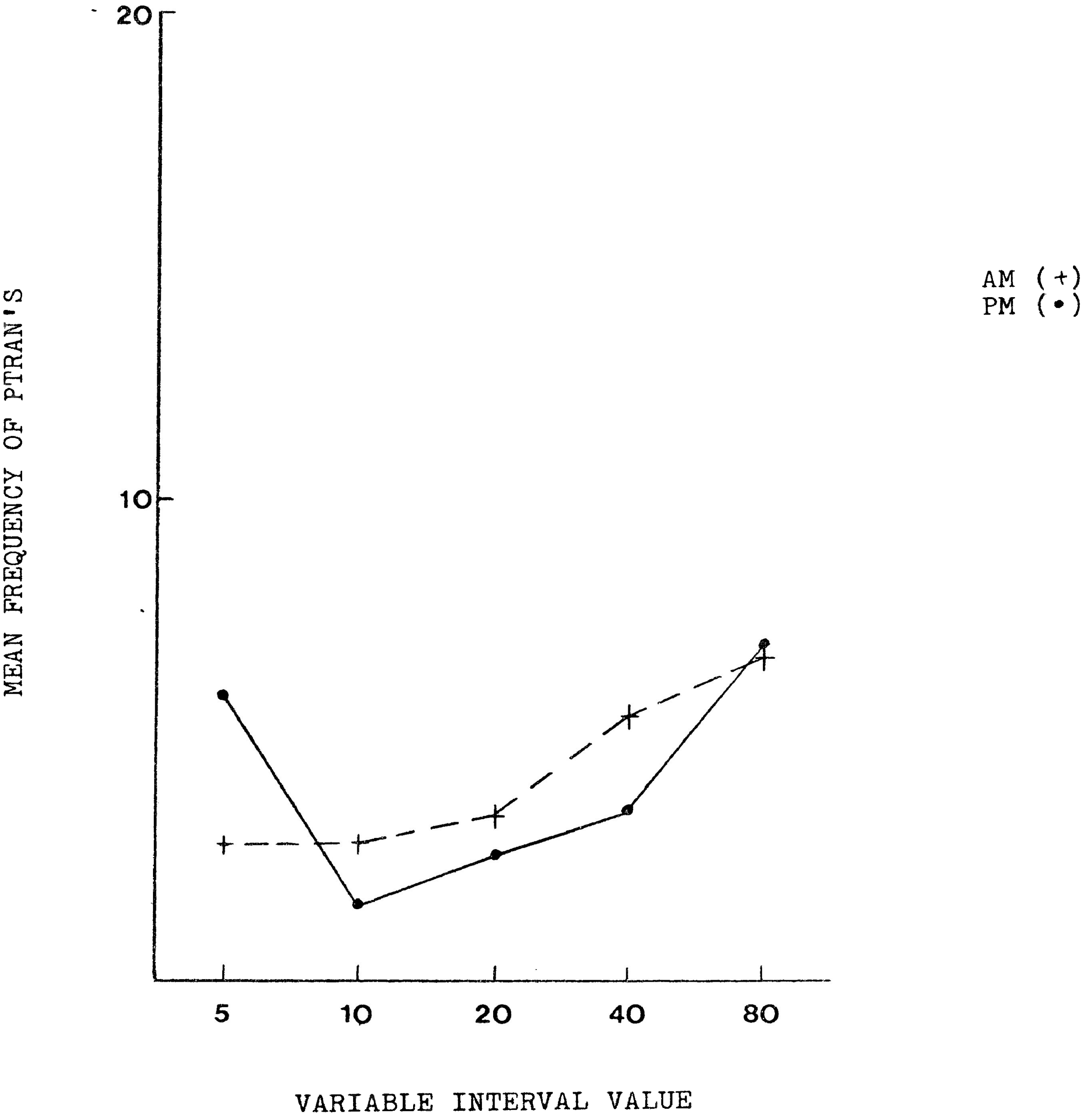


Figure 22. Mean number of occasions on which a PTRAN dispersion change occurred during each VI schedule.

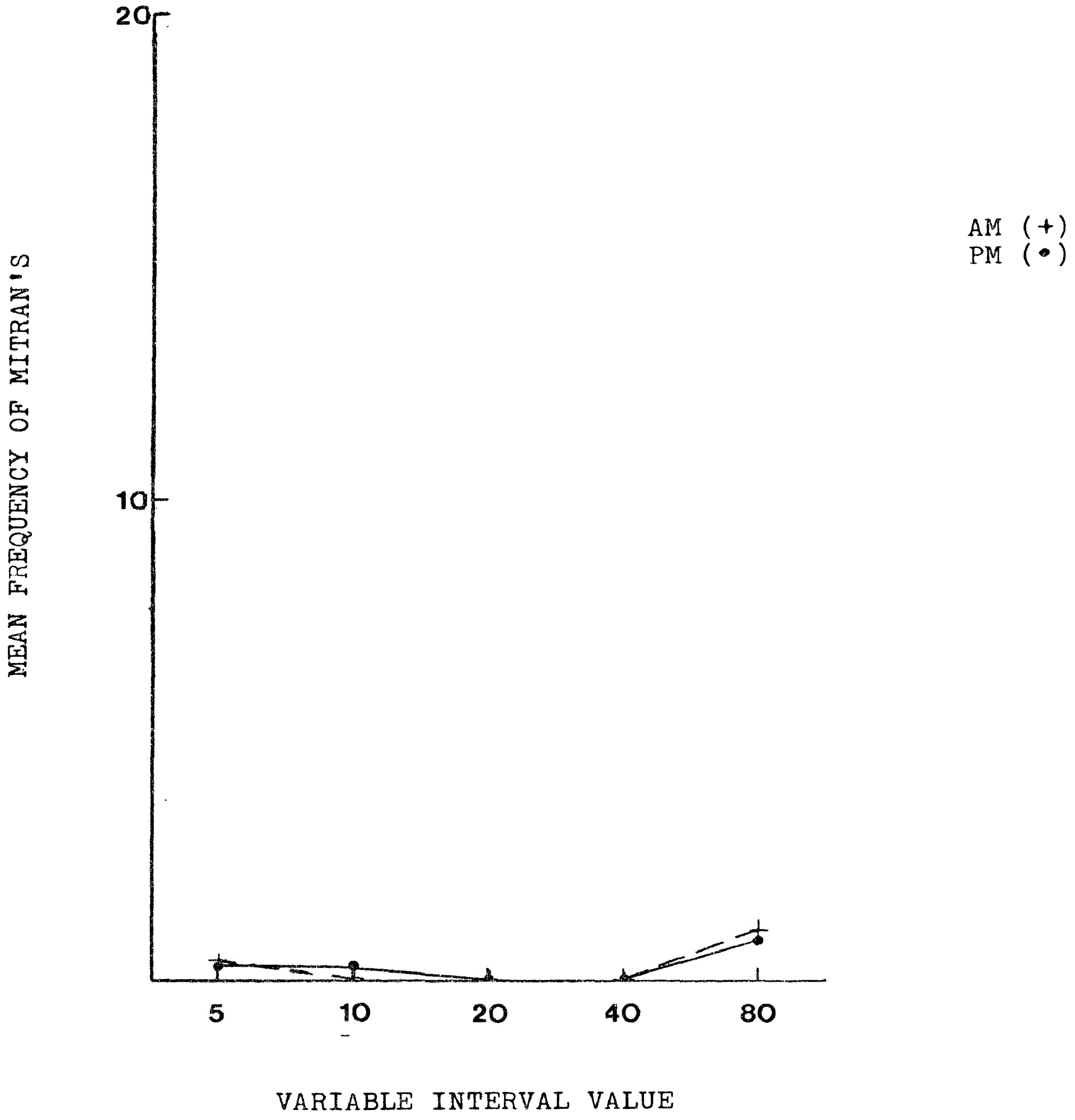


Figure 23. Mean number of occasions on which a MITRAN dispersion change occurred during each VI schedule.

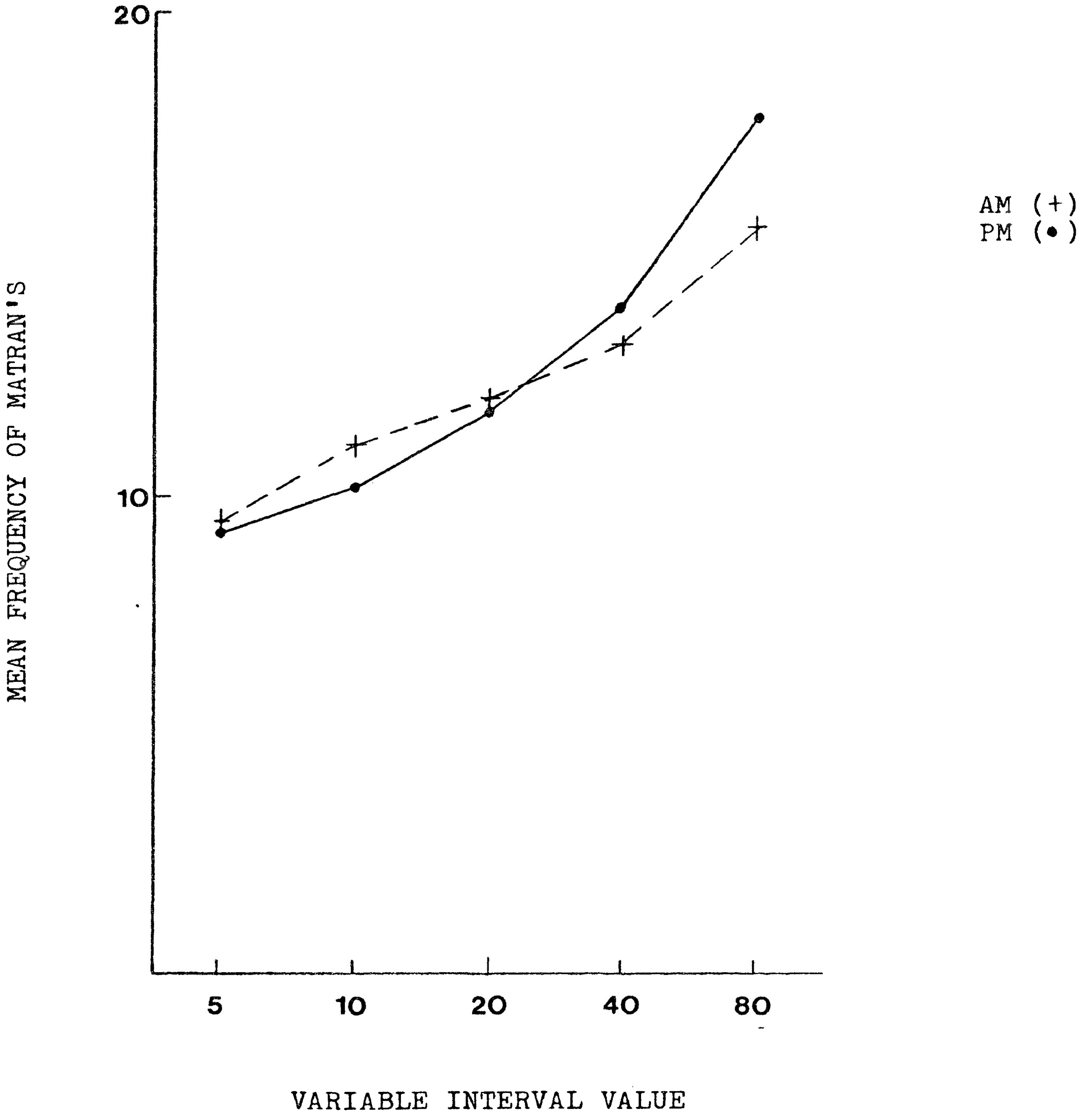


Figure 24. Mean number of occasions on which a MATRAN dispersion change occurred during each VI schedule.

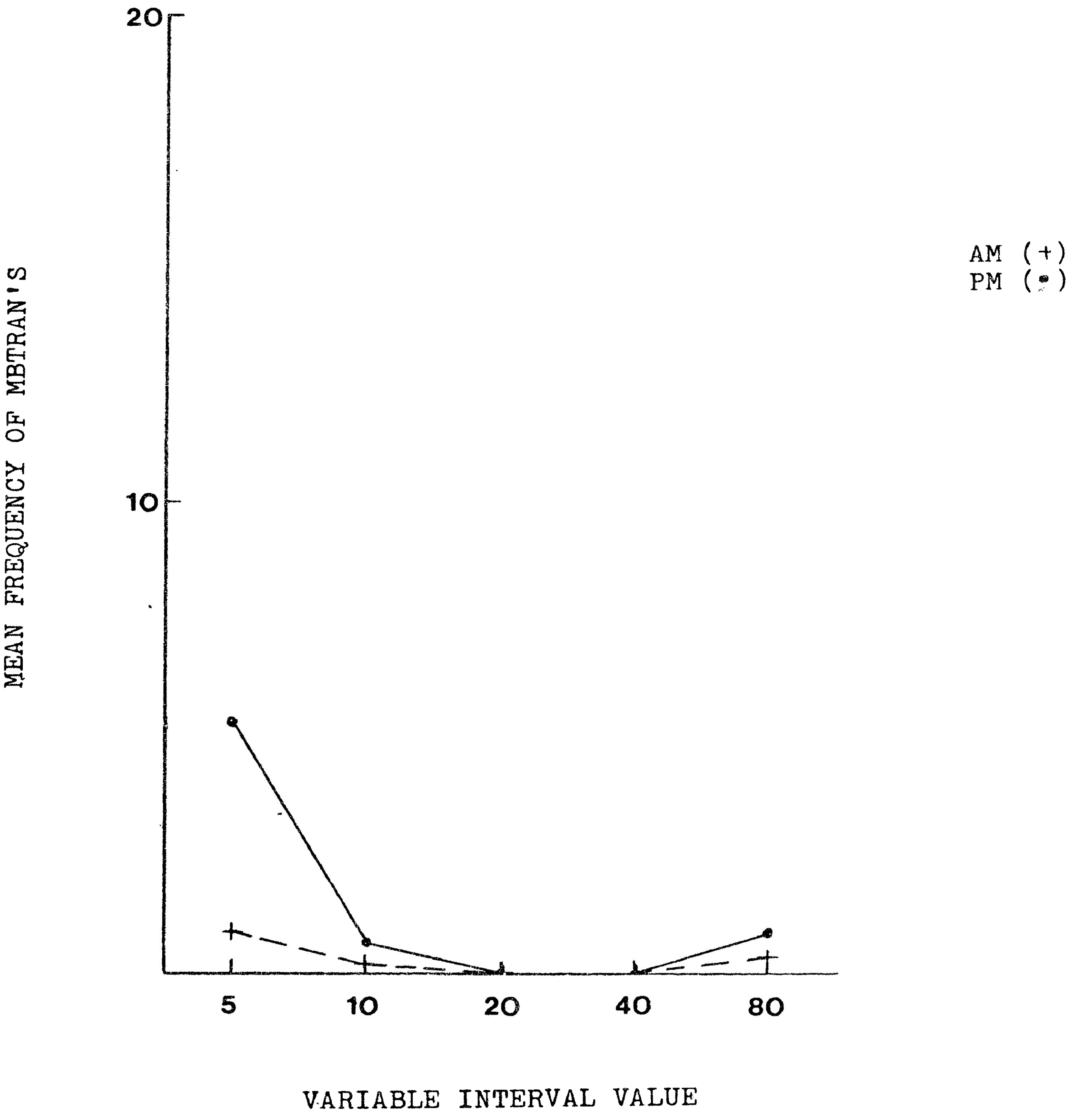


Figure 25. Mean number of occasions on which a MBTRAN dispersion change occurred during each VI schedule.

The average number of ITRANS out of 30 observations over 20 sessions was relatively low under VI5 and then increased to the highest average under VI10. The average number of ITRANS continued to decrease sequentially over schedules VI40 to VI80. The average number of PTRANS out of 30 observations over 20 sessions was relatively high under VI5. It decreased under VI10 and then again increased under VI20, VI40 and VI80 respectively. The MITRAN occurred least often of all the Transition types. Under VI5 the highest average was obtained. Under VI10 this average dropped until there were no MITRANS observed under VI20 and 40. MITRANS again occurred under VI80. The MATRAN was found to be the most common type of Transition. The lowest average MATRAN occurred under VI5 and steadily increased to a maximum under VI80. The MBTRAN average was relatively high under VI5. It then decreased to zero under VI10, VI20 and VI40 and again increased under VI80. Generally these results suggest that temporal stability was greatest under the mid-VI schedules and least under the extreme schedules VI5 and 80 as displayed in Figure 26.

Ancillary data that shows work output and food intake was recorded and analysed in terms of rates of responses and reinforcement. The highest average number of group responses per session was produced under VI20 and 40, decreased under VI10 and 80 and was lowest under VI5. Figure 27 and

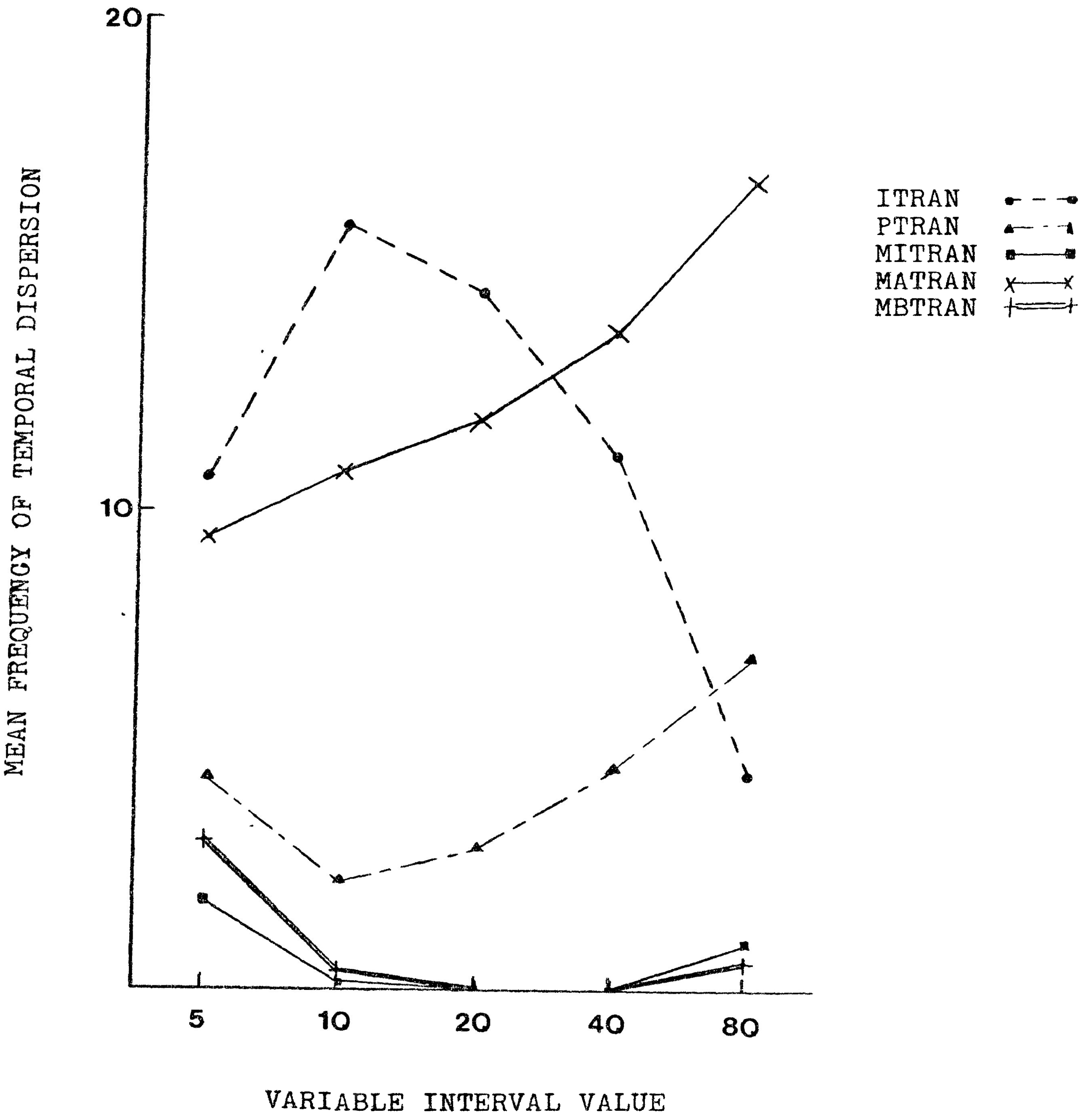


Figure 26. Mean number of occasions on which each temporal dispersion change (ITRAN, PTRAN, MITRAN, MATRAN, and MBTRAN) occurred during each VI schedule.

Table 14 show in detail the AM and PM differences in response rate and Figure 28 displays the average number of responses made during each AM and PM session per VI schedule. The mean number of responses made per session increased from VI5 to VI20 and then decreased between VI20 and VI80. The collective response rate was generally lower under the extreme VI schedules and higher under the mid-VI schedules VI20 and 40. This shows that an inverted U-shaped curvilinear relationship over schedules between collective response rates and VI values existed.

The number of reinforcements procurred collectively each AM and PM session is depicted in Figure 29 and Table 15. There was little difference in the number of reinforcements obtained under AM and PM sessions. Figure 30 illustrates the mean frequency of group reinforcements acquired per schedule. A maximum number of reinforcements was obtained under VI5. It decreased under VI10, VI20, and VI40 to a minimum under VI80. Generally there was an inverse relationship between the number of reinforcements produced and the VI schedule value.

The first measure of economy, the mean daily COP ratio as illustrated in Figure 31 and Table 16, shows an increase over the five schedules. The COP was lowest under VI5 and gradually increased over VI10, VI20, and VI40 until it reached a maximum COP ratio under VI80. There

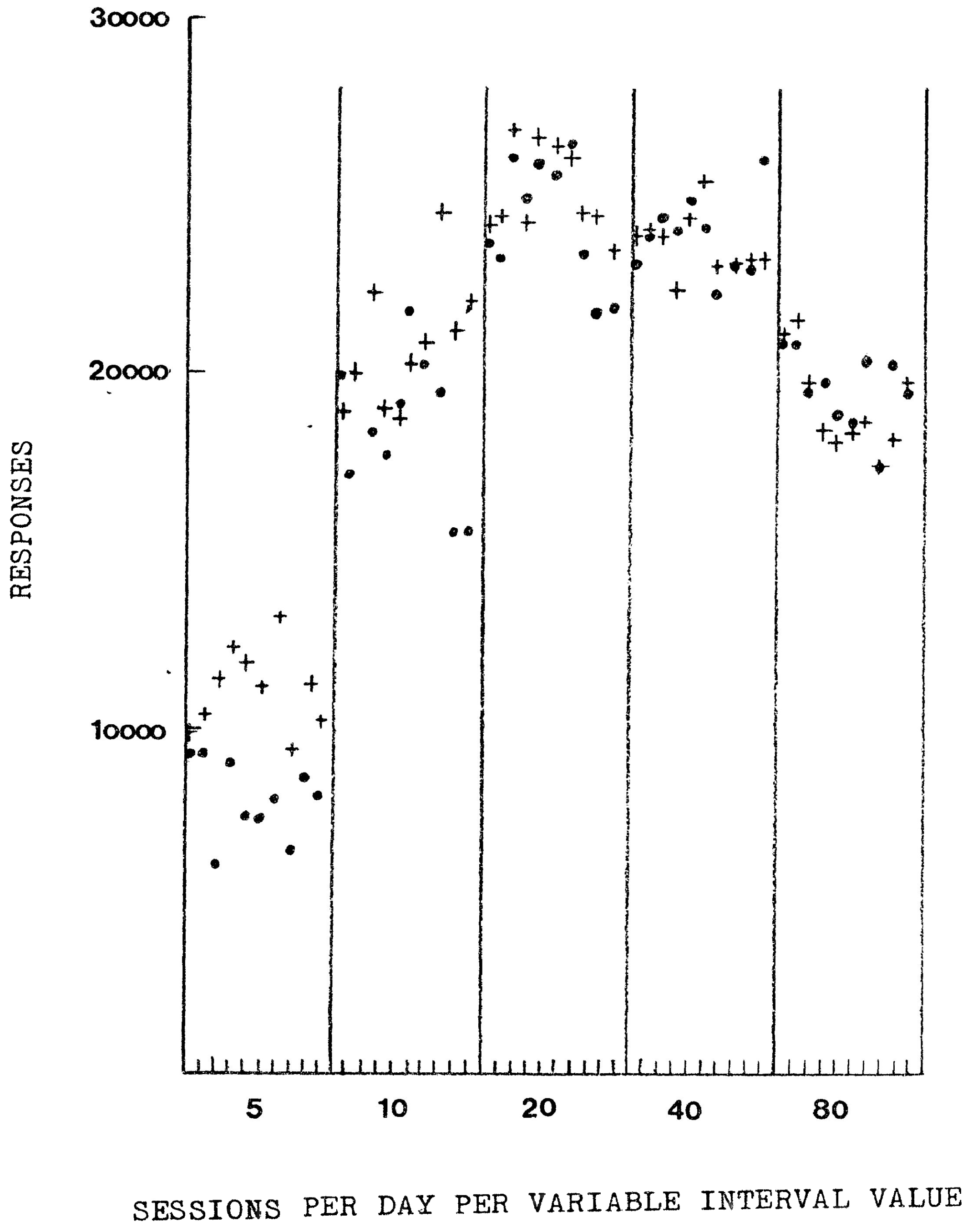


Figure 27. Average number of responses made during each AM (+) and PM (•) session.

Table 14

Total and mean number of responses made during each AM and PM session and each Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	9675	9109	18704	19760	24020	23509	23721	22877	20957	20657
2	10940	9109	19912	17071	24207	23030	23901	23748	21362	20513
3	11225	5898	21125	18281	26576	25925	23732	24246	19563	19341
4	12095	8765	18820	17570	23998	24815	22184	23829	18201	19664
5	11607	7284	18511	18969	26581	25833	24112	24714	17819	18759
6	11088	7112	20133	21609	26203	25462	25293	23933	18188	18271
7	12979	7738	20735	20082	25977	26210	22882	22010	18469	20202
8	9148	6264	24464	19351	24344	23135	22924	22967	17157	17079
9	11023	8383	21012	15371	24256	21432	23008	22729	18011	20158
10	10136	7825	21936	15361	23289	21677	23098	25893	19518	19261
AM Mean	10992		20535		25129		23486		18922	
AM SD	1129		1794		1163		863		1385	
PM Mean		7749		18343		24103		23695		19391
PM SD		1125		2029		1782		1117		1116
Total Mean	9370.15		19438.85		24523.95		23540.05		19156.15	
SD	1992.80		2177.00		1556.00		1555.53		1247.14	

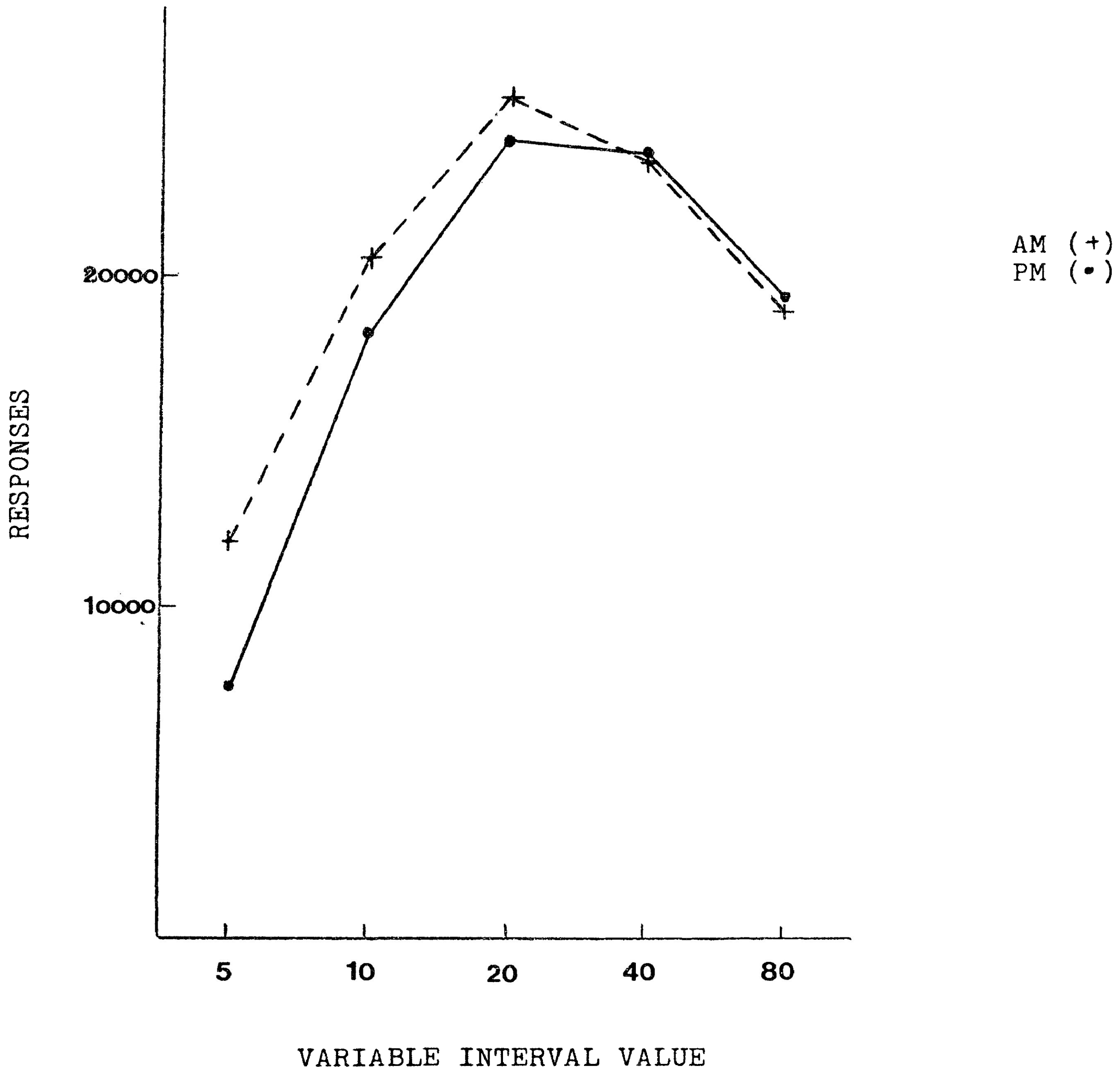


Figure 28. Mean number of responses made during each VI schedule.

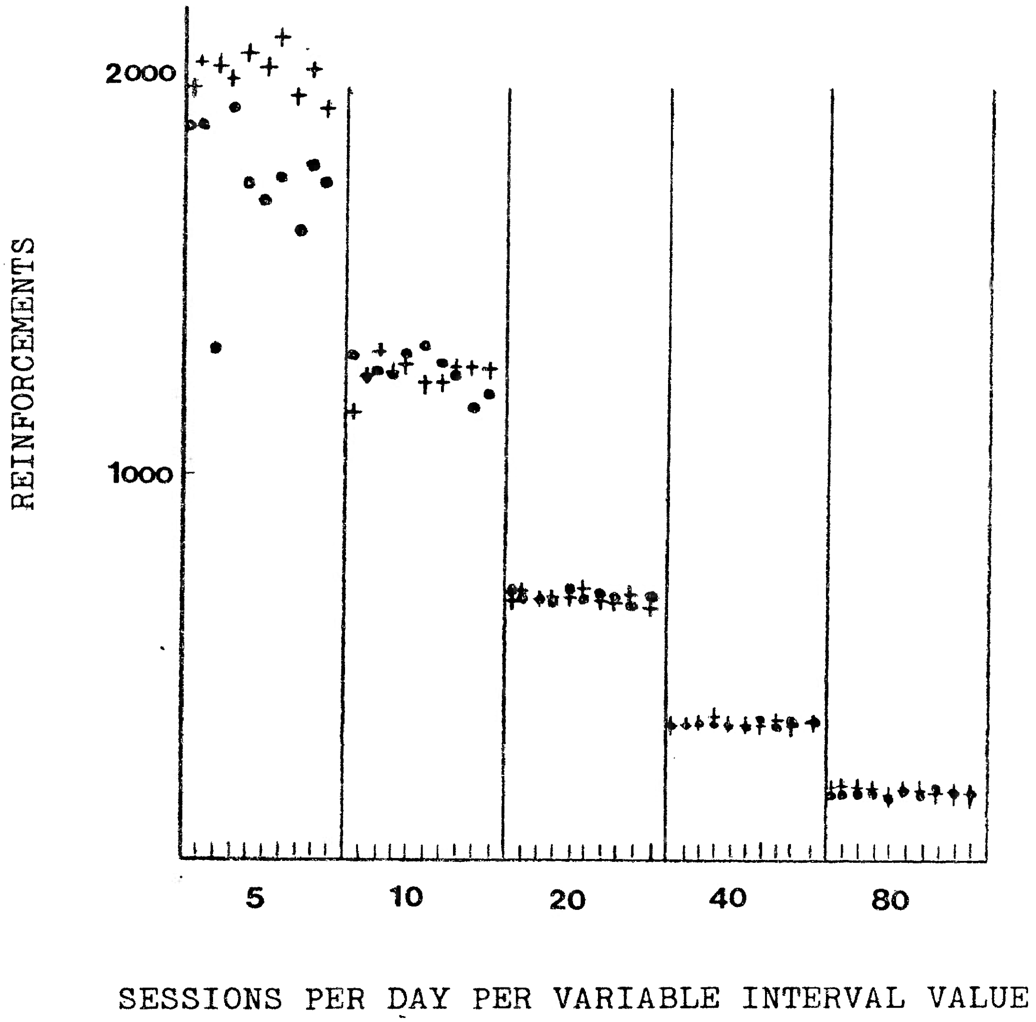


Figure 29. Total number of reinforcements obtained during each AM (+) and PM (•) session.

Table 15

Total and mean number of reinforcements obtained during each AM and PM session and each Variable Interval schedule.

Day	Frequency per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	2045	1909	1169	1308	679	681	357	353	188	178
2	2066	1909	1255	1257	695	678	352	353	195	178
3	2034	1326	1315	1265	612	679	352	359	184	171
4	2029	1948	1264	1251	678	662	367	347	182	174
5	2092	1752	1282	1319	680	698	351	347	171	164
6	2056	1703	1238	1336	706	677	352	350	180	173
7	2135	1770	1239	1281	667	676	352	360	178	188
8	1983	1631	1274	1259	669	680	357	347	172	179
9	2059	1807	1265	1179	692	658	347	355	180	182
10	1941	1750	1265	1205	651	685	360	365	178	175
AM Mean	2044		1257		679		355		181	
AM SD	54		38		16		6		7	
PM Mean		1751		1266		677		354		176
PM SD		179		49		11		6		6
Total										
Mean	1897.25		1261.30		678.15		354.15		178.50	
SD	198.20		42.72		13.31		5.82		7.04	

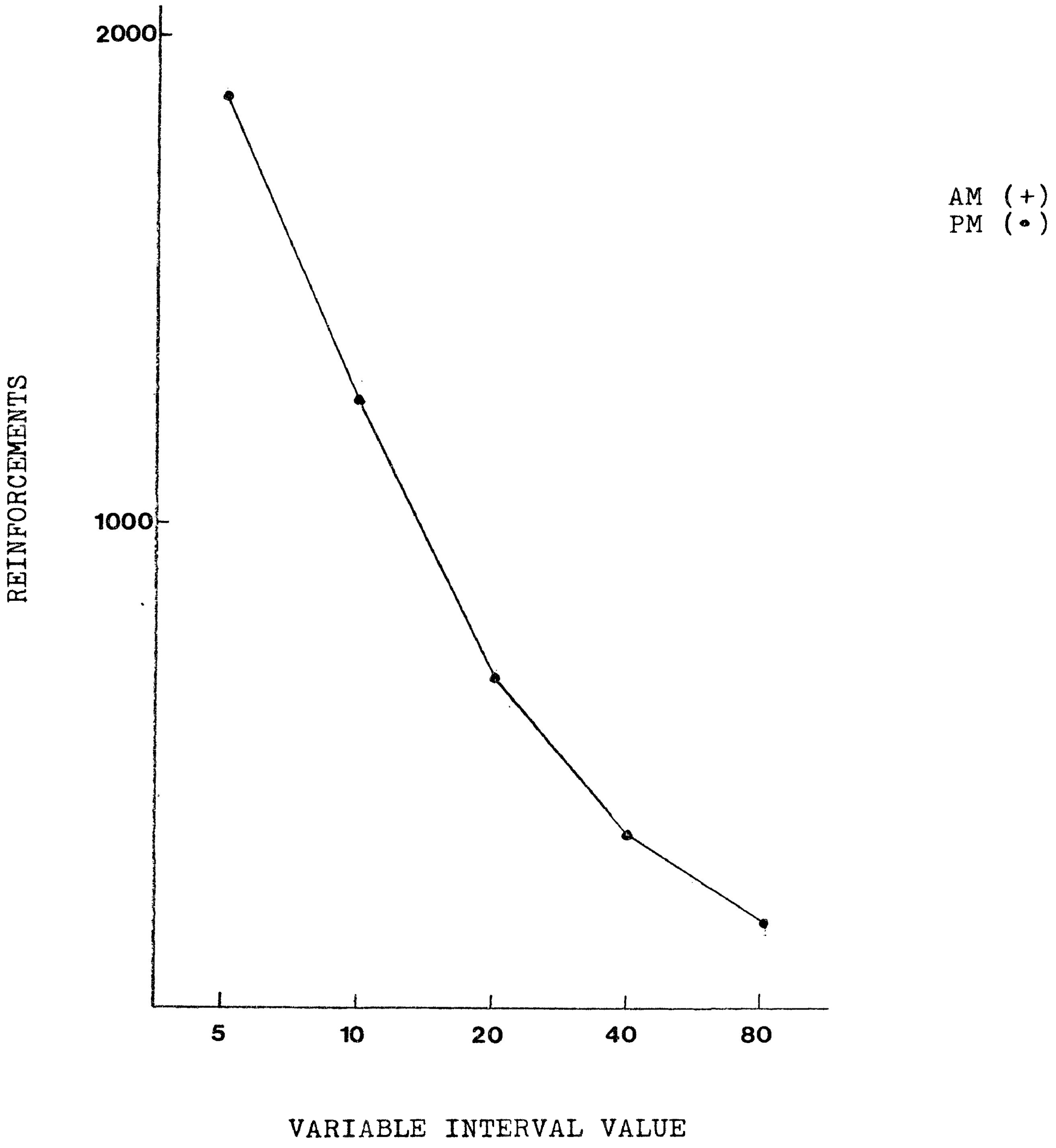


Figure 30. Mean number of reinforcements obtained during each VI schedule.

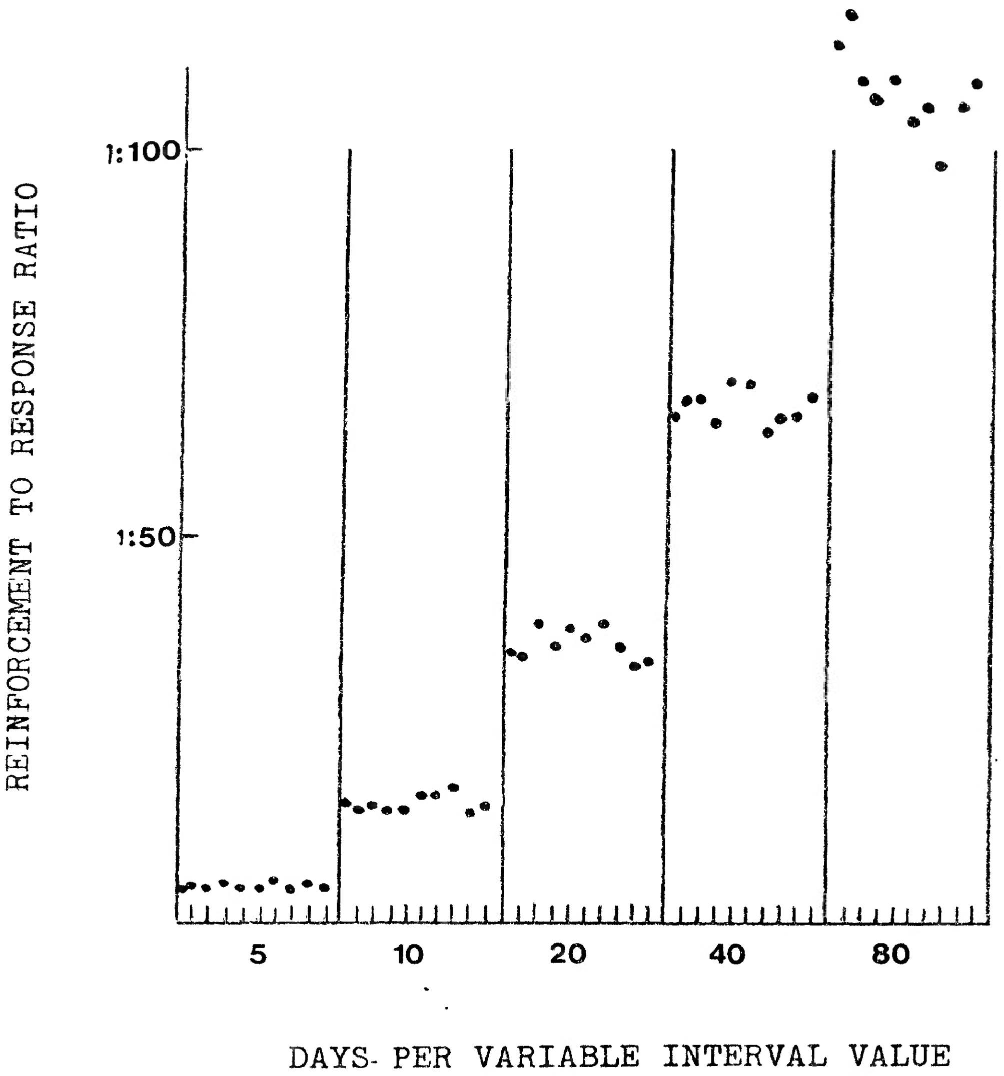


Figure 31. Mean Cost of Pellet (COP) observed on each day.

Table 16

Total and mean reinforcement to response ratios (Cost of Pellets) for each day per Variable Interval schedule.

Day	Mean COP per day per schedule				
	VI5	VI10	VI20	VI40	VI80
1	4.75	15.56	34.95	65.63	113.76
2	5.04	14.73	34.40	67.59	117.01
3	4.99	15.26	38.87	67.48	109.64
4	5.23	14.47	36.44	64.56	106.51
5	4.86	14.41	38.05	69.96	109.29
6	4.79	16.22	37.36	70.12	103.33
7	5.23	16.21	38.86	63.08	105.61
8	4.23	17.29	35.21	65.20	97.58
9	5.00	14.83	33.81	65.17	105.41
10	4.85	15.05	33.71	67.55	109.86
Total Mean	4.89	15.44	36.17	66.63	102.34
SD	0.62	1.54	2.22	3.04	22.18

appears to be a relatively direct relationship between the COP and VI value. The cost of the food was proportional to the Interval value. Figure 32 and Table 17 illustrate, in detail, the second measure of economy, Percentage of Food Obtained, (POFO). This measurment revealed an increase over the schedules. The average percentage of food obtained per schedule is shown in Figure 33 which shows that efficiency was lowest under VI5 where the lowest number of the reinforcements was obtained, and highest under VI80 where the highest number of reinforcements was obtained. Under VI10, 20 and 40 there was a linear increase. This again shows that there is a relatively direct relationship between the level of efficiency and VI schedule value such that efficiency in terms of utilization of available resources increases with VI value.

Figure 34 and Table 18 show that the mean PRP's over ascending VI values resulted in a curvilinear U-shaped relationship. The longest mean PRP was obtained under VI5 and decreased in VI10. The shortest PRP was under VI20. The PRP's again increased under VI40 to a maximum under VI80. This demonstrates that the time elapsed between the obtainment of a reinforcement and a bar press response at the food station is lowest under mid-VI schedules.

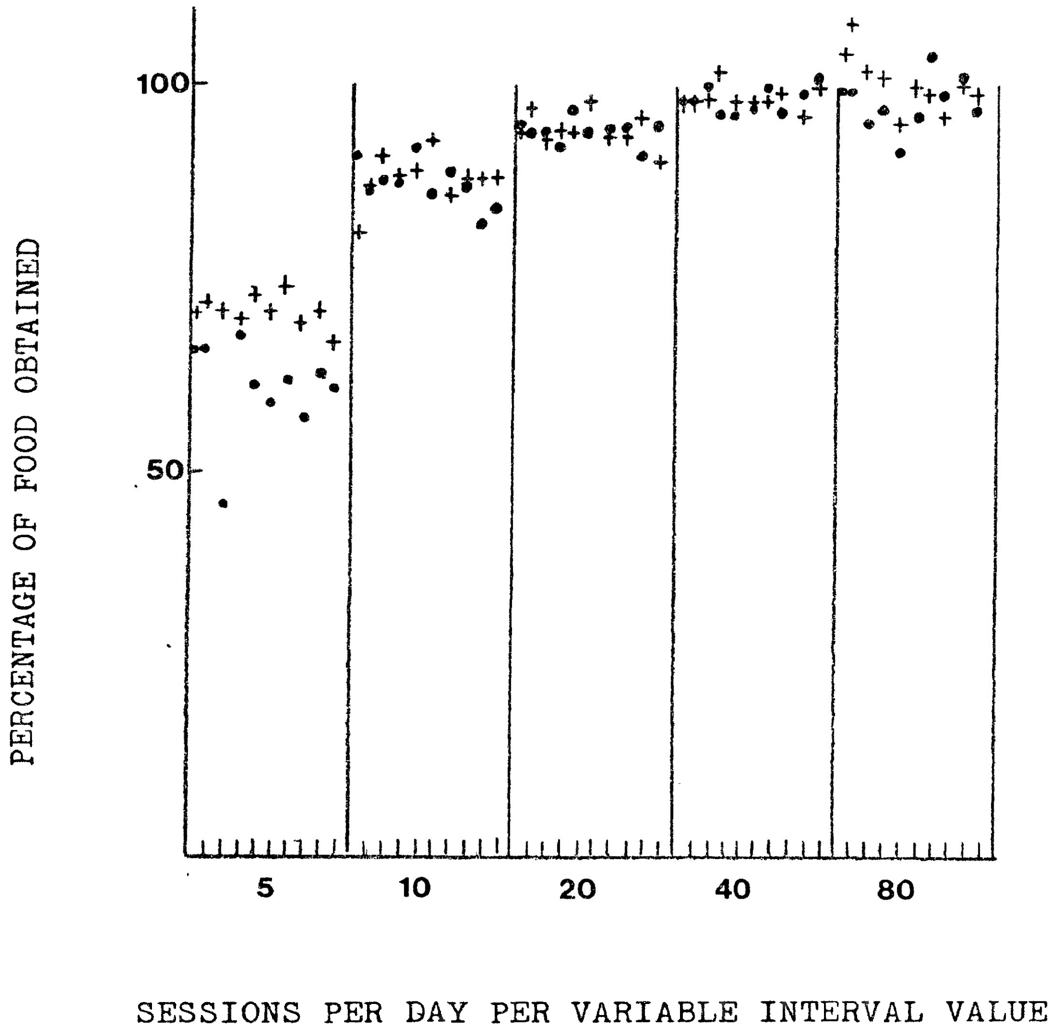


Figure 32. Average percentage of the available food that was obtained during each AM (+) and PM (•) session.

Table 17

Total and mean Percentage of Food Obtained during each AM and PM session and each Variable Interval schedule.

Day	POFO per schedule									
	VI5		VI10		VI20		VI40		VI80	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
1	71	66	81	91	94	95	98	98	104	99
2	72	66	87	87	97	94	98	98	108	99
3	71	46	91	88	93	94	98	100	102	95
4	70	68	88	87	94	92	102	96	101	97
5	73	61	89	92	94	97	98	96	95	91
6	71	59	93	86	98	94	98	97	100	96
7	74	62	86	89	93	94	98	100	99	104
8	69	57	88	87	93	94	99	96	96	99
9	71	63	88	82	96	91	96	99	100	101
10	67	61	88	84	90	95	100	100	99	97
AM Mean	71.0		88.0		94.0		98.5		100.0	
AM SD	2.0		3.0		2.0		2.0		4.0	
PM Mean		61.0		87.0		94.0		98.0		98.0
PM SD		6.0		3.0		2.0		2.0		4.0
Total Mean	65.90		87.10		94.10		98.35		99.10	
SD	6.82		3.23		1.94		1.69		3.78	

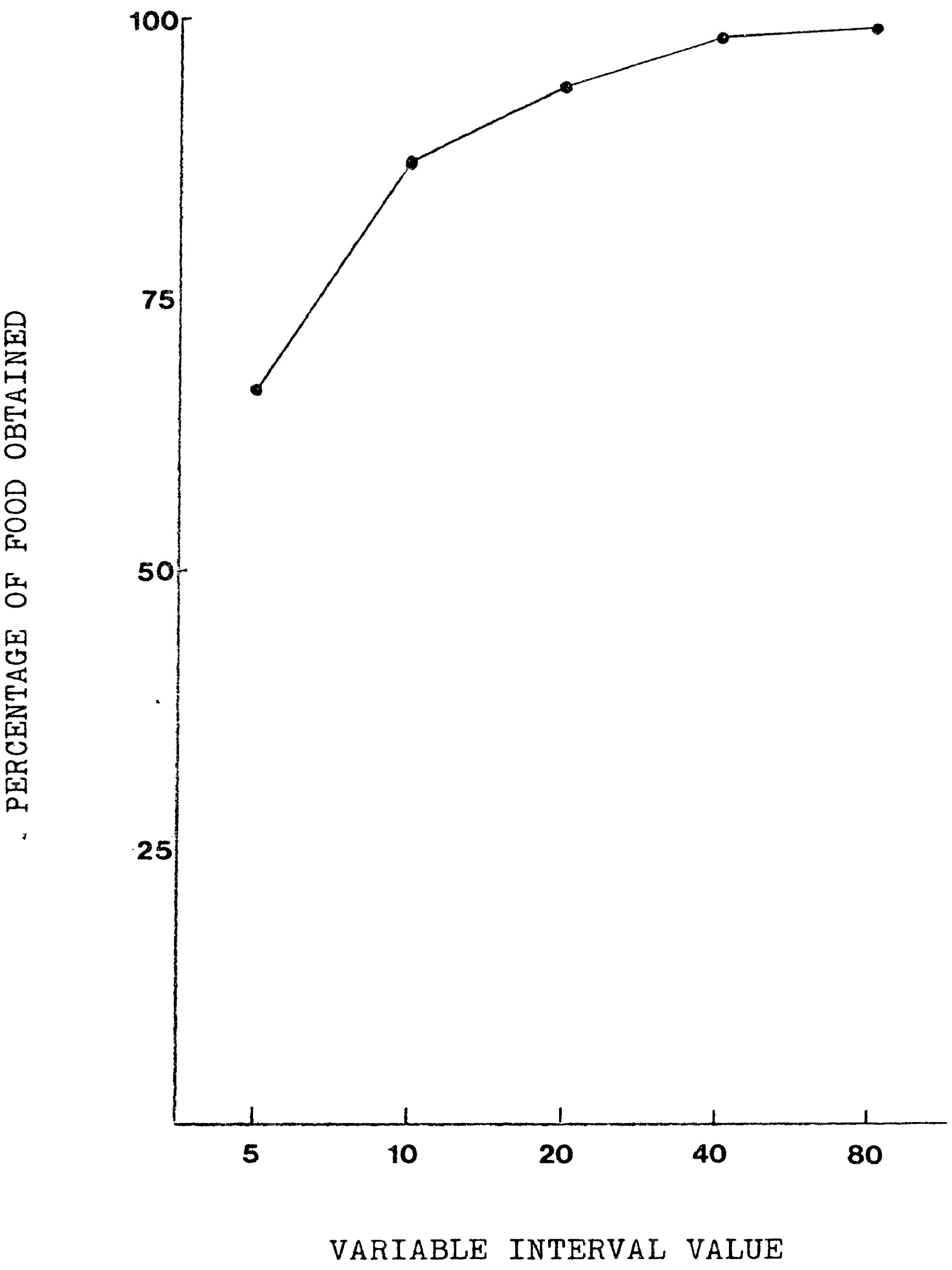


Figure 33. Mean percentage of the available food that was obtained during each VI schedule.

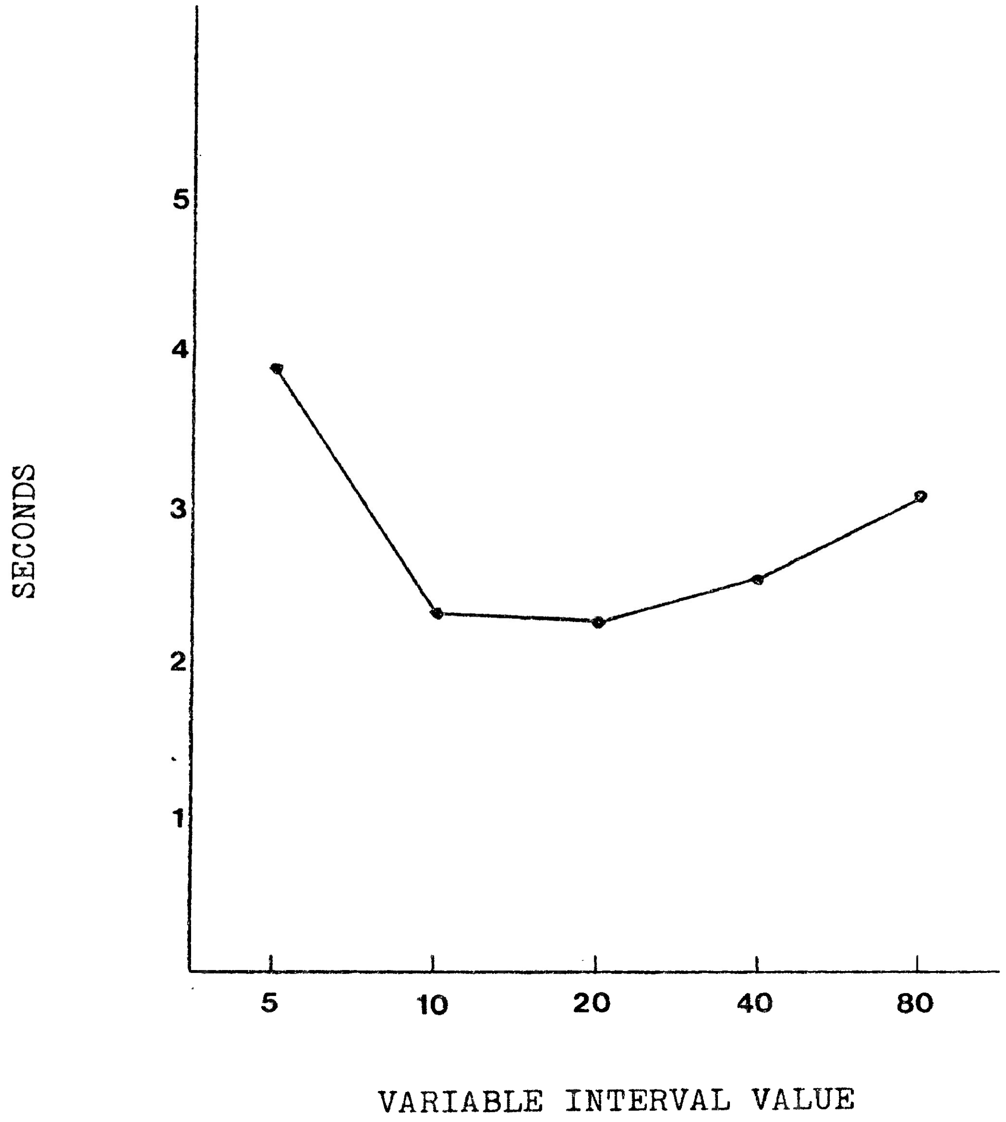


Figure 34. Mean post-reinforcement pauses observed during each VI schedule.

Table 18

Mean length of the Post-reinforcement Pauses observed during each Variable Interval schedule.

Schedule	Seconds of PRP	
	Mean	SD
VI5	3.92	2.1
VI10	2.33	0.9
VI20	2.29	1.4
VI40	2.56	1.5
VI80	3.06	1.2

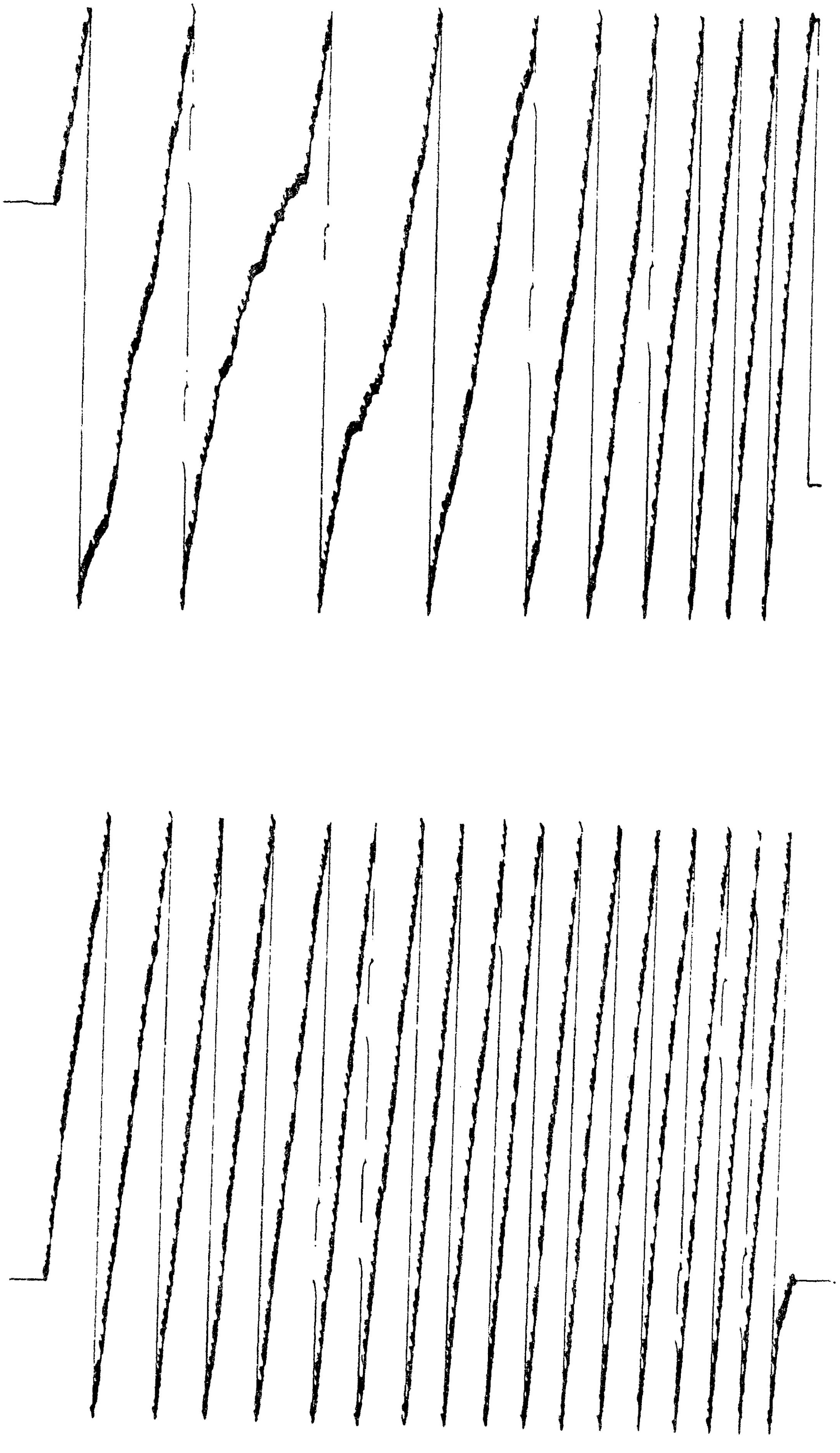


Figure 35. Cumulative graphic recording of response and reinforcement rates for the AM and PM sessions under VI5.

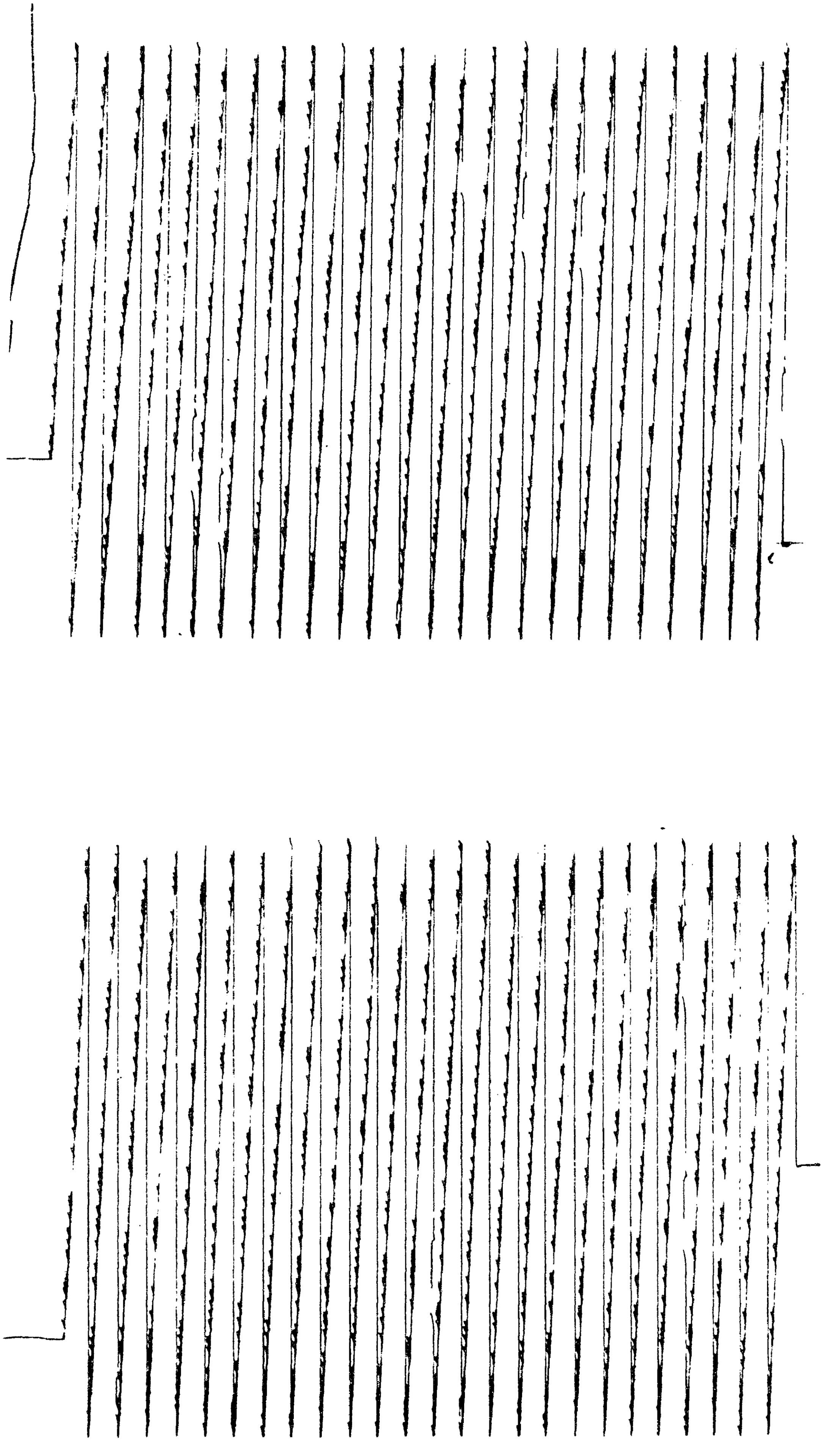


Figure 36. Cumulative graphic recording of response and reinforcement rates for the AM and PM sessions under VI10.

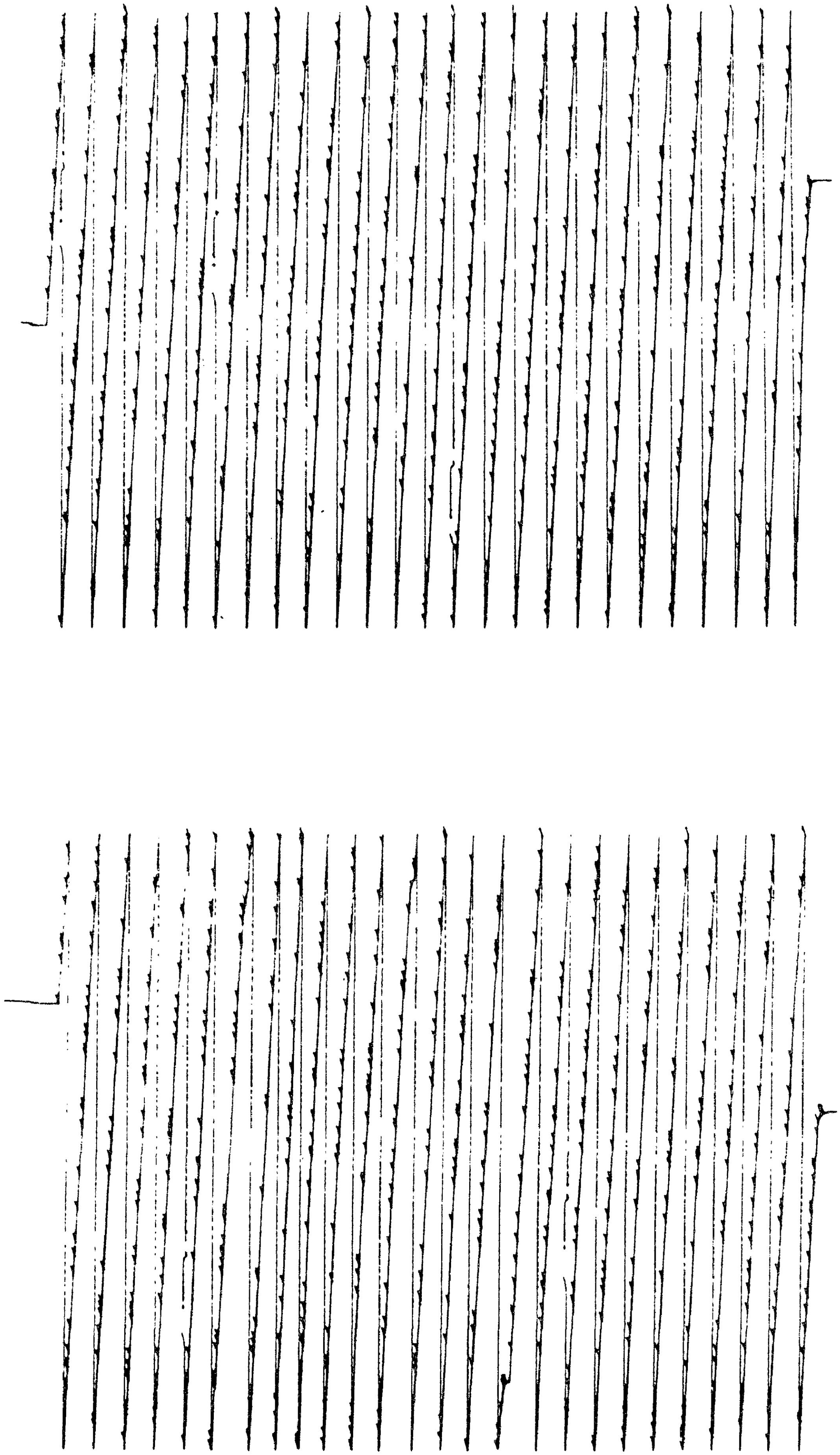


Figure 37. Cumulative graphic recording of response and reinforcement rates for the AM and PM sessions under VI20.

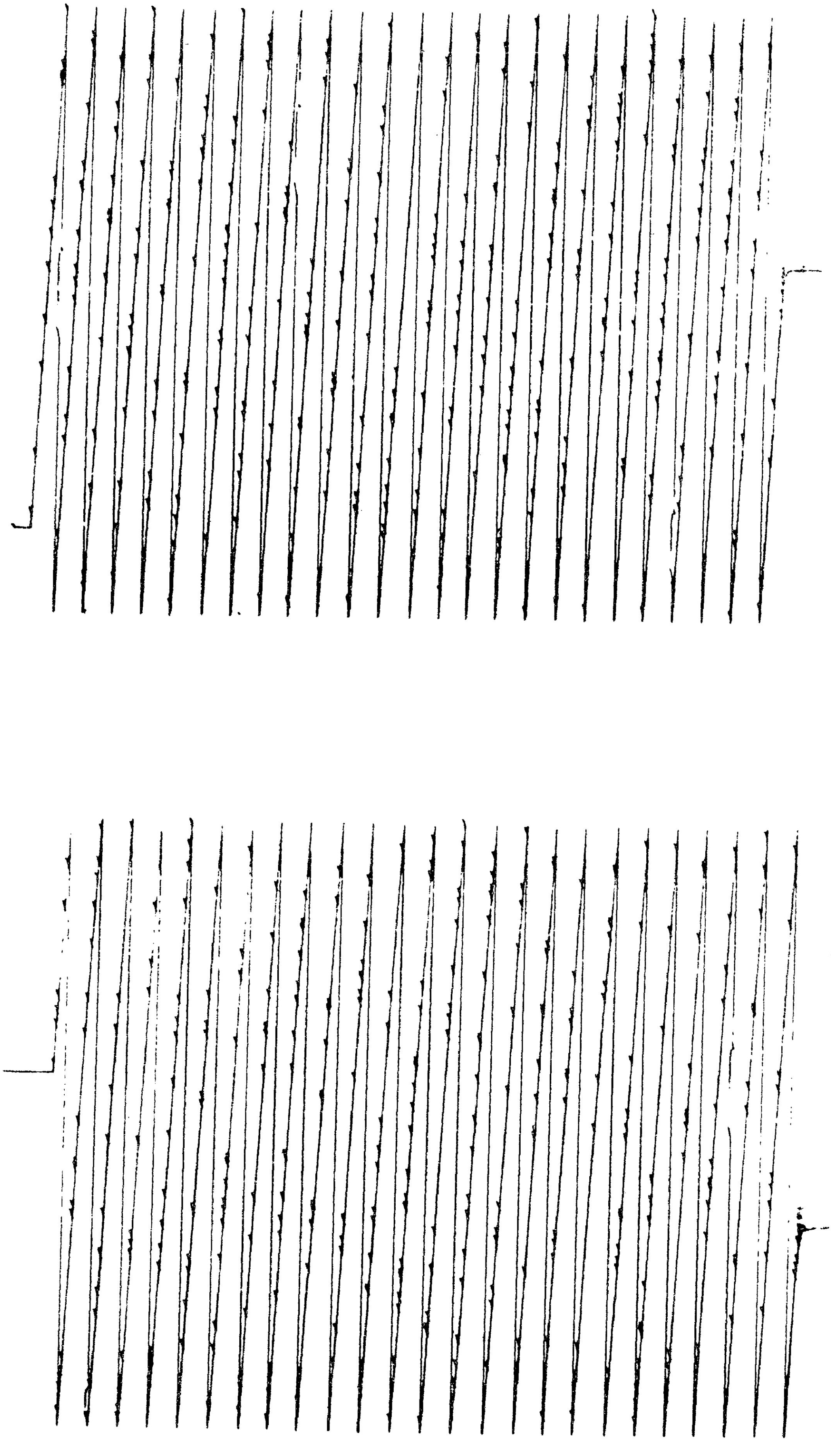


Figure 38. Cumulative graphic recording of response and reinforcement rates for the AM and PM sessions under VI40.

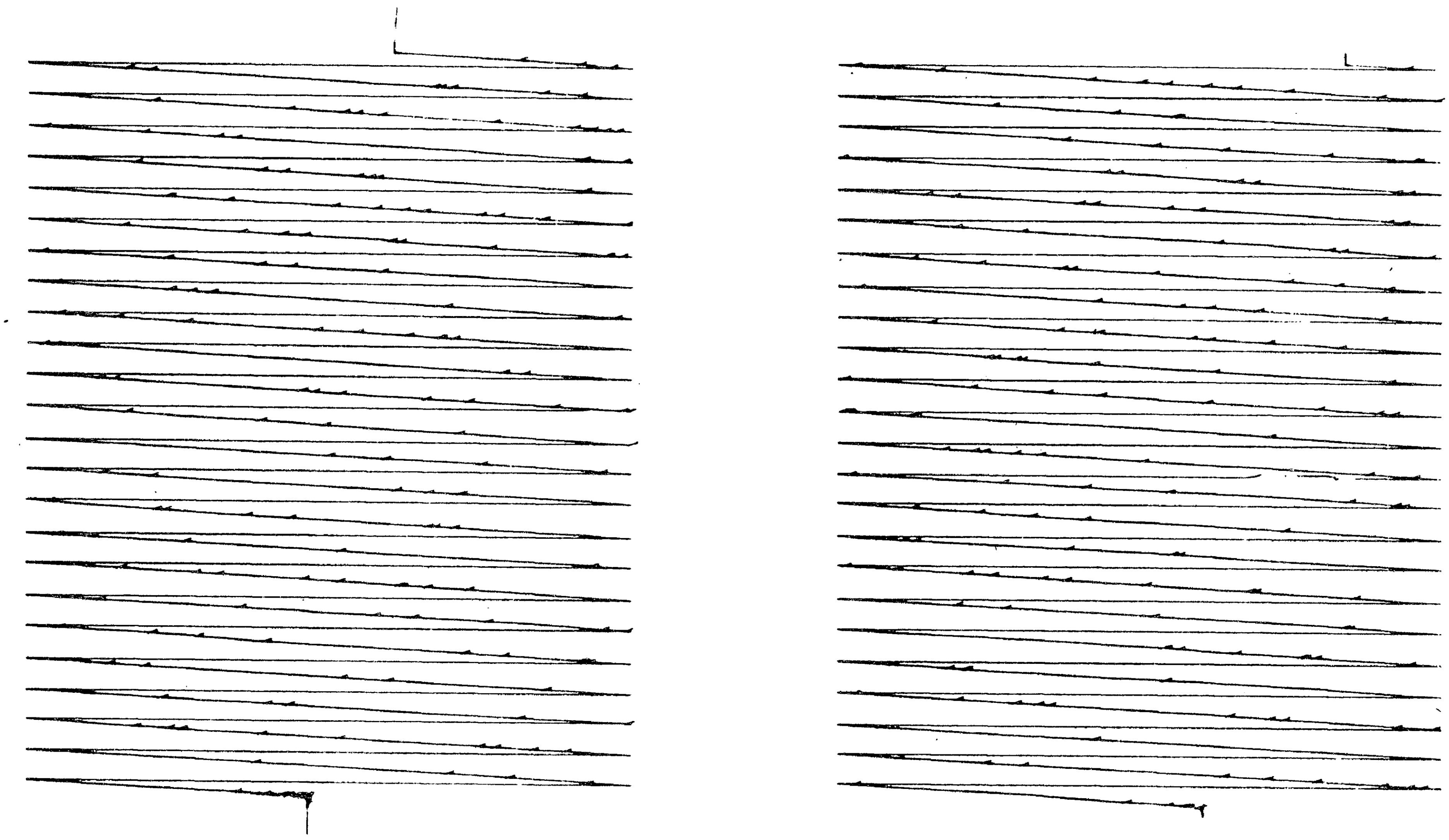


Figure 39. Cumulative graphic recording of response and reinforcement rates for the AM and PM sessions under VI80.

The graphic cumulative recordings are shown in Figures 35, 36, 37, 38 and 39. It became evident that the rate of responding increased, then leveled and finally decreased slightly over ascending VI schedules. There was a prominent difference between the AM and PM sessions in VI5. In the latter half of the PM sessions the rate of responding decreased considerably. Consistent AM and PM response and reinforcement rates were observed in each of the remaining schedules.

DISCUSSION

The behaviour of a population's members can be discussed in terms of measurable units or responses. These responses can be shown to come under the control of contingencies of reinforcement. These results demonstrate that there are changes in spatial and temporal dispersion and density of the individual members in relation to changes made in the reinforcement schedules. The changes were gradual over the ascending VI schedule values and demonstrated curvilinear relationships. This indicates that under extreme low and high VI schedules dispersion was more irregular than under the mid value VI schedules of reinforcement.

Similar trends were found in a separate study using Fixed Interval schedules of reinforcement on eight rats in the operant arena (Goldstein, Johnson and Ward, 1984). The Fixed Interval (FI) schedule differs from the Variable Interval (VI) schedule only in that an organism must wait for equal amounts of time to pass, once a reinforcement has been obtained, before any response can produce another reinforcement, rather than waiting differing lengths of time as in VI schedules. Goldstein, Johnson and Ward (1984) found that the frequency of regular dispersion patterns observed during equivalent Fixed Interval values (FI5, 10, 20, 40 and 80) produced similar curvilinear relationships under both the FI and VI schedules, although the actual amount of dispersion was lower under the FI schedules.

In another experiment using the operant arena, Fixed Ratio (FR) values were instituted. The frequency of regular dispersion over ascending FR schedules did not show the same curvilinear relationship (Goldstein and Mazurski, 1982) as seen in the Interval schedules. Instead, a direct increase in regularity was observed between FR1 and FR32. Goldstein, Johnson and Ward (1984) in a later study extended the analysis of Ratio value reinforcement control on dispersion patterns to see if the direct increase in regularity, found under the above FR study, was a function of the controlling factors inherent to Ratio schedules or, if the ratio values used simply did not go high enough to test the effect on regularity, i.e., to find out whether or not regularity would first increase, plateau and then begin to decline as was seen in the Interval schedules. They used FR schedules of 5, 10, 20, 40, and 80 and they found there was an increase in the regularity of the dispersion patterns toward the mid-FR value, followed by a decrease. This formed a curvilinear dispersion curve similar to those found under the Interval values. This suggests that both Interval and Fixed-Ratio schedules exert control over the dispersion patterns of the rats in the arena such that regularity is relatively curvilinear to ascending schedule values. Variable-Ratio (VR) schedules of 5, 10, 20, 40 and 80 were also studied In VR schedules an organism has to make a specific number of responses before a reinforcement can be obtained and the number of responses for each reinforcement is randomly generated around an average VR value. Although the regularity increased from VR5 to 40 the regularity stabilized under VR80. However, it was not known if regularity would decline to form a curvilinear relationship over ascending schedule values above VR80.

Evidence for naturally occurring changes in cluster formation, that correspond to changes in food availability, has been described by Davies and Houston (1981). The pied wagtail species motacilla alba was observed in its coastal feeding territory. They found that the owner of a territory (the bird that has domination over a food site) sometimes allows another member of its species (satellite) to feed in its territory and this represents clumping. This occurred most frequently when the food supply was high because the satellite helped defend the food from other members (excess clumping) by scaring them off. It was suggested that the owner of the territory tolerated the satellite to the extent that it could maximize its own feeding rate; the satellite's aid in defending the food site outweighs the cost of sharing the food supply. As the food supply diminishes the food consumption of the satellite is too costly in relation to the food saved through defense of the territory. The satellite is then evicted (resulting in a more regular dispersion pattern).

Foraging strategy as a function of maximization and minimization

Real (1980) suggested that the non-linearity of a foraging strategy is representative of the diversity that animals show in finding food in nature. When food resources are abundant and time is not limited animals act conservatively until they have acquired sufficient food (energy) and then engage in less conservative, more risk taking and/or exploitive strategies. This represents a time minimization strategy. Under VI5 PM the rats acted more as time minimizers. They foraged for food in such a way as to consume enough food to become satiated and leave time to engage in other activities during periods when food was still potentially available. In contrast, time maximizers have a limited time in which they have access to food in order to meet their energy requirements. This foraging constraint seemed apparent under VI5 AM and all the other VI schedules. When resources are scarce or time is limited animals will adopt risky strategies (i.e., exploration of new, unpredicatable food patches) in an effort to escape near starvation. In this case the exploitive strategy is more representative of local maximization than time minimization. That is, the animals adopt a strategy that has the highest probability of reinforcement from moment to moment while food is available. Otherwise, when food is neither overly abundant nor overly scarce, animals usually prefer conservative foraging strategies in favour of the risky ones. According to Staddon (1980) the conservative strategy represents global maximization. That is, animals will engage in a strategy that provides the highest probability of food obtainment over an entire feeding session. Local maximizing may or may not necessarily lead to global maximization. Staddon (1980) observed that, rats in particular, behave as if they can not see too far ahead in a temporal sense and therefore tend to behave more as local maximizers in complex environments. They tend to maximize globally, if at all, only in simple foraging situations. In this study there was evidence that the animals demonstrated both local and global time maximization as well as time minimization (described below).

Trends in this analysis of VI control of population dispersion showed that the dispersion patterns in both the lowest and highest schedule conditions were similar. The daily dispersion averages of both VI5 at one extreme and VI80 at the other demonstrated irregular disperion patterns. The contingencies of the two divergent schedules produced similar patterns due perhaps to different economic or operant constraints. AM and PM differences in disperion were found under VI5 but not under the other VI conditions (note that these AM and PM differences found under VI5 are partialled out when daily averages are compared) and are evident through the following: 1) the number of responses and reinforcements and the POFO were found to be higher in every AM session than over the PM sessions during VI5, 2) the latter half of the PM sessions showed a slowed rate of responding and fewer obtained reinforcements as seen in the graphic cumulative recordings, 3) attrition levels were lower in the AM sessions than they were in the PM sessions, 4) ritualized fighting and climbing was seen only in the latter half of the PM sessions, and 5) more regularity was seen throughout the AM sessions whereas regularity was seen mostly in the first half of the PM session rather than in the latter half.

The AM and PM differences in VI5 may be explained in terms of the time differential between the sessions. Between the AM and PM sessions there was a 5 1/2 hour separation while there was a 17 1/2 hour separation between the PM and AM sessions. As a result there was a longer period of food deprivation leading up to the AM session and this could have encouraged the rats to remain at the food stations for a longer period of time during that session rather than during the PM session. It is not unreasonable to consider therefore, that the members of the colony were more hungry by the beginning of the AM than by the PM sessions and the rate of responding was such that enough food was obtained to carry them through to the beginning of the PM session. At the start of the PM sessions the colony would again need more food but, because the time between sessions was relatively low the rats became satiated and slowed their rate of responding thus altering their dispersion patterns. The economy in the latter half of the PM session is hypothetically exploitive and geared toward minimization. This is to say that the rate of response of the members of the colony ensured that the minimal amount of food (reinforcement) needed to ward off hunger was obtained at a minimal work level (rate of responding). Excess work (responding) to overproduce food (reinforcement) for future consumption (conservative, global maximizing strategy) was not emitted, though possible. This lack of excess work to produce excess food has been described elsewhere in detail by Houston and McNamara (1981). They presented rats with a choice of independent VI schedules. The animals tended to maximize reward relative to their immediate situation but not over a global period of time.

In contrast to VI5 the VI80 schedule can be considered a hypothetical, desperation, risk-taking strategy that promotes local maximization. Firstly, the COP was already very high and secondly, the maximum level of efficiency (in terms of POFO) had nearly been reached (99.1%). Under VI80 the cost of food being produced was already expensive in terms of response rate and any additional responding merely produced diminishing returns in terms of food (energy input) to work (energy output) ratio (additional work produces proportionally less food). Because the economy was poor already, the rats engaged in risky behaviours in a desperate attempt to maximize immediate reinforcement.

This shows that in addition to using both conservative and expoitive foraging tactics rats can behave as both time minimizers and time maximizers (Pyke, Pullman, and Charnov, 1977; Smith, 1978).

Dispersion as a function of concurrent VI schedule switching choice

The mid-VI schedules produced the greatest amount of spatial and temporal regularity per session. VI10 demonstrated the most regularity followed by VI20 and VI40 respectively. This reflects a conservative strategy which produces global maximization. Under these conditions a stay/never-switch strategy was implemented most often. A stay/never-switch strategy is one in which an animal will rarely leave an abundant food source for a much less abundant, less predictable or distant one (Baum, 1982; Houston and McNamara, 1981). The energy-saving gained by staying and obtaining a pellet within a maximum of 20 seconds in VI10, 40 seconds in VI20 and 80 seconds in VI40, may have outweighed the energy cost attributable to the Changeover Delay (COD) or the time it takes to move to another food site. Therefore the rats chose to travel less and consequently did not use the stay/stay or stay/switch strategies as often as they did under VI5 and 80. In independent concurrent VI schedules of differing values an organism will spend more than a moment of time in each schedule before switching. This is refered to as the stay/stay strategy (Baum,1982; Houston and McNamara, 1981). In independent, concurrent VI schedules that have relatively large differences in value an animal will spend most of its time working in the schedule that has the lowest COP but make periodic visits to the other schedule to pick up a waiting pellet then immediately return to the previous schedule. This is called a stay/switch strategy (Baum, 1982; Houston and McNamara, 1981). When the rats did switch the distances travelled were relatively short. Evidence of this fact was the reduction to zero in the attrition under VI20 and 40 as well as shorter PRP's. This suggests that when dispersion to new food sites did occur under these mid-VI schedules, there was less waiting and less long distance travelling.

The decrease in the regularity of the dispersion patterns from the mid-VI schedules to VI80 may be explained as a change in adaptive food production strategy. Hypothetically, by remaining in a regular dispersion, less food would be produced in the time alloted than if an irregular dispersion pattern was engaged in. Therefore the rats switch from a conservative foraging strategy under the mid-VI values to an exploitive foraging strategy under VI80. This can represent a change in reinforcement-obtainment strategy from a stay/never-switch choice under the mid-VI schedules to the stay/stay and stay/switch strategies under VI80. It can be seen that under VI80, reinforcement can be withheld for a maximum of 159 seconds before a bar press will provide food. This maximum, potential, waiting time could be avoided by movement to another station where time has been elapsing and there may be less than the maximum 159 seconds at the immediate foodsite. The advantage of moving is offset by the probability of a reinforcement becoming available immediately or at least within a relatively shorter period of time (Baum, 1982). Evidence for this comes from the fact that travel and waiting time increased under VI80. Travel under VI80 was recognized by an increase in the non-regular temporal Transitions and an increase in spatial clumping. In addition, an increase in waiting behaviour was evidenced by an increase in post-reinforcement pauses as well as a decrease in group response rates (bar pressing) compared to VI10 through VI40. The increase in aggregations as a strategy to adapt maximally to the schedule demands during VI80 was also measured in terms of an increase in the percentage of food obtained to 99.1% from 87% under VI10.

A stay/never-switch strategy was encouraged to some extent in VI80; the probability of getting a reinforcement quickly for the appropriate response discouraged movement when the odds of obtaining reinforcement from another food station were no longer significantly better and could have potentially been worse. This may account for the occurrence of regular spatial/temporal dispersion for roughly 33% of the time under VI80.

Generally, as the schedules increased between VI10 and VI80 a change in strategy became apparent, e.g., there was a change from the stay/never-switch to the stay/stay and stay/switch strategies. Even though the increase in the frequency of aggregated dispersions did not allow the members of the colony to produce enough food to meet minimum daily caloric requirements it may still be considered the best strategy as it allows for the optimal production of food that is available e.g., 99.1% under VI80.

Elasticity in reinforcer demand and dispersion

The dispersion and density of animal populations is also dependent upon the availability of free food which in turn affects response rates. The response rate of animals depends in part on whether or not the system in which the animal forages is open or closed (Berryman, 1981). Hursh (1980) reviewed both FR and VI research of response rate in relation to increased schedule values. He found that in some cases response rates decreased over VI schedules while in others the response rate increased. He concluded that in an open economy (a system in which the animals have access to supplemental food after an experimental session) response rates decreased because the response was under the control of the experimenter's free food to a greater extent than it was under the control of the food available under the schedule of reinforcement during the session. In the closed economy (a system in which the animal does not have access to a supplemental food supply and therefore must obtain all of its food during the experimental session) response rates increased because the animal's food consumption was solely determined by the animals interaction with the schedules of reinforcement. He described this as the elasticity of demand. In a closed economy demand is inelastic (an animal's demand for food is relatively constant) and when the schedule values increase, higher rates of responding are required to maintain a sufficient supply of food. This infers that the COP increases and therefore becomes increasingly more elastic as schedule values increase. In the open economy the demand is elastic during an experimental session because the food supply can be provided later by the experimenter. Therefore the animal will respond at a lower rate than it would under the higher schedules because of the needless extra work that is required to obtain a sufficient supply of food that can otherwise be acquired through supplemental feeding. Therefore COP is more constant relative to ascending schedule values thereby remaining proportionally more inelastic.

The curvilinear rise and fall in the response rates in the current investigation can also be explained in terms of open and closed economies. Under VI5 and 10 the economy was closed (no food supplement was provided) and the response rate increased. This is consistent with Hursh's (1980) observations. A small food supplement was offered during VI20 but supposedly it was not enough to offset the demand for food during the sessions and therefore the highest rate of responding resulted during VI20. VI20 is the beginning of an open economy. As the economy became more open as in VI40 and 80 the response rate decreased. This may have occurred, in part, because an even larger food supplement was provided to offset the decrease in total amount of food available during the sessions under the higher schedules. This is also consistent with Hursh's (1980) observations.

Further support for the idea that an open or closed economy affects response rate is apparent in the changes in COP over VI schedules. The COP was lowest under VI5 but then increased nearly three-fold as the VI-value only doubled to VI10. This shows more elasticity in the COP as the schedule increased under the closed economy of VI5 and 10. However, the COP only doubled as VI schedules doubled from VI10 to 20, 40 and 80. This represents relative consistancy and inelasticity over ascending VI schedules.

The rise and fall of the rate of responding therefore may be, in part, the result of changing from a closed to an open economy. In the open economy the demand for food during the experimental sessions was somewhat elastic and therefore the animals' bar press response was under less control of the VI schedule than in the lower VI schedules. Once satiated rats were not under the same contingency control as they were when they were hungry; the reinforcing value of the food pellets lessens. This demonstrates the elasticity, or flexibility, of the demand for a particular reinforcer (Hursh, 1980; Rachlin, 1980) and concomitant changes in the schedule control of dispersion.

As the demand changed, so did the dispersion patterns. When demand was low, and thus elastic, dispersion was more aggregated under VI5. This may indicate that other variables took on higher reinforcing value, (i.e., social interaction exerted more control over dispersion than a food reinforcer). Under VI80 the rats again aggregated but for a different reason; the demand for food was higher because less food was available during the sessions. More likely the rats aggregated as a result of the controlling factors of the schedule of reinforcement under VI80 than as a result of other factors such as social interaction. Under VI80 then, the rats acted as time maximizers. They used all the available time for foraging. This suggests that as the demand for a reinforcer increases other factors will have less control over behaviour. If the reinforcer is food, satiated animals will act as time minimizers and hungry animals will act as time maximizers.

Discriminative stimulus control and dispersion

The last controlling function of population dispersion in operant terms is the power of ecological variables to act as discriminative stimuli. Discriminative stimuli may include members of the same species, empty food sites, rats working alone at food sites (Goldstein, 1981), as well as the individual organism's rate of responding per reinforcement (Baum, 1981; Herrnstein, 1974; Skinner, 1969). In this study, for example, if a rat working at a food station acted as a S for high probability of reinforcement the other rats tended to approach him in order to obtain more food for less work than they could obtain by working alone. At other times a roaming rat would eat alternately with a rat that was already bar pressing without having to bar press for himself.

Often a rat would acquire more than one pellet before stopping to eat under VI5. This behaviour was reduced when another rat approached. Two or more rats would sometimes work together in a response/reinforcement sharing fashion. In this situation two rats potentially could obtain more food collectively than each could separately for relatively the same amount of work. Sometimes when two rats were at the same station one rat would retrieve a food pellet while the other took up bar pressing. The latter would then retrieve a pellet and the former rat would then start to bar press so that the two were generally switching places after every reinforcement was delivered. The time spent in switching used up time that would otherwise have been spent making non-reinforced bar presses. Therefore fewer bar presses were made before a reinforcement was produced. For instance, under VI5 one rat may make 15 responses, on average, to obtain one food pellet where as two rats working together at the same station may impede each other's access to the bar using up time so that on the average only 10 responses occurred before a reinforcement was delivered. In other instances roaming rats would pick up free pellets that other rats produced without themselves pressing the bars.

Clusters of two or, to a lesser extent, three rats per station reduced the COP ratio whereas clusters larger than this reduced this advantage at local food sites, e.g., one pellet per eight rat aggregation is less advantageous than one pellet per rat. Under each schedule then, there are limits to the type of foraging behaviours that can be engaged in at any one time. The schedule creates a saturation point which when surpassed by a critical number of the members results in less food obtainment for the population members collectively because the probability of reinforcement decreases. This also helps to explain why there was a certain level of stability in the extreme schedules VI5 and VI80. An individual rat can increase its amount of food intake by cooperating with the other organisms rather than competing independently and without regard for the behaviour of its fellow mates. An individual rat can obtain more food for less effort by working with, rather than apart from, the other rats in the colony when the rate of reinforcement is very high as in VI5 or very low as in VI80.

The mid-VI schedules tended to encourage independent foraging. The effect of the contingencies under VI10 and 20 did not encourage COD in the form of travelling and waiting. Empty food stations and rats working at other food sites do not act as a positive SD under these schedules (Goldstein, 1981a: Goldstein and Mazurski, 1982). This may happen because they do not increase the probability of reinforcement to a point greater than that which could be obtained by working alone. A regular dispersion would, in this case, have a positive SD advantage. Further more, once bar pressing commenced, it would be disadvantageous to leave because of the likelihood of increasing the COP by making possibly more bar presses at another food site and risking a further delay in the obtainment of a food pellet. In VI10, 20 and 40 dispersion regularity hypothetically leads to maximization throughout each session. Too much movement or clumping would increase the incidence of missed and therefore unretrievable food pellets. Leaving a food station vacant increases the probability that a pellet is scheduled to be delivered but can not be delivered without a bar press at that station. Each pellet that is left waiting in this way leads to a reduction in the total number of obtainable pellets for that session. Grouping under these schedules acts as a negative SD in that when a roaming rat approaches, after the resident rat has been bar pressing, the resident rat is at a high

COP disadvantage if the roaming rat eats the pellet before the resident rat has the chance. The rats discourage their mates from coming near the food trough by hovering over the food trough and/or batting the other rat away. In this way a resident rat was a negative SD and therefore may have helped to lower the frequency of roaming by other rats. As the schedule increased to VI80 a regular dispersion would lower the COP advantage gained by the stay/never-switch strategy adopted during the mid-VI schedules. Clumping, roaming, and waiting become SD's for reinforcement under VI80 but not under the mid-VI schedules.

Conclusions

How can the observed curvilinear relationship between regularity and schedule value be explained in measurable and predictable ways? Descriptively, a curvilinear relationship indicates change in foraging strategy. It is a change in the accumulation of effects of the individual members such that each simultaneously and independently chooses a different strategy in order to achieve the greatest adaptive advantage in the least time in wake of the possibility that the competition or, environmental conditions, do the worst (Smith, 1978). In order to operationalize this description the nature of choice, adaptation and time need elaboration.

Choice herein, does not infer the rationality or irrationality in a cognitive or motivational sense. Rather, it indicates a course of action (behaviour) (Rachlin, 1980). The term adaptation implies fitness based on some criterion. Theory of adaptation assumes that the fitness of a foraging organism is a function of the efficiency of foraging measured by some "currency" (usually energy). Natural selection (adaptation) has resulted in animals that forage so as to maximize this fitness (Pyke, Pulliam and Charnov, 1977). By definition, when an organism reaches total fitness it would no longer evolve (Smith, 1978).

Maximizing fitness has come to be described partially in terms of models of optimal foraging. Optimal foraging is described generally as the tendency of an organism to maximize its rate of energy intake while minimizing energy output per unit time (Krebs, Kacelnik and Taylor, 1978; Staddon, 1980). The aim of optimal foraging theory is to provide an objective framework in which to analyse behaviour and environmental forces which are consistent with natural observation (Real, 1980). Nature shows that there is interdepedent feedback between behaviour and environment such that adjustment in one creates change in the other (Baum, 1981; Berryman, 1981; Staddon, 1980). Behaviour, in these terms, is guided by the outcome it produces and reinforcement is the label given to that outcome by which operant behaviour is guided (Staddon, 1980). From this definition adaptation now can be described in terms of optimal foraging theory which itself can can be viewed in terms of rates of response (dispersion) and reinforcement (food obtained per unit of time). Optimal foraging can be further measured by using other operant terminology, e.g., level of efficiency (POFO) and COP in relation to specific patterns of dispersion under specific VI schedules of reinforcement.

Response and reinforcement in terms of energy output/input are dynamically interdependent. The absolute value of the reinforcer, which in itself includes a certain amount of responding (Staddon, 1980), is flexible over time. An organism will work at different rates for the same amount of food, depending on whether it has access to other food; sources (Hursh, 1980) or whether or not the food's stimulus value changes from positive to neutral (once the organism becomes satiated) (Real, 1980) or changes from positive to aversive (under different schedules of reinforcement) (Rachlin, 1980). In this study the number of reinforcers available decreased while the corresponding percentage obtained continued to increase as the VI values increased. In addition, both the regularity of dispersion and the number of responses made first increased and then decreased curvilinearly as the VI values increased.

A high level of efficiency does not necessarily indicate that optimal foraging has been reached (except by definition in terms of 100% POFO). Measures of efficiency, nonetheless, can define whether or not a foraging tactic is statistically optimal either immediately or in the long term. If an organism's food requirement is much less than the amount of food available and it is satiated, then additional food procurement becomes less than optimal in the short term because the organism is still working but eating less and therefore the COP would be high. Even if there is an increase in the POFO and a decrease in COP it may not indicate that the organism is foraging optimally (to the point where maximum adaptive fitness is reached). Rather, the strategy being used could at best be considered to be approaching an optimal level of adaptive fitness under the existing environmental conditions.

Determining the fitness by calculating COP tells little about the maximizing value when the figures are used out of context (Baum, 1981). Part of the problem is that the measures of efficiency are not absolute and therefore very difficult to quantify. For instance, COP ratios by themselves do not indicate the optimal level of foraging. The usefulness of the COP is that it provides an inference about what is more optimal. The problem with COP ratios is that they lie on a continuum between infinitely small and infinitely large. Smaller is better but does not necessarily represent perfect fitness. As an example of this, Allison (1981) compared baseline free responding for food to contingent responding for food and found that the COP's were not equivalent. The animals procured less than the maximum rate of reinforcement found under baseline free responding conditions. This shows that maximizing does not necessarily imply perfect fitness. Rather, it is a description of the best COP obtainable under the prevailing environmental contingencies.

There is also a problem with the POFO measure in describing optimal foraging. The POFO by itself does not provide a reliable measure of optimal foraging. It fails to provide specific information about caloric output or input in regard to meeting daily nourishment needs. One hundred percent efficiency is "optimal" in a tautological sense and anything less, by definition, would not be "optimal." This conception of "optimal" in terms of POFO fails to suggest whether the total amount of pellets obtained (be it 100% or not) is sufficient to meet an organisms energy requirements. From this perspective POFO could be small (e.g., 5%), and yet more than meet an organism's caloric requirements. This fulfills the criterion of optimal foraging strategy. In some cases even though POFO is 100% the foraging may be "optimal" yet not necessarily adaptive (i.e., when evolutionary change does not keep up with a rapid change in the environment leading to extinction). From this conception it can be seen that adaptation is contingent upon optimal foraging strategy such that the more productive the strategy, in terms of COP and POFO, the greater the fitness. However, this does not suggest that optimal foraging strategies ensure adaptation.

Finally, the element of time needs elaboration in order to complete the present analysis of optimal foraging. That is, can optimal foraging best be analysed in short term or long term acquisition of food and is it a function of either probability or rate of reinforcement? In response to the former part of the question, the optimal response to reinforcement ratio has been viewed in terms of both local (short term) time intervals and global (long term) time intervals. Local and global time intervals are on an infinite time continuum and therefore arbitrary time parameters have been designated for the study of optimal foraging. Maximizing food obtainment can be measured from moment to moment, over a feeding session, or for a lifetime. This shows that optimal foraging does not have to be confined to the study of only one time frame. In many cases it has been found that organisms change their strategy over the long term. An organism may maximize the probability of reinforcement globally at some times (as seen in VI5 AM, VI10, 20, 40, and 80); locally, at other times (as seen in VI5 PM) and both locally and globally within a given time frame. Mellgren (1982) has shown that rats will search all food patches in a new habitat thus discovering the probability of reinforcement at each food site. This is an inefficient method of foraging in the short term because time is wasted at low probability food sites. This is an example of a conservative foraging strategy which promotes global maximizing and is used by time maximizers. Once the rat sampled the food patches a change in foraging strategy was observed. The rat spent more time and effort procuring food at the sites that had the highest probability of reinforcement. This exploitive foraging strategy likely produces local maximizing. It is quite conceivable that an organism also adapts a strategy that comprises both the conservative and exploitive strategies which may produce neither local nor global maximizing within a feeding session. In this hypothetical, middle of the road, strategy an organism would spend some of its time and effort exploitively but also use conservative strategies if the probability of reinforcement went below a certain level.

In response to the latter part of the question regarding rate or probability as a controlling factor, the literature shows that in terms of moment to moment conditions maximizing the probability of reinforcement (local maximization) is different from maximizing the rate of reinforcement from moment to moment (melioration) (Herrnstein and Vaughan, 1980). Just as animals may hypothetically use both conservative and exploitive foraging strategies, they may also make use of both rate and probability of reinforcement as cues to optimal foraging. That is, a rat may determine the probability of reinforcement from the rate of reinforcement and note a change in probability when the rate changes (Staddon, 1980). The questions regarding local versus global strategies and rate versus probability of reinforcement may be answered by asking how and to what extent are these parameters important to optimal foraging rather than which are important.

Optimal foraging has been described above in terms of the factors that are used to measure it. Emphasis has been placed on the notion that an organism will try to use a foraging strategy that produces the most benefits in the least amount of time. In behavioural language an organism will disperse itself and respond in a way that creates either the highest rate and/or probability of reinforcement. The present study shows that ecological data can be studied experimentally and in terms of operant behavioural principles which may lead to a useful methodology for the prediction of population trends. Thus dispersion and density can be analysed in terms of time maximization or minimization, switching choice, open or closed systems and discriminative stimulus control. This information can then be used to aid in planning resource allocation and availability in a systematic manner.

REFERENCE NOTE

Goldstein, S. R., Johnson, P. A. and Ward, G. T. (1984). Schedules of reinforcement as regulators of dispersion patterns. Manuscript presently under review for publication.

REFERENCES

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

Allison, J. (1981). Paired baseline performance as a behavioral ideal. *Journal of the Experimental Analysis of Behavior*, *35*, 327-366.

Baum, W. M. (1982). Choice, changeover and travel. *Journal of the Experimental Analysis of Behavior*, *38*, 35-49.

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

Baum, W. M. (1981). Optimization and the matching law as accounts of instrumental behavior. *Journal of the Experimental Analysis of Behavior*, *36*, 387-403.

Berryman, A. A. (1981). *Population systems: a general introduction*. New York: Plenum Press.

Birch, L. C. (1965). *The role of weather in determining the distribution and abundance of animals*. In E. J. Kormondy (Ed.), Readings in ecology. New Jersey: Prentice-Hall Inc.

Blenkkenhorst, H. J. and Goldstein, S. R. (1983). A PET interface to control reinforcement delivery. *Behavioural Research Methods and Instrumentation*, *15*, 398.

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

Caswell, H., Koenig, H. E., Resh, J. A., and Quentin, R. (1972). *An introduction to systems science for ecologists*. In B. C. Patten (Ed.), Systems analysis and simulation in ecology. New York: Academic Press.

Chitty, D. (1970). *Animal numbers and behavior*. In L. Adams (Ed.), Population ecology. Belmont: Dickson Publishing Co.

Colinvaux, P. (1978). *Why big fierce animals are rare*. New Jersey: Princeton University Press.

Covich, A. P. (1976). Analysing shapes of foraging areas: some ecological and economic theories. *Annual Review of Ecology and Systematics*, *7*, 235-257.

Curio, E. (1976). *The ethology of predation*. New York: Spinger-Verlag.

Davies, N. B., and Houston, A. I. (1981). Owners and satellites: the economics of territory defence in the pied wagtail, Motacilla Alba, *Journal of Animal Ecology*, *50*, 157-180.

Dempster, J. P. (1975). *Animal population ecology*. London: Academic Press.

Eibl-Eibesfeldt, I. (1975). *Ethology: the biology of behavior*. New York: Holt, Rinehart, and Wilson.

Elton, C. (1971). *Animal ecology*. London: Methuen and Co.

Emmel, T. C. (1973). *Ecology and population biology*. New York: W. W. Norton and Co.

Fantino, E., and Logan, C. A. (1979). *The experimental analysis of behavior*. San Francisco: W. H. Freeman and Co.

Fraser, D. F., and Thomas, E. S. (1980). Observations on stream minnows in a patchy environment: a test of a theory of habitat distribution. *Ecology*, *61*, 790-797.

Fretwell, S. D. (1972). *Populations in a seasonal environment*. New Jersey: Princeton University Press.

Giesel, J. T. (1974). *The biology and adaptability of natural populations*. St. Louis: The C. V. Mosly Co.

Goldstein, S. R. (1981a). Schedule control of dispersion and density patterns in rats. *Behavioral Analysis Letters*, *1*, 283-295.

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

Goldstein, S. R., Blenkkenhorst, H. J., and Mayes, L. W. (1982). Computerization of the operant arena. Behavior Research Methods and Instrumentation, 14, 369-372.

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

Graft, D. A., Lea, S. E. G., and Whitworth, T. L. (1977). The matching law in and within groups of rats. Journal of the Experimental Analysis of Behavior, 25, 183-194.

Grant, P. R. (1972). Interspecific competition among rodents. Annual Review of Ecology and Systematics, 3, 79-106.

Grott, R., and Neuringer, A. (1974). Group behavior of rats under schedules of reinforcement. Journal of the Experimental Analysis of Behavior, 25, 183-194.

Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. OIKOS, 38, 210-221.

Herrnstein, R. J.)1974). Formal properties of the matching law. Journal of the Experimental Analysis of Behavior, 21, 159-164.

Herrnstein, R. J and Vaughan Jr., W. (1980). Melioration and behavioral allocation. In J. E. R. Staddon (Ed.), Limits to action. New York: Academic Press.

Holling, C. S. (1959). The components of predation as revealed by a study of small- mammal predation of the European Pine Sawfly. The Canadian Entomologist, 91, 293-320.

Houston, A., and McNamara, J. (1981). How to maximize reward rate on two variable-interval paradigms. Journal of the Experimental Analysis of Behavior, 35, 367-396.

Huffaker, C. B. (1958). Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia, 27, 343-383.

Hursh, S. R. (1980). Economic concepts for the analysis of behavior, Journal of the Experimental Analysis of Behavior, 1980, 34, 219-238.

Krebs, C. J. (1978). Ecology: the experimental analysis of distribution and abundance (2nd ed.). New York: Harper and Row.

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

Levin, S. A. (1976). Population dynamic models in heterogeneous environments. Annual Review of Ecology and Systematics, 7, 287-310.

Lewis, T., and Taylor, L.R. (1967). Introduction to experimental ecology. London: Academic Press.

Mac Arthur, R. H. (1972). Geographical Ecology. New York: Harper and Row.

Margalef, R. (1965). On certain unifying principals in ecology. In E. J. Kormondy (Ed.), Readings in ecology. New Jersey: Prentice-Hall Inc.

Mellgren, R. L. (1982). Foraging in a simulated environment: there's a rat loose in the lab. Journal of the Experimental Analysis of Behavior, 38, 93-100.

Murdock, W. W., and Oaten, A. (1975). Predation and population stability. Advances in Ecological Research, 9, 1-131.

Odum, E. P. (1965). Relationships between structure and function in ecosystems. In E. J. Kormondy (Ed.), Readings in ecology. New Jersey: Prentice-Hall Inc.

Phillipson, J. (1967). Ecological energetics. London: William Clowes and Sons Ltd.

Pimentel, D. (1966). *Complexity of ecological systems and problems in their study and management*. In K. E. F. Watt (Ed.), Systems analysis in ecology. New York: Academic Press.

Pyke, G. H., Pulliam, H. R., and Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, *52*, 137-154.

Racklin, H. (1980). *Economics and behavioral psychology*. In J. E. R. Staddon (Ed.), Limits to action. New York: Academic Press.

Real, L. A. (1980). *On uncertainty and the law of diminishing returns in evolution and behavior*. In J. E. R. Staddon (Ed.), Limits to action. New York: Academic Press.

Smith, M. J. (1978). Optimizing theory in evolution. *Annual Review of Ecology and Systematics*, *9*, 31-56.

Staddon, J. E. R. (1980). *Optimality analysis of operant behavior and their relation to optimal foraging*. In J. E. R. Staddon (Ed.), Limits to action. New York: Academic Press.

Skinner, B. F. (1969). *Contingencies of reinforcement: a theoretical analysis*. New York: Appleton-Century-Crofts.

Soloman, M. E. (1969). *Population dynamics*. New York: St. Martin's Press.

Stueck, K. L., and Barrett, G. W. (1978). Effects of resource partitioning on the population dynamics and energy utilization strategies of feral house mice (Mus musculus) populations under experimental field conditions. *Ecology*, *59*, 539-551.

Terborsh, J. (1971). Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the Avifauna of the Cordillera Vilcabamba, Peru. *Ecology*, *52*, 26-36.

Watt, K. E. F. (1966). *The nature of systems analysis*. In K. E. F. Watt (Ed.), Systems in ecology. New York: Academic Press, 1966.

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

Wilson, E. O. (1975). *Sociobiology: the new synthesis*. Cambridge, Mass.: Harvard University Press.

Wynne-Edwards, V. C. (1962). *Animal dispersion in relation to social behaviour*. Edinburgh: Oliver and Boyd.