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Optimal time vs distance: A study of optimal foraging theory

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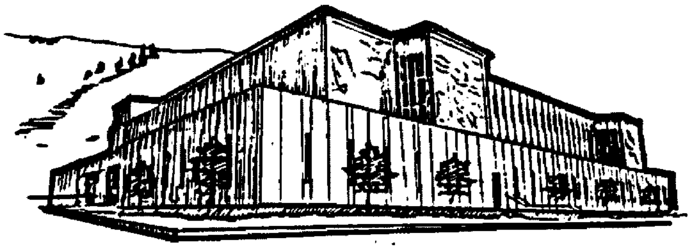

OPTIMAL TIME VS DISTANCE:
A STUDY OF OPTIMAL FORAGING THEORY

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Optimal Time vs. Distance:
A Study of Optimal Foraging Theory (81 pp.)

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Sociobiological explanations of the foraging activities of most animals involve a cost/benefit analysis of the behavior of the foraging animal. Optimal foraging theory is a more complete explanation of the sociobiological cost/benefit model. An assumption of optimal foraging theory is that animals who are the most proficient at determining the correct foraging costs with regard to benefits, will survive longer and reproduce more offspring.

One problem with testing this assumption is that it is very difficult to arrive at meaningful dependent measures. Therefore, preliminary investigations into optimal foraging theory must include the determination of variables that the animals under study find important. This investigation was designed to determine which of two variables, time or distance, is the most important to foraging rhesus macaques. Using a video-game format, two rhesus monkeys were presented with a foraging situation in which the longest distance path to a prey object was the shortest time path. The shortest distance path took more time to traverse than the longer, quicker path. Choice of the optimal time path by the monkeys indicated a preference for time minimization, and choice of the optimal distance path indicated a preference for distance minimization. Several control conditions were used to test the effects of absolute speed and position bias. Monkey A chose the time solution for the first half of the experiment, and a combination of the time and distance solution for the second half of the experiment. Monkey B chose the distance solution for the entire experiment. The consistency of the choices made by the animals indicate a preference for one or the other optimal solutions, meaning that the animals did chose to use one of the optimal pathways instead of using neither. However, the individual selections of the animals may be due to an order effect and not to variance within the species.

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Introduction

Optimal foraging theory is based on the notion that since all animals require food, the animals that are the most efficient at attaining food are the animals that will contribute the most genetic material to the species' gene pool. Since the genetic material contributed will have some inherent variability, the process of natural selection will result in ranges of possible foraging behaviors that maximize fitness. The average behavior of a foraging animal in any given situation should be close to that which maximizes fitness (Pyke, Pulliam, and Charnov, 1977). Smith (1983) states that while the exact currency of fitness cannot be measured, proxy currencies are used. Usually, the measured currency that an animal optimizes is the net rate of energy intake or total nutrients per unit foraging time.

Pyke et al. (1977) and Pyke (1984) suggest that there are five areas of optimal foraging theory that should be studied, four of which are decisions the animal must make when foraging, and one based on where the animal begins when foraging. These decisions are: 1) Which patch types to visit. 2) How long to stay in each patch. 3) Which food types to eat in each patch. 4) Which foraging path to employ in each patch type. The fifth category of optimal foraging literature is called central place foraging, which includes studies on how animals forage when their home site or nest is located in one particular spot to which they must return after foraging. The other four decisions are also pertinent to central place foraging.

The present study investigated the fourth decision the animal makes, which concerns the optimal path to employ. This literature review will emphasize research concerning optimal speeds of movement and optimal pathways.

Surprisingly little research has been done on the movement of foraging animals, and most of the existing literature is concentrated on between-patch behavior. However, if a patch can be conceptualized in the same way as a single food object (which sometimes occurs within patches) the results of the between-patch literature can be applied to within-patch movement as well.

Pyke (1984) in a critical review of optimal foraging theory presents an analysis of models of foraging movement. These models contain the assumption that movements of an animal that increase the rate of food intake also increase fitness in a linear fashion. One of the two models that he reviews predicts an optimal direction to a food item based on the probabilities with which animals will turn in one of four directions. If 1.) the direction of movement depends only on the direction of the previous movement, 2.) movements can only occur between one point on a grid and one of its four nearest neighbors, and 3.) the animal obtains no food at revisited grid points, the optimal pathway is uniquely determined by the probability of the animal going backwards subtracted from the probability of the animal turning right. These probabilities are obtained by discrete approximation to a normal distribution with a mean angle of 0 degrees and a range of +180 degrees to -180 degrees. The optimal directionality minimizes path recrossing. Using computer simulation, Pike also showed that the optimal directionality prediction increases with increases in the size of the grid. When the time of the foraging bout was limited, the optimal direction depended on the behavior of the animal at the grid boundary. For realistic grid sizes and foraging bout lengths, the model predicts directionalities with very little turning.

The second model that Pyke (1984, 1977) reviews predicts that animals will move linearly from one randomly distributed resource point to the next, closest resource point when the animal does not know in advance the contents of the resource points.

The first model seems to explain within patch movement, while the second explains between patch movement. Both models predict that the animal will move linearly toward a prey object or patch with minimal turning. However, Zimmerman (1979) points out that optimal directionality should decrease if food renewal is rapid or if the animal leaves some of the available food. Under these circumstances, random movement could be expected. This conclusion is valid under conditions in which the animal is free to forage for as long as it likes. If the amount of time allotted to foraging is limited, the animal should forage as efficiently as possible for that amount of time.

Cody (1974) and Pyke (1977) argue that animals will exhibit patterns of movement which result in the maximum net rate of food intake and that this path would be one in which the animal's frequency of path recrossing were minimized. All things equal, the most optimal path to a food object would obviously be a straight line. But in the natural environment, all things are not equal and the animal must confront obstacles that may change its speed of movement, the direction of its path, and the distance it must cover to come in contact with a prey object.

Speed of movement is an important variable in determining the efficiency with which an animal gathers food. Cody (1974) suggests that one reason hawks may situate their nests centrally within their foraging territory, (or their foraging territory around their nests) would be to minimize the time taken to get to any point in the territory, gather food, and return to the nest. Confounded with this finding, however, is the fact that by centrally locating the nests the hawks have also decreased the distance they must cover.

Many studies in foraging literature support the idea that animals prefer to feed in patches with the highest intake per unit time. Lewis (1980) studied the behavior of gray squirrels and found that they chose patches in which they could eat the most nuts per unit time. Fantino and Abarca (1985) found that animals maximize reinforcement using the shortest VI schedule available.

Logue, Smith, and Rachlin (1985) in a study to determine the sensitivity of pigeons to post vs. pre reinforcement delays found that pigeons tend to act impulsively and always choose the reinforcement with the least amount of prereinforcement delay. The pigeons make this choice even when a larger reinforcement is offered for a larger prereinforcement delay, and even when the density of reinforcement is increased with longer prereinforcement delays. In other words, the pigeons do not maximize reinforcement over long intervals but instead always choose the schedule of reinforcement that offers the reinforcement closest to the actual operant behavior. This is consistent with Mazur's (1981) finding that animals choose to match their behavior with the presented schedules of reinforcement even when in doing so they do not maximize their total rate of reinforcement. However, Logue et al (1985) conclude their article with the statement that outside of the laboratory, prereinforcer delay often varies inversely with the rate of reinforcer access. Therefore, the pigeon may be using a rule of thumb that is very useful in its natural habitat over long intervals.

Pyke (1981) in a computer simulation of animal foraging behavior found that by making the prey completely seen to the animal, and by assuming that all encountered food items are detected, the optimal search rate was the maximum speed that the animal could sustain over the search period.

One conclusion that can be drawn from these articles is that the animal may seek to minimize the amount of time spent foraging while maximizing the amount of food gathered. The mechanism that the animal uses for doing this may be that the animal seeks situations in which it can gain an immediate reinforcement for its efforts. No matter how the data are interpreted however, one obvious conclusion is that animals try to obtain the most food possible during foraging time (Fantino and Abarca, 1985).

Distance between patches is usually confounded with time between reinforcements in most tests of this kind. Pyke (1981) investigated the visual cues a hummingbird uses when deciding which patch of flowers to forage in and found that the birds did not use distance information alone but also used a measure of the number of flowers per patch. Pyke (1981) found that the best predictor of movement was made by evaluating which flower patches had the greatest n/d ratio, where n is the number of flowers in the patch and d is the distance to the patch. Obviously, the shorter the distance to the flower patch, and the more flowers per patch, the more attractive it is to the birds. However, the shorter distances also involve shorter flight times.

Mellgren, Misasi, and Brown (1984) found that rats stayed in a patch and foraged for longer periods of time when the travel between patches was difficult. They defined difficult travel as longer distances that took more time to cover. When travel was easy, the rats stayed in each patch for shorter amounts of time and visited more patches. Again, from this study it is difficult to tell whether the animal is basing its giving up time decision on effort, time between patches or distance between patches.

MacDonald and Wilkie (1990) investigated the spatial memory of yellow-nosed monkeys in a simulated foraging environment and found that the animals had very efficient spatial memories. The experiment was designed to test the memory of the monkeys on two types of memory problems using eight separate food cups located on eight separate sites within the foraging environment. The first problem, the win-shift problem, involved baiting four of the food cups, allowing the monkey to find the four food items, removing the animal, baiting the other four food cups, and after a specified amount of time allowing the monkey to forage in the patch again. The monkey exposed to this problem was very efficient at visiting the sites in which he had not found food the previous time. The second problem, the win-stay problem, involved baiting four of the food cups, allowing the monkeys to find the four food items, baiting the same four food cups, and after a specified period of time allowing the monkeys to forage in the patch again. The monkeys were very efficient at returning to the same sites in which they had previously found food. One important finding of this study was that the monkeys minimized the distance traveled between food cups in the re-search phases of the experiment. Although no time constraint was imposed on the animals, and they were in no way food deprived, they traveled using the most efficient pathway between baited food cups. They also minimized the total distance traveled by picking the next closest site from the one they were currently visiting. Time did not seem to be important to the animals because once they reached the food site, they examined the cup itself at length. However, it is possible that the animals were minimizing travel time for some other reason.

This leads to the central question of the present research. Do rhesus monkeys optimize while foraging using time or distance?

Krebs, Stephens, and Sutherland (1983) state that optimal foraging models do not test the idea that animals forage optimally. Rather, they test the constraints under which optimality occurs and the specific mechanism used by a species to solve foraging problems. However, Meyers (1983) asserts that the question of whether an animal optimizes at all is also an important one. He also maintains that there are several reasons for why an animal may not optimize, including phylogenetic constraints and trade-offs. Although it is possible to find an overall optimal strategy for living, it may not be possible to pin down optimal foraging strategies. The question of whether Rhesus Macaques will optimize at all during foraging is addressed in this study, as well as whether the monkeys use time or distance as an optimal criterion and whether that choice changes as a function of absolute speed of movement.

Rationale

The procedure for the current experiment involved the use of the graphics capability of a Commodore 64 computer used in the same way as most commercial video games. This methodology provided visual information about the contingencies for reinforcement to the animal. The videogame format was such that the animal maneuvered a Pacman figure on a television monitor with a joystick. Pilot work using this methodology demonstrated effective control of the monkey's behavior through this presentation of visual stimuli. The animals appear to make the association between their movements of the joystick and the movements of the Pacman figure on the screen.

The procedure described in this paper used this methodology to assess the monkeys' ability to choose an optimal path to a red-square prey object, and to make a decision as to whether to make that choice on the basis of time or distance. This was done by presenting a video screen to the animal containing two separate sections, one in which the speed of the Pacman movement was faster than the speed of movement in the other section. These two sections will henceforward be called media. The ratio of allowable speeds within the two media was such that in some phases, the animal could choose a pathway that covered less distance but took more time than a longer, quicker pathway. The speeds of the ratios chosen reflect pilot work that suggested that if the Pacman travels at fewer than about 10 pixels per second, the animal becomes frustrated and performance declines. If the Pacman travels at speeds of more than about 100 pixels per second, the animal looses the ability to completely control Pacman movement. Phases were also included in which the ratio of the two media were such that there was only one pathway that optimized both time and distance. The results from these single pathway phases were used to answer the question of whether the animals chose to optimize during this task at all.

Pyke (1984) discusses the sampling behavior of animals with regard to optimality and states that if there is a known amount of time remaining for foraging, an animal should allocate some of that time to sampling the environment (also Krebs, Kacelnik, and Taylor, 1978). As applied to this study, it may be optimal for the animals to sample the environment somewhat. In order to allow the animals to sample the environment on a regular basis without detracting from the actual test trials in this study, and to allow some assessment of motivation to be made, pretest trials were introduced every five trials. These pretest trials consisted of the placing of a prey-object directly below or across from the Pacman starting position in both media which allowed sampling behavior.

Smith (1983) offers several criteria for operationalization in a good test of optimal foraging theory. These criteria and the counter parts in the present study were as follows:

1). Currency (such as energy). In the present study the currency of fitness was the net energy intake, which was presumed to have a direct influence on fitness. The energy allotted to the monkeys was 28 biscuits of monkey chow (61 grams), which was approximately the free feeding intake of the monkeys.

2). A set of constraints or factors that limit the range of options for the duration of the process studied. The constraints in the present experiment were the limited amount of food, the limited space available for foraging, and only one choice of food item.

3). A set of options to be left open to the forager. The choices left open to the foraging animal in this study are which of an unlimited number of paths to use: and if the animal chooses to optimize, a choice between whether to optimize using time or distance.

Rhesus monkeys energy requirements should be fixed in the present housing situation, and they require time for other tasks such as grooming. Therefore, a prediction was made that the fitness of the animal should be greatest when it minimizes the time it takes to get from the starting point to the prey object, which would minimize the time spent foraging. However, when the ratio between the fast and slow medium is such that the time differential between optimizing in terms of time or distance is minimal, a prediction was made that the monkeys' behavior would be randomly distributed between the two options.

Do monkeys choose to forage in an optimal manner? If they do choose to behave optimally, is time or distance the important component to optimize? The design and methodology of this optimal foraging experiment was used to asses the efficiency of the animal's behavior with regards to these questions.

Method

Subjects

The subjects in this study were two male Rhesus monkeys (Macaca mulatta), each approximately 5 years old. Both subjects have had shaping experience using the video game apparatus. Neither of the animals had experience with the present task. The animals were reared in social group housing, and rotated periodically into separate cages in which all testing occurred. The study was done under conditions of a closed economy where the animals were maintained at approximately their free feeding weight, with one of the animals experiencing insignificant weight loss. Food given during testing consisted of 9 1/3 biscuits of Purina Monkey Chow (65 grams), cut in thirds. A half orange was provided at random intervals about four hours after the end of each session.

Apparatus

The testing chamber consisted of the monkey's home cage (61 cm x 92 cm x 61 cm) attached to a removable cart containing a monitor, Commodore joystick, feeder, and camera apparatus connected to the front panel. Water was available in the home cage at all times. The monitor was placed approximately 15 cm from the face of the cage. The joystick was centered beneath the monitor and protruded out from the apparatus 8 cm into the home cage where the monkey had access to it when sitting near the front of the cage. The feeder dispensed single biscuit chunks into a bowl on the right side of the monitor for Monkey A, and on the left side of the monitor for Monkey B.

The task was programmed in PROMAL on a Commodore 64 machine. The computer controlled the feeder reinforcement dispensers and recorded data onto floppy discs for permanent storage. Monitors were also installed in an adjacent experimental control room so the monkey's progress could be observed. Monkeys were watched via a camera installed on the top of the cart and pointed at a split mirror over the testing chamber.

Procedure

Shaping. Both monkeys underwent a systematic shaping procedure to guarantee familiarity with the apparatus and the testing situation. The shaping procedure consisted of exposing the animal to a program in which red-square prey figures (3 mm by 3 mm) were arranged at varying distances from the centrally located white Pacman figure (5 mm in diameter) on a blue screen background. The monkey then moved the Pacman with the joystick toward any one of the prey figures. When the Pacman figure overlapped with a prey object, a reinforcement was dispensed. Movement of the Pacman figure consisted of linear movement (up, down, right, and left) accompanied by opening and closing of the Pacman mouth. Nine pixels were traveled from the time the Pacman mouth opened to the time it closed.

The number of captured prey items required for the screen to be reset to its original position ranged from 1 to 7. The distance from the Pacman figure to the prey object ranged from 1 to 20 (5 mm to 8 cm). The number of trials was thirty. The monkey's were trained on the Shape program until a criterion of 7 prey items per reset at distance 20 (about 8 cm) was reached for five consecutive days. The animals continued at this level for 45 days, or 1350 trials. The number of reinforcements per day was 30 (65 grams). Both monkeys in the present study successfully completed the shaping program with an average session time of 15 minutes. Both monkeys showed the ability to move in all directions, including diagonally.

Testing

The present study consisted of a task in which the computer screen was divided into two parts. One part of the screen was the fast medium, which was the width of the screen (200 pixels) and the height of the Pacman figure (20 pixels). The remaining part of the screen was the slow medium and was 200 pixels across and 180 pixels in height. The object of the task was for the monkey to move the Pacman across the fast medium until the edge of the screen, and then to shift into the slow medium and travel toward a red 20 by 21 pixel square (3 mm by 3 mm) designated as a prey object, or to move the Pacman along a diagonal line to the prey object. Upon the Pacman figure's "eating" of the red square prey object, the monkey received 1/3 of a biscuit.

In order to provide an opportunity for the monkey to determine which of several conditions it was in, two types of pretest trials were presented at the beginning of the session and every five trials afterward. There were two purposes for the pretest trials: 1.) to expose the animal to the ratio condition it would experience in subsequent trials. 2.) as an indicator of the motivational level of the animal.

In the pretest trials the prey object was located 180 pixels across the screen from the Pacman in the fast medium in one instance and 180 pixels above or below (depending on which phase was currently being tested) the Pacman on the screen in the slow medium in the other. Measurements during the pretest trials consisted of the total amount of time per reinforcement, and an efficiency ratio of the number of pixels in the best path over the number of pixels in the path the animal traveled. Although this ratio was peripheral to the study, it was used to gauge changes in motivation and motor skill coordination. The pretest trials were ordered at each presentation, with the first pretest trial through the fast medium, and the second through the slow medium for each series of pretest trials for each day. The first optimality trial of the session was then presented.

There were 8 kinds of trials, four different ratios, and two sets.

The trials were labeled 1a, 1b, 2a, 2b, 3a, 3b, 4a, and 4b. An "a" trial was a trial in which there were two possible "optimal" solutions. The first optimal solution was one in which the animal traveled across the fast medium and then through the slow medium, minimizing time. In the other optimal solution, minimizing distance, the animal traveled on a straight diagonal path from the starting position to the prey object. The "b" trials were trials in which there was only one optimal solution: minimizing both time and distance. This solution was a diagonal line from the Pacman start point to the prey object. For ratio 1, the speed of continuous Pacman movement in the fast medium to the slow medium was 60 pixels per second /9 pps. For ratio 2 the speeds were 60 pps/25 pps. Ratio 1 was used in all "a" trials of Set A, and ratio 2 was used in all "b" trials of Set A. A set was a complete randomized presentation of all Pacman starting positions using the same speed of movement in the fast medium. For Set A the speed of movement in the fast medium was 60 pps.

Ratio 3 was 90 pps/18 pps and was used for all "a" trials of Set B. Ratio 4 was 90 pps/60 pps and was used in all "b" trials of Set B. For Set A, the speed in the fast medium was 60 pps. For Set B, the speed in the fast medium was 90 pps.

For Set A, trial 1a, the Pacman was located at the top, left hand corner of the screen and the prey square was located 180 pixels down the right edge of the screen (see Figure 1). The ratio of the fast medium to the slow medium was 60 pps/9 pps, such that the best strategy to use if the animal was optimizing in terms of time would be to go straight across the top, turn at the right edge of the screen, go straight down the right edge in the slow medium, and eat the prey object. The best strategy to use if the animal was optimizing in terms of distance was to move the Pacman diagonally across the slow medium at a 45 degree angle from the Pacman starting point.

For Set A, trial 1b, the Pacman was located at the top left of the screen with the prey located 180 pixels down on the right edge of the screen (see Appendix B, Figure 1). The monkey was required to move the Pacman in a straight diagonal path to the prey object from the starting point. The ratio of the fast medium to the slow medium was 60 pps/25 pps, such that both time and distance were optimized using this strategy.

The same was true for Set B, trials 1a and 1b, except that ratio 3, 90 pps/18 pps was used in "a" trials and ratio 4, 90 pps/ 60 pps was used in "b" trials.

Trials 2a and 2b were equal to 1a and 1b except the Pacman figure started at the top right-hand corner and the prey object was located 180 pixels down the left edge of the screen (see Appendix B, Figure 1). Trials 3a and 3b were the same as trials 1a and 1b except that in trials 3a and 3b the fast medium was at the bottom of the screen and the Pacman figure started at the bottom right corner (see Appendix B, Figure 2). The prey object was located 180 pixels up the left edge of the screen. Trials 4a and 4b were the same as trials 2a and 2b except that in trials 4a and 4b the Pacman figure began at the bottom left-hand corner of the screen and the prey object was 180 pixels up the right side of the screen (see Appendix B, Figure 2). In this way, a balance was established in order to account for position biases. All trial types were run using both Set A and Set B.

There were 28 trials per session, including the eight pretest trials. Each session consisted of the same type of trial, (i.e. all 20 were of type 1a). Sessions were run in blocks of three days, with the order of presentation determined using the following rules:

1) No two consecutive a or b trials

2) The a and b pair of the same number were not allowed to follow one another.

This procedure was designed to prevent the transference of learning between blocks of sessions. The complete sequence was run through once, 24 days with Set A (ratios 60 pps/ 9 pps and 60 pps/25 pps), and 24 days with Set B (ratios 90/18 and 90/60). Ratios 60/9 and 90/18 were used on all "a" trials and ratios 60/25 and 90/60 were used on all "b" trials. Monkey A was presented with Set A for the first run of 24 days in which all conditions were presented. He was then presented with Set B for the second run of 24 days. Monkey B was presented with Set B for the first run of 24 days, and Set A for the second run. The purpose of the two separate ratios was to control for the effects of absolute speed.

The sessions were run as follows:

1) For Monkey A, the order of presentation for the first run (with Set A) was 2a, 1b, 3a, 4b, 1a, 3b, 4a, and 2b. For the second run (with Set B) the order was 4b, 3a, 2b, 1a, 3b, 4a, 1b, and 2a.

For Monkey B, the order of presentation was 1a, 2b, 3a, 4b, 2a, 1b, 4a, and 3b (with Set B) for the first run. For the second run (with Set A) the order of presentation was 1b, 2a, 4b, 3a, 2b, 4a, 3b, and 1a.

The study was conducted for 48 consecutive days.

The measurements taken from these trials were as follows:

1) The time taken from the first movement of the Pacman figure to when the prey was eaten by the Pacman. The optimal time was divided by this measure to provide the total-time efficiency ratios.

2) The total distance traveled from the first movement of the Pacman figure to when the prey was eaten by the Pacman. The optimal distance was divided by this measure to provide to distance efficiency ratios.

3) The total time in which the animal was moving per trial. The optimal time was divided by this measure to provide the move-time efficiency ratios.

4) Every start, stop, and direction change the animal made. This was measured by recording every x,y coordinate in which the changes occurred, and the order in which they occurred.

5) Move-time was subtracted from total-time to form the down-time measure. This measure represented the amount of time in seconds that the animals were not moving in each trial.

Results

The data generated from this study were analyzed in several ways. Therefore the results and then the discussion section of this document were broken up into three parts: 1) The efficiency ratios, 2) The pathways, and 3) The motivation trials. Since no position biases were seen, the data will not be analyzed by position.

The Efficiency Ratios

For each trial, three efficiency ratios were computed. The first efficiency ratio, the pixel efficiency ratio, was made by dividing the number of pixels in the shortest possible pathway, the optimal pathway, by the number of pixels the animal actually travelled.

The second efficiency ratio, the total-time efficiency ratio, was formed by dividing the shortest amount of time that the monkey could take between the Pacman starting point and the prey object, the optimal time, by the total amount of time the animal required for the completion of that trial.

The third efficiency ratio, the move-time ratio, was formed by divding the optimal time by the amount of time the monkey was actually moving during the trial.

Two comparisons were then made. The information from the comparisons was compiled in Appendix A, Tables 1 through 4. The numbers in the first column of the tables indicate which day the trials came from. The second and third columns of the tables are labeled "time" and "distance". The numbers in the "time" column indicate the number of trials, out of twenty, that the time efficiency ratio was nearer to unity than the distance efficiency ratio when the trials were "a" trials. "A" trials were trials in which there were two disparate optimal solutions, one in which time could be minimized, and one in which distance could be minimized.

The numbers in the third column from the left, the column labeled "distance", indicate the number of trials in which the distance efficiency ratio was nearer to one than the time efficiency ratio for each day of "a" trials.

The numbers in the fourth column, labeled "correct", indicate the number of trials out of 20 that the efficiency ratio for the distance in the correct solution for "b" trials, (the solutions that minimized both time and distance) were closer to unity than to a solution that mimicked the optimal time solution in "a" trials. The numbers in the fifth column, labeled "other", indicate the number of trials out of twenty in which the efficiency ratio using the time pathway for "a" solutions over actual time was closer to unity than the ratio of optimal distance over distance in the correct solution. In other words, the numbers in the "correct" column indicate how many trials out of 20 the animal chose the diagonal solution (which minimizes both time and distance in "b" trials). The "other" column indicates how many trials out of 20 the animal chose a different path.

Due to space limitations in the Commodore 64, 119 starts, stops, and changes of direction was the upper limit of data that could be recorded. When the limit of 119 was reached, the machine went to the next trial and the animal received no reinforcement. The numbers in the sixth column, labeled "missed", indicate how many trials out of twenty in which the animal missed reinforcement for this reason.

The numbers in the seventh column, labeled "not valid", indicate how many trials out of twenty were removed due to a computer malfunction. Since these malfunctions formed a very small percentage of all the trials, these trials were not made up. When this malfunction occurred, the computer skipped that trial and went on to the next one, usually dispensing a reinforcement. There was no consistent pattern to when these malfunctions occurred.

The days are also divided into blocks of three, each block indicating a new Pacman starting position. The eighth column contains the starting point for the Pacman for that set of three days. It can be seen from the table that there is no difference in solution choices based on Pacman starting positions.

The tables containing the results of the comparison between distance efficiency ratios and total-time efficiency ratios for Monkey A can be seen in Appendix A, Table 1, and for Monkey B in Appendix A, Table 3.

These comparisons were made with no ratio criteria used, meaning all valid ratios (no missed trials) were included in the comparison.

Because the move-time measurements were lower than the total-time measurements, the move-time ratios were also compared to the pixel ratios. These comparisons for Monkey A can be seen in Appendix A, Table 2, and for Monkey B in Appendix A, Table 4. These figures should be viewed as a general estimate however due to a data recording problem. Seconds were not added to the move-time measure when the animal made perseveration errors by bouncing the Pacman along the wall. Therefore, the move-time measure may be in error in terms of a one to thirty second range. This error makes the move-time ratios somewhat untrustworthy, but interesting none the less.

The Pathways

Graphing of all of the trials for each animal proved to be unsatisfactory for several reasons. The first reason was that the first two days of each phase for each animal were somewhat erratic, producing lower ratios and unintelligible graphs. Therefore, the comparisons of the efficiency ratios themselves produced a better understanding of the actual choice the animal made. The second reason was that graphing of all of the trials produced 2,688 graphs, which are more than can be examined without confusion. Therefore, only a representation of the third day of select phases will be presented in Appendix C in this document. Figures 3 - 16, Appendix C, are maps indicating where on the screen the Pacman was located at particular times. The x and y axes represent the bottom and left side of the screen. The points (signified by letters and numbers) on the screen are simply mapped pixel locations of the Pacman. The numbers and letters themselves on the screen represent the time points at which the pacman was at that location. Since only starts, stops, and changes of direction were recorded with pixel locations, the time points represent when the monkey was starting, stopping, or changing the direction of the Pacman. Figures 3-9, Appendix C, represent pathways traveled by Monkey A, and Figures 10-16 represent pathways traveled by Monkey B. Figure 3, Appendix C shows one of the better paths traveled by Monkey A when he was attempting to optimize in terms of time. Although the total time taken during this trial was not very low, the plot shows the animal attempting to stay on the optimal path solution. Figure 4, Appendix C shows one of the worst and most unstable trials by Monkey A. The path taken was not direct, and he did not minimize either time or distance. Figure 5, Appendix C shows a representation of the average path traveled by Monkey A during the ratio 60/9pps Since the monkey seemed to oscillate between one of two patterns of behavior, another average path for this ratio was included. This path can be found in Figure 6, Appendix C. Figure 7, Appendix C shows an average path traveled by Monkey A during the 60/25pps ratio. It can be seen clearly that during this ratio, the animal attempted to take the diagonal, correct pathway. Figure 8 Appendix C shows an average pathway traveled by Monkey A during the 90/18pps ratio. Figure 9, Appendix C shows an average pathway traveled by Monkey A during the 90/60pps ratio. Again, it can be seen that the animal preferred the distance solution in this ratio.

Figure 10, Appendix C gives an example of one of the best solutions by Monkey B. His path was a direct diagonal, beginning at 1, to the prey object, located at W. Figure 11, Appendix C gives an example of one of the worst solutions by Monkey B. It can be seen that this worst solution is much worse than the poorest solution by Monkey A. Figure 12, Appendix C, shows a representative path exhibited by Monkey B during the

60/9pps ratio. It can be seen from this representative path that the monkey preferred the optimal distance diagonal solution. Figure 13, Appendix C, shows a representative pathway traveled by Monkey B during the 60/25pps ratio. This plot again indicates that the animal preferred the optimal distance solution. Figure 14, Appendix C, shows a representative pathway for Monkey B during the 90/18pps ratio. Again, the animal chose the diagonal solution. Figure 15, Appendix C, shows a representative pathway traveled by Monkey B during the 90/60pps ratio. This plot again shows the animal choosing the correct diagonal pathway. Figure 16, Appendix C, shows a representation of where Monkey B moved the Pacman during missed pretest trials. It can be clearly seen from this plot that Monkey B moved the Pacman to the area of the screen most frequently reinforced, and continued to bounce the Pacman against the wall until the trial was missed.

The Pretest Trials

The pretest trials were the two trials in which the prey object was inserted directly across from the Pacman starting position in both the fast medium and then the slow medium. The purpose of these trials was to allow the animal to sample both media without contamination of the test trial data and to be able to gauge the motivation level of the animal.

The pretest trials were somewhat successful in allowing the animal to sample the environment. Out of 384 total pretest trials, Monkey A missed six and Monkey B missed 57. Therefore, the animals did sample both media to some extent.

However, the pretest trials were not very good indicators of the motivation level of the animal. Two dependent measures that should be reflections of the animals' motivation level are the number of starts, stops, and changes of direction the animal exhibits per trial, and the amount of time per trial that the animal is not moving, called the downtime. For Monkey A, the correlation coefficient of these two measures for all trials was .40 ($n = 2675$, $p < .05$). For Monkey B, the correlation of these two measures was .34 ($n = 2580$, $p < .05$). These correlations indicate that these two measures are related. The starts, stops, and changes of direction measure for the pretest trials was then correlated with the starts, stops, and changes of direction measure for the next two trials. This correlation was not significant for either animal. The correlation coefficient for Monkey A was .23 (n = 378) and Monkey B was .10 (n = 327). The start, stop, and change of direction measure for each pretest trial was then correlated with the second pair of regular trials. For instance, the first two pretest trials were correlated with trials five and six. The second two pretest trials which occurred on trials eight and nine were correlated with trials twelve and thirteen, etc. For Monkey A, this correlation coefficient, .31 (n = 378), was significant at the .05 level. However, in realistic terms, accounting for 15% of the variance is not very informative. For Monkey B, this correlation coefficient was .13 (n = 327), and was not significant.

The same procedure was followed with the measure of how much time the monkey was not moving per trial, henceforward called the downtime measure. This comparison is not as accurate as the previously described one because of problems with the downtime measure itself. Downtime was calculated by subtracting the amount of time the animal was moving from the total time per trial. As was previously mentioned, the movetime measure did not include time the animal spent bouncing the Pacman against the wall. The correlation coefficient when the downtime measure for the pretest trials was correlated with the next two trials for Monkey A was .095 (n = 378), and for Monkey B was .094 (n = 327). When the downtime measure for the pretest trials was correlated with the next two trials, for example when trials one and two were correlated with trials five and six, the correlation coefficient for Monkey A was .098 (n = 378), and for Monkey B was .052 (n = 327). None of these correlation coefficients were significant.

Discussion

The Efficiency Ratios

The tables containing the summaries for the efficiency ratios (see Appendix A) are very informative and interesting for several reasons. The first reason is that the tables show a definite preference for one optimal solution for each monkey. Monkey A seems to prefer to optimize in terms of time and Monkey B seems to prefer to optimize in terms of distance, at least when examining the comparison of distance and total-time.

Using the comparison of distance and total-time, the pattern used by Monkey A (see Appendix A, Table 1) is very enlightening. He began by choosing the time solution over the distance solution for the first three days. For days four through six, he begins by choosing the same pattern as was the optimal time solution in the previous ratio, however, by day six he has chosen the correct diagonal solution more often than the other solution. For days seven through nine, he begins by choosing the diagonal solution more frequently, but by day nine he has chosen each solution equally often. At this point, it is possible that if this ratio were to be continued to be presented to the animal, its behavior may have shifted over totally to choosing the time solution. On days ten through twelve, he again began by choosing the wrong solution, but slowly shifted over to the correct one. On days thirteen through fifteen, he chose the time solution consistently, and by days sixteen through eighteen, he seems to have learned to understand what ratio he is in and to react accordingly while minimizing time. Days nineteen through twenty-one are again spent minimizing time, with the animal's behavior becoming shifted in the time direction on day twenty-one. For days twenty-two through twenty-four, Monkey A has chosen the correct solution more often than the incorrect one.

Days twenty-five through twenty-seven mark the shift in absolute speed from the 60/9pps and 60/25pps ratios to the 90/18pps and the 90/60pps ratios. The second set of ratios, 90/18pps and 90/60pps represent less of a time differential between the optimal time solution and the optimal distance solution. For the first set of ratios, 60/9pps presents a time differential of six seconds between the optimal time and the optimal distance solutions. For the second set of ratios, 90/18pps presents a time differential of only three seconds between the optimal time and the optimal distance solution. Day twenty-five was the first day of new absolute speeds for each animal.

Days twenty-five through twenty-seven for Monkey A consisted of trials where the correct solution was the diagonal. Monkey A spent the majority of his trials in the correct pathway. Days twenty-eight through thirty however, presented a radical shift from the solution chosen on the first twenty-four days of play. On days twenty-eight through thirty, Monkey A chose the distance solution more frequently than the time solution. Explanation of this finding is confounded by the fact that the animal had just experienced six straight days in which the correct solution had been the diagonal path, as well as an absolute speed change. Therefore, his choice of paths could have been due to either the decreased amount of time lost by choosing the diagonal, or behavioral perseveration from the last six days. Days thirty-one through thirty-three show that the animal had chosen the correct path more often than the other, and days thirty-four through thirty-six show that the animal had a definite preference for the optimal distance path. On days thirty seven through thirty-nine, the animal again chose the correct path more often than not.

Days forty through forty-two show less of a preference for the distance solution, with day forty-one showing a distinct preference for the optimal time solution. Days forty-three through forty-five show inconsistent behavior, with the animal ending up on day forty-five almost evenly split between the correct solution in terms of time and distance and the other solution. Days forty-six through forty-eight may show the beginnings of a preference for the optimal time solution again, with the animal ending up almost evenly split between optimal time and optimal distance. It is possible that if the animal were allowed to continue for another three days of this ratio, he may have switched back to choosing the optimal time solution again. For Monkey A, the totals at the bottom of Table 1 are less informative of his choices than the progression of his choices. According to the totals he preferred to use the solution that optimized in terms of time by a small margin. He also showed strong optimizing behavior in that he chose the correct solution more often than the incorrect one when time and distance could be optimized in the same diagonal solution. But the progression of his choices seems to indicate some matching behavior, and the solution that the monkey was matching, at least for the first twenty-four days, was the optimal time solution. He may have been headed that way at the end of the last twenty-four days as well.

The comparisons between the distance and move-time ratios for Monkey A (see Appendix A, Table 2) are not nearly as interesting. The monkey chose the optimal time solution consistently throughout all trials, and changed to the diagonal solution when it was optimal in terms of time as well. The larger number of optimal time solution choices in this table may reflect a tendency of the monkey to follow the optimal time path for at least part of the trial, and then spend some time not moving, therefore decreasing the time efficiency ratio. However, the problem with the move-time measure must be considered. It is possible that if time were added to the move-time measure when the animal was bouncing the Pacman against the wall that Table 2 would look exactly like Table 1.

Monkey B's behavior was definitely less stable than Monkey A's behavior, missing a total of 51 test trials, whereas Monkey A missed only seven. Also, it must be noted that the actual ratios for Monkey B were lower overall than Monkey A. However, Appendix A, Table 3 shows that Monkey B clearly showed an overall preference for the distance solution, especially by day fifteen. This may be due to the fact that Monkey B's first twenty-four days were spent using the ratios in Set B, and the time differential between the optimal time solution and the optimal distance solution in Set B was only three seconds. For days twenty-five through forty-eight Monkey A seemed to prefer the distance solution in the absolute speed of Set A as well. One reason why Monkey B may not have switched to the optimal time solution for days twenty-five through forty-eight could be that it had learned to use the diagonal so completely it was unable to switch to another solution. Another reason may have been that it preferred the optimal distance solution to the optimal time solution.

The move-time distance comparison shown in Appendix A, Table 4 shows less consistent behavior, with a definite preference for the optimal time solution. This may be due to the animal staying on the optimal time path but spending a great deal of time not moving. It also may be due to the fact that this particular animal spent a great deal of time bouncing the Pacman against the wall, and this time is not evident using the move-time measure but is using the total time measure.

Several important conclusions may be drawn from the efficiency ratio comparisons. One is that the animals do tend to behave optimally in terms of time and distance. For all of the "b" trials, each animal approached the correct solution more often than any other solution, meaning that they were sensitive to the minimization of either time or distance. For Monkey A at least, the efficiency ratio comparisons show that the monkey was sensitive to a time differential of only six seconds, and not to a time differential of only three seconds. This puts the sensitivity boundary somewhere between three and six seconds for this animal. This shows that Monkey A is able to make fine discriminations in terms of time.

The results of the efficiency ratio comparisons for Monkey B may be confounded with order so clear conclusions are difficult to draw. However, it would appear that the animal had an optimal strategy that it used consistently throughout the experiment.

The Pathways

As can be seen by examining the graphs of the best and worst trials of each of the animals (see Appendix C), they exhibited a range of behaviors. However, it can be seen from the most representative of the plots that the animals were very consistent in their choice of solutions. The plots also show that although sometimes one of the monkeys exhibited perfect behavior resulting in efficiency ratios of one, more often the animal chose some middle solution between time and distance. The solution Monkey A chose most often was closer to the optimal time solution, and the solution Monkey B chose most often was closer to the optimal distance solution.

An example of a pretest trial missed by Monkey B is also included (Figure 16, Appendix C). It can be seen from the graph that the animal consistently bounced the Pacman against the wall in the position that the prey object was most often found. This is discussed in the section headed "The Pretest Trials".

The plots of the pathways indicate highly stable behavior. For Monkey A, this behavior was amenable to manipulation by changing the requirements for optimizing in terms of time. Again, this seemed to indicate some matching behavior, with the monkey matching his behavior to the optimal time solution.

The Pretest Trials

It must be concluded that the pretest trials were unsuccessful in measuring the motivation or interest level of the animals. The low correlation coefficients between the pretest trials and the other trials showed that there was not a relationship between how the animals did on the pretest trials and the test trials. For Monkey B, one reason for this finding may have been that he was using a game strategy where he moved the Pacman to the screen position where the prey object was most frequently found. In other words, he was moving the Pacman to a screen position and not to the red square prey object. This could account for the large number of missed pretest trials exhibited by this animal. It also could account for the large number of missed test trials on test days with new Pacman starting positions. Since the prey object was in a different location during the pretest trials from where it was located during the test trials, the monkey missed the reinforcements on the pretest trials. Since the monkey eventually learned to move the Pacman to where the prey object was located during the pretest trials, but would have a difficult time moving the Pacman to the prey object on days where the Pacman starting position was different, it could be hypothesized that the animal was optimizing in terms of effort. If the animal does not have to watch the screen to get a reinforcement, it may entail less cognitive effort than paying attention to the screen and moving the joystick in such a way as to get to the red square prey object every time. When the monkey used this particular strategy, the maximum number of reinforcements that he could lose in one day was the number of pretest trials per day, eight. For the first five days of this experiment, the animal was losing at least the eight pretest trial reinforcements every day.

It is also possible that the animal had learned during shaping to move the Pacman to certain positions to receive reinforcements, and this strategy transferred to the experiment. If the animal had been using this position strategy at the beginning of this experiment,he had lost it by the end because by day 30 he no longer was missing pretest trials.

The low correlation levels between the pretest trials and the test trials for Monkey A are more difficult to explain because Monkey A was more stable in his behavior and showed far less missed trials than Monkey B. Perhaps these supposedly easy trials that required only one directional movement on the animal's part were actually more difficult and confusing because of the different location of the prey object. Perhaps the motivation level of the animal is not possible to measure using the present dependent measures. It does seem clear, however, that these pretest trials do not tap into the constructs of motivation or interest level for these two monkeys.

The fact that the two monkeys performed differently by choosing different solutions is a problem in that it cannot be fully explained by the present design. However, the question of whether animals minimize any foraging behavior posed by Meyers (1983) can be answered quite adequately by this study.

Both monkeys did use one solution that optimized either time or distance, and they did so consistently.

For Monkey A, the important variable seemed to be time. As in the research performed by Fantino and Abarca (1985), this animal maximized reinforcements by minimizing time. If the movement of the Pacman can be conceptualized as a Fixed Interval schedule, Monkey A chose to work in the shortest fixed interval schedule available to him.

For some of the trials, Monkey B seemed to perform much like the animals studied by McDonald and Wilkie (1990). The animals in that study often traveled on the path that would minimize time, but stopped frequently. This could indicate some inclination to take the minimum time solution when actually working, and to use some of the "saved" time for leisure activities.

Future studies of this kind could manipulate the time difference between an optimal time and an optimal distance solution even further. Even though some sensitivity to the time differential presented in this study was evident, the time differential could be made to be larger by the addition of another fast medium down the side of the screen. Doing so could separate the solutions by as much as the experimenter chooses. Even more optimal solutions may be shown using this procedure.

Further research should also allow more days in each phase to allow the behavior to stabilize completely. The present study hints at the beginnings of stable strategies. Additional sessions at each phase could show them more thoroughly. Since it is undesirable for the animals to remain out of their social environments for long periods of time, experimental time could be saved by reducing the number of control phases. Since the animals did not seem to show position biases in the present experiment, phases to control for the effects of position are not necessary.

The present study allows many interesting conclusions to be reached. One is that Rhesus macaques optimize some variable while foraging, and that their foraging behavior follows a strategy that is stable for each animal. Much more research is needed to understand whether preference for the minimization of time or distance is an individual preference for the animal, or a species preference.

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Appendix A

Table 1

Monkey A: Pixels and Total-Time

Day	Time	Dist.	Cor.	Oth.	Mis.	N.V.	Pos.
1	12	3			4	1	R.U.
2	17	3					
3	15	4				1	
4			2	16	2		L.U.
5			4	16			
6			11	9			
7	8	11			1		L.D.
8	6	12				2	
9	10	10					
10			6	14			R.D.
11			10	9		1	
12			11	8		1	
13	18	1				1	L.U.
14	14	4				2	
15	14	6					
16			15	4		1	L.D.
17			12	8			
18			13	7			
19	13	7					R.D.
20	15	5					
21	17	3					
22			14	5		1	R.U.
23			11	9			
24			14	6			
25			16	4			L.U.

Day	Time	Dist.	Cor.	Oth.	Mis.	N.V.	Pos.
26			12	8			
27			18	2			
28	7	12				1	R.U.
29	4	16					
30	9	10				1	
31			15	5			L.D.
32			11	9			
33			13	7			
34	0	20					R.D.
35	10	9					
36	2	18					
37			14	6			R.U.
38			16	4			
39			18	2			
40	7	13					L.U.
41	14	6					
42	5	15					
43			16	4			R.D.
44			13	7			
45			11	8		1	
46	7	13					L.D.
47	6	14					
48	11	9					
Tot	241	224	296	177	7	15=	960

Table 2

Monkey A: Pixels and Move-Time

Day	Time	Dis	Corr	Oth	Miss	N.V.	Poss
1	14	1			1	1	R.U.
2	19	1					
3	19					1	
4				18	2		L.D.
5				1	19		
6				1	19		
7	19				1		L.D.
8	17	1				2	
9	19	1					
10			2	18			R.D.
11			5	14		1	
12			7	12		1	
13	19					1	L.U.
14	18					2	
15	20						
16			13	6		1	L.D.
17			7	13			
18			14	6			
19	20						R.D.
20	20						
21	20						
22			12	7		1	R.U.
23			6	14			
24			11	9			
25			7	13			L.U.

Day	Time	Dis	Corr	Oth	Miss	N.V.	Poss
26			12	8			
27			12	8			
28	19					1	R.U.
29	20						
30	19					1	
31			12	8			L.D.
32			8	12			
33			6	14			
34	20						R.D.
35	19					1	
36	20						
37			11	9			R.U.
38			15	5			
39			17	3			
40	20						L.U.
41	20						
42	20						
43			9	11			R.D.
44			14	6			
45			12	7		1	
46	20						L.D.
47	20						
48	20						
Tot	461	4	214	259	7	15=	960

Table 3

Monkey B: Pixels and Total-Time

Day	Time	Dis	Corr	Oth	Miss	N.V.	Poss
1	7	12				1	L.U.
2	3	17					
3	1	19					
4			4	11	5		R.U.
5			13	7			
6			9	11			
7					19	1	L.D.
8	4	14				2	
9	4	15				1	
10			12	7		1	R.D.
11			11	9			
12			14	6			
13	13	7					R.U.
14	13	7					
15	8	12					
16			8	9	3		L.U.
17			12	6	2		
18			19	1			
19	9	10				1	R.D.
20	9	11					
21	6	13				1	
22			17	3			L.D.
23			11	3	5	1	
24			16	4			
25			11	1	8		L.U.

Day	Time	Dis	Corr	Oth	Miss	N.V.	Poss
26			20				
27			16	1	3		
28		15			5		R.U.
29	3	16				1	
30	4	15				1	
31			14	5		1	R.D.
32			13	6		1	
33			16	3		1	
34	17	3					L.D.
35	12	8					
36	10	10					
37			14	5		1	R.U.
38			12	8			
39			13	7			
40	7	13					R.D.
41	4	16					
42	2	18					
43			16	4			L.D.
44			19	1			
45			16	2		2	
46	2	16				2	L.U.
47		19				1	
48	2	17				1	
Tot	140	303	326	119	51	21=	960

Table 4

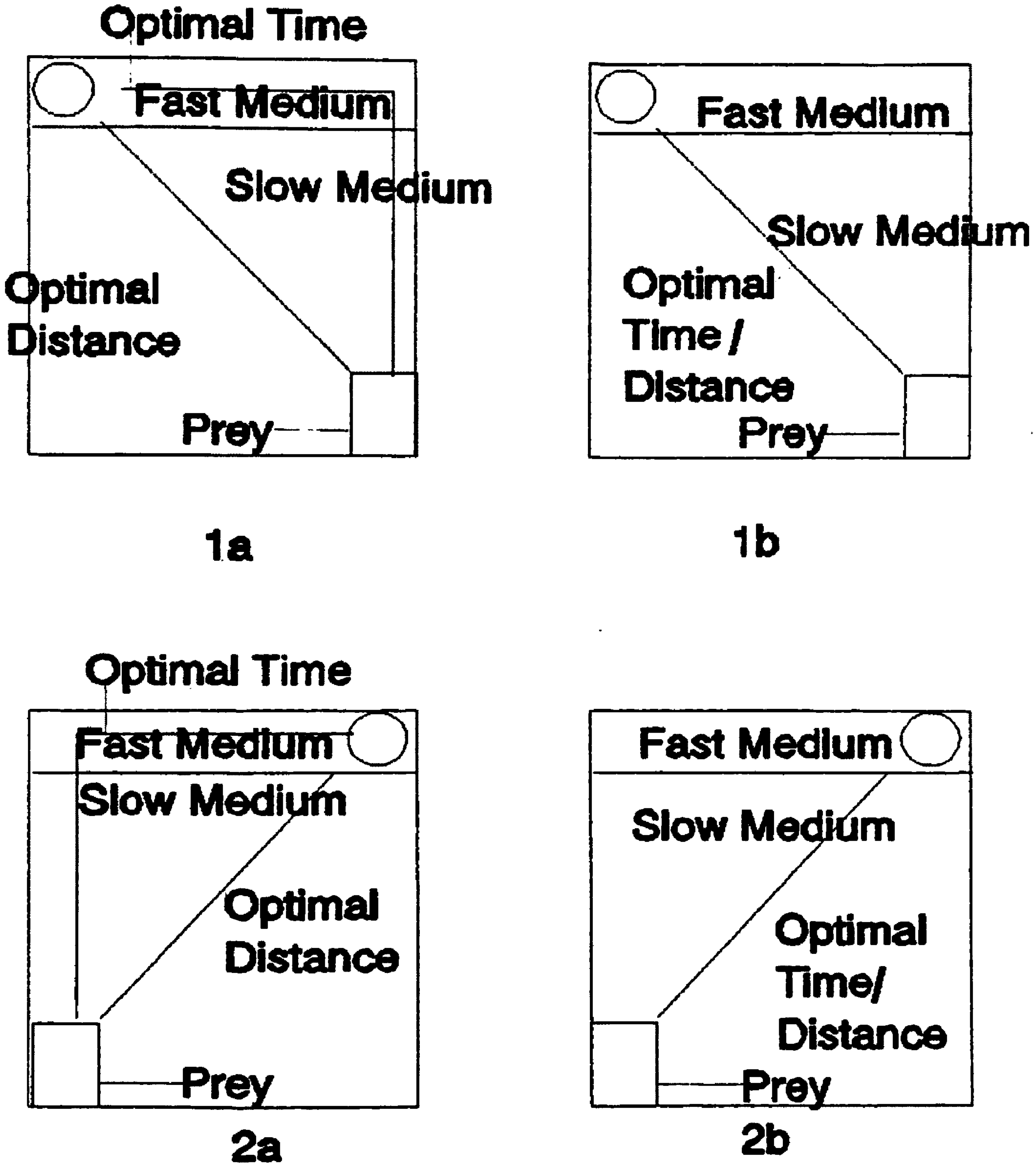
Monkey B: Pixels and Move-Time

Day	Time	Dis	Corr	Oth	Miss	N.V.	Poss
1	16	3				1	L.U.
2	16	4					
3	12	8					
4			1	14	5		R.U.
5			1	19			
6			1	19			
7					19	1	L.D.
8	18					2	
9	17	2				1	
10			10	9		1	R.D.
11			12	8			
12			14	6			
13	20						R.U.
14	20						
15	20						
16			5	12	3		L.U.
17			9	9	2		
18			15	5			
19	18	1				1	R.D.
20	20						
21	12	7				1	
22			8	12			L.D.
23				14	5	1	
24			2	18			
25			10	2	8		L.U.

Day	Time	Dis	Corr	Oth	Miss	N.V.	Poss
26			16	4			
27			13	4	3		
28	14	1				5	R.U.
29	19					1	
30	19				1		
31			7	12		1	R.D.
32			15	4		1	
33			16	3		1	
34	19	1					L.D.
35	20						
36	20						
37				19		1	R.U.
38			2	18			
39			5	15			
40	20						R.D.
41	20						
42	20						
43			13	7			L.D.
44			18	1		1	
45			15	3		2	
46	17	1				2	L.U.
47	19					1	
48	19					1	
Tot	415	28	208	237	51	21=	960

Appendix B

Figure 1: Trials 1a, 1b, 2a, 2b



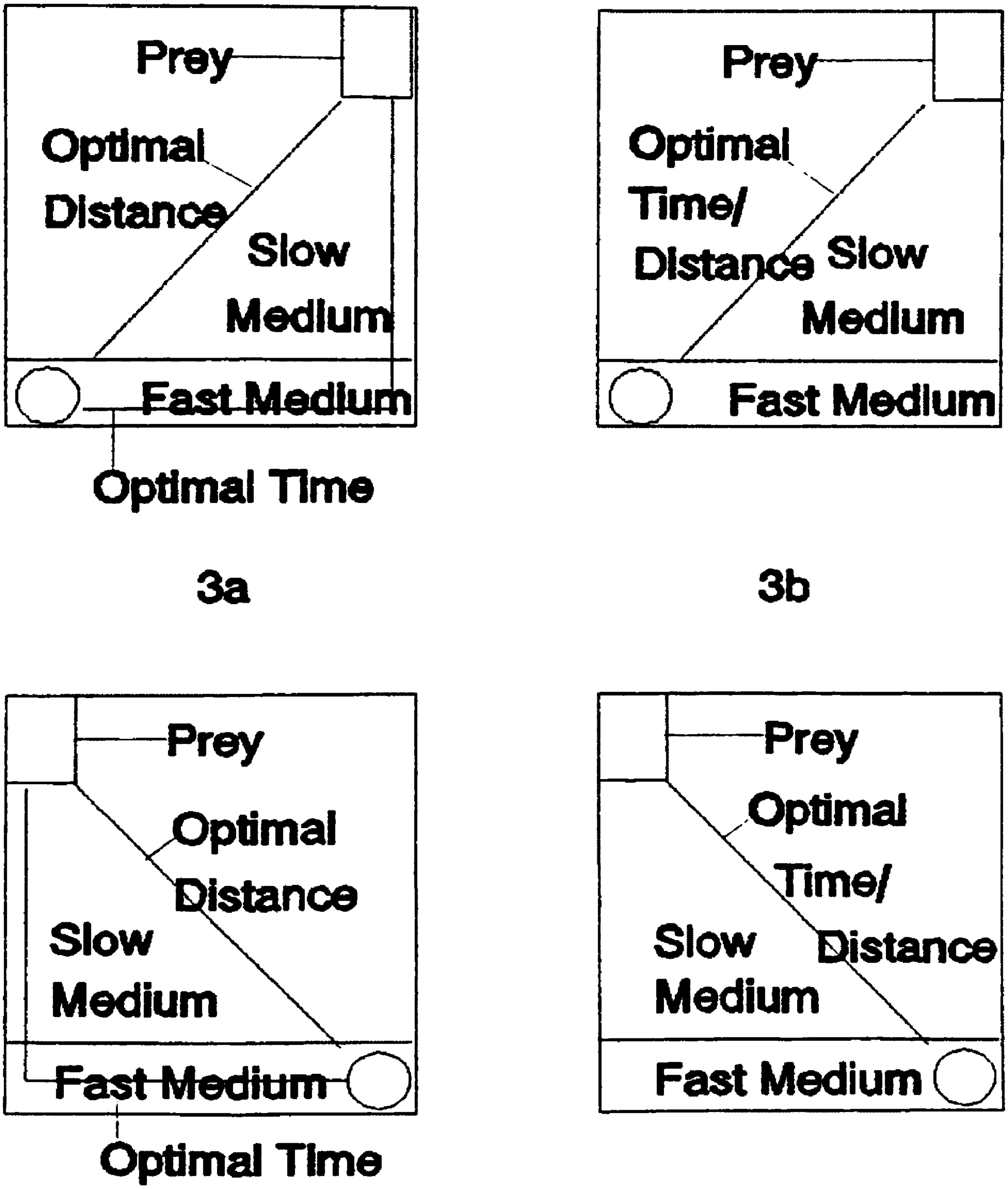
1a

1b

2a

2b

Figure 2: Trials 3a, 3b, 4a, 4b

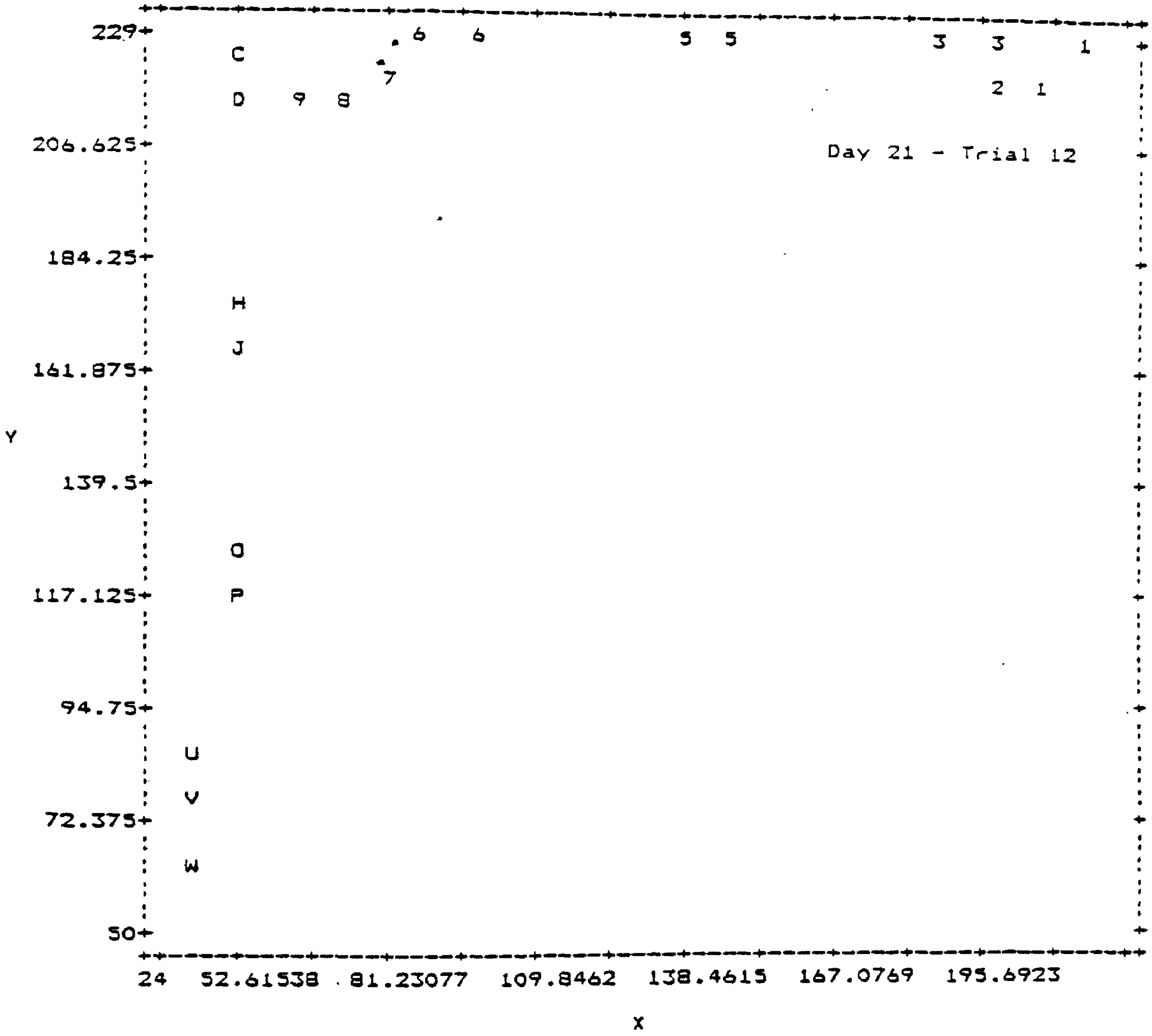


3a 3b

4a 4b

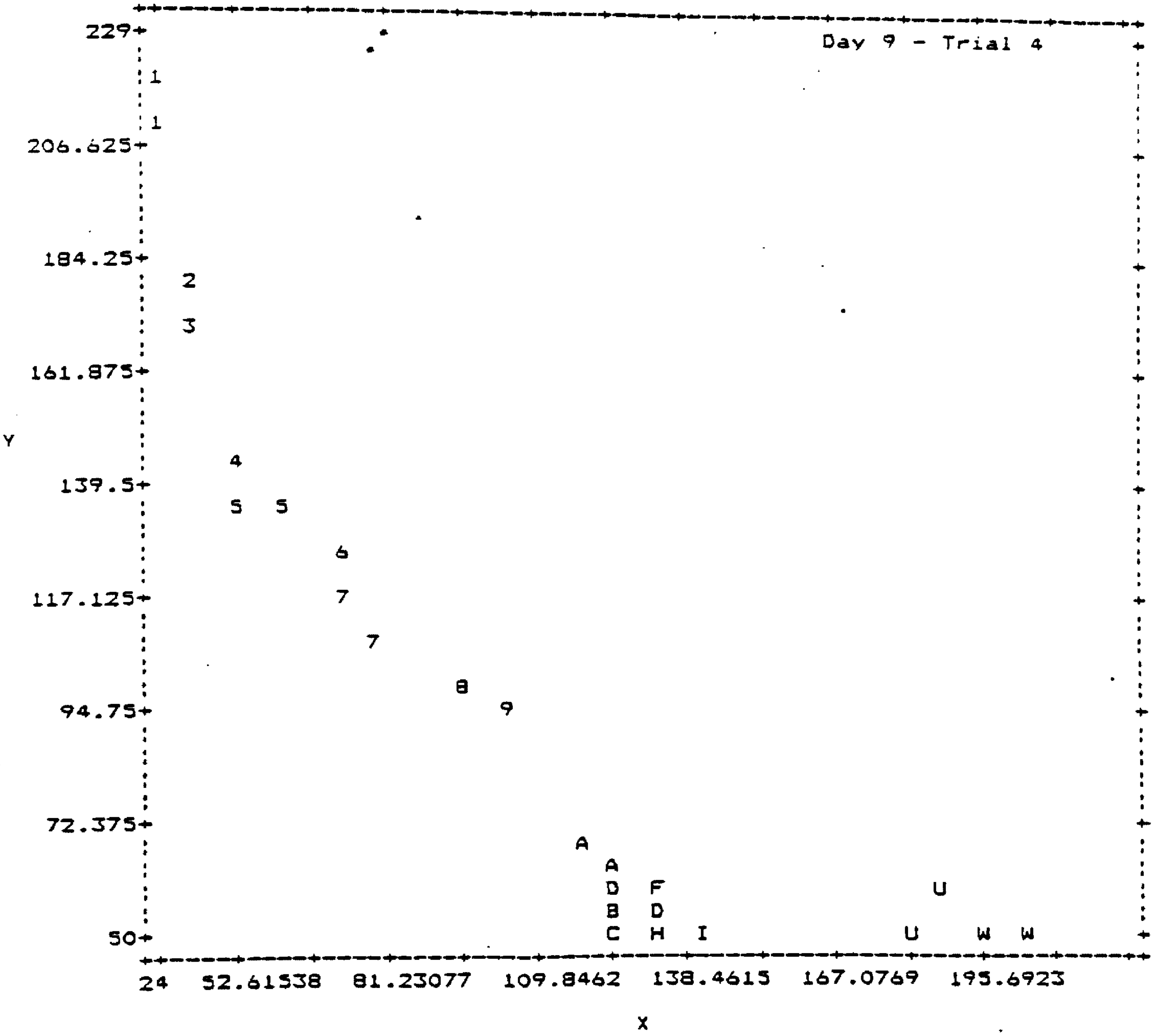
Appendix C

Figure 3: Monkey A - Ratio 60/9 pps best day.



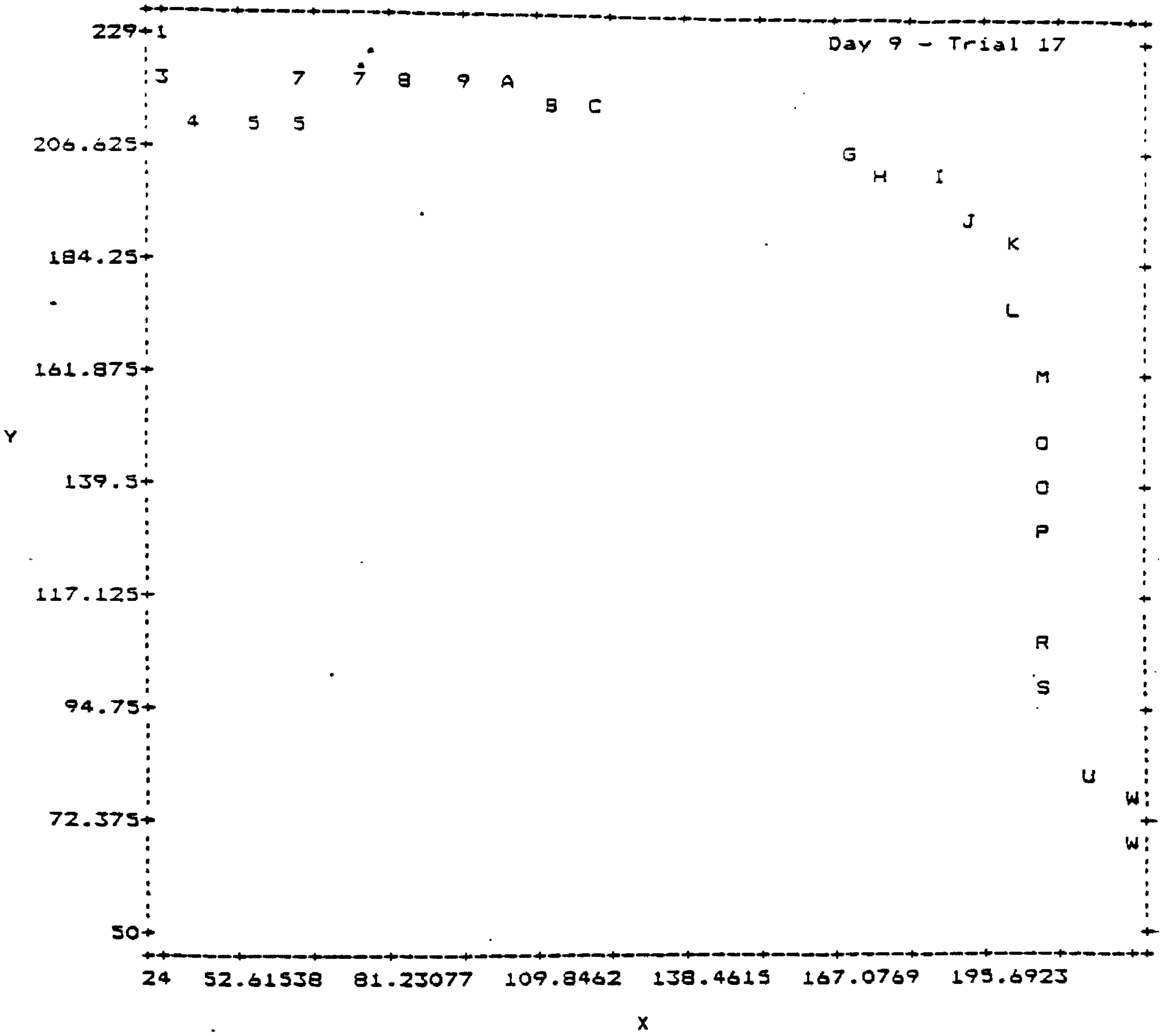
```
           22 cases plotted. The bounds of TIME are defined as follows:
  1:     3.000-    4.000  2:     4.000-    5.000  3:     5.000-    6.000
  4:     6.000-    7.000  5:     7.000-    8.000  6:     8.000-    9.000
  7:     9.000-   10.000  8:    10.000-   11.000  9:    11.000-   12.000
  A:    12.000-   13.000  B:    13.000-   14.000  C:    14.000-   15.000
  D:    15.000-   16.000  E:    16.000-   17.000  F:    17.000-   18.000
  G:    18.000-   19.000  H:    19.000-   20.000  I:    20.000-   21.000
  J:    21.000-   22.000  K:    22.000-   23.000  L:    23.000-   24.000
  M:    24.000-   25.000  N:    25.000-   26.000  O:    26.000-   27.000
  P:    27.000-   28.000  Q:    28.000-   29.000  R:    29.000-   30.000
  S:    30.000-   31.000  T:    31.000-   32.000  U:    32.000-   33.000
                 V:    33.000-   34.000  W:    34.000-   35.000
```

Figure 4: Monkey A - Ratio 60/9 pps worst day.



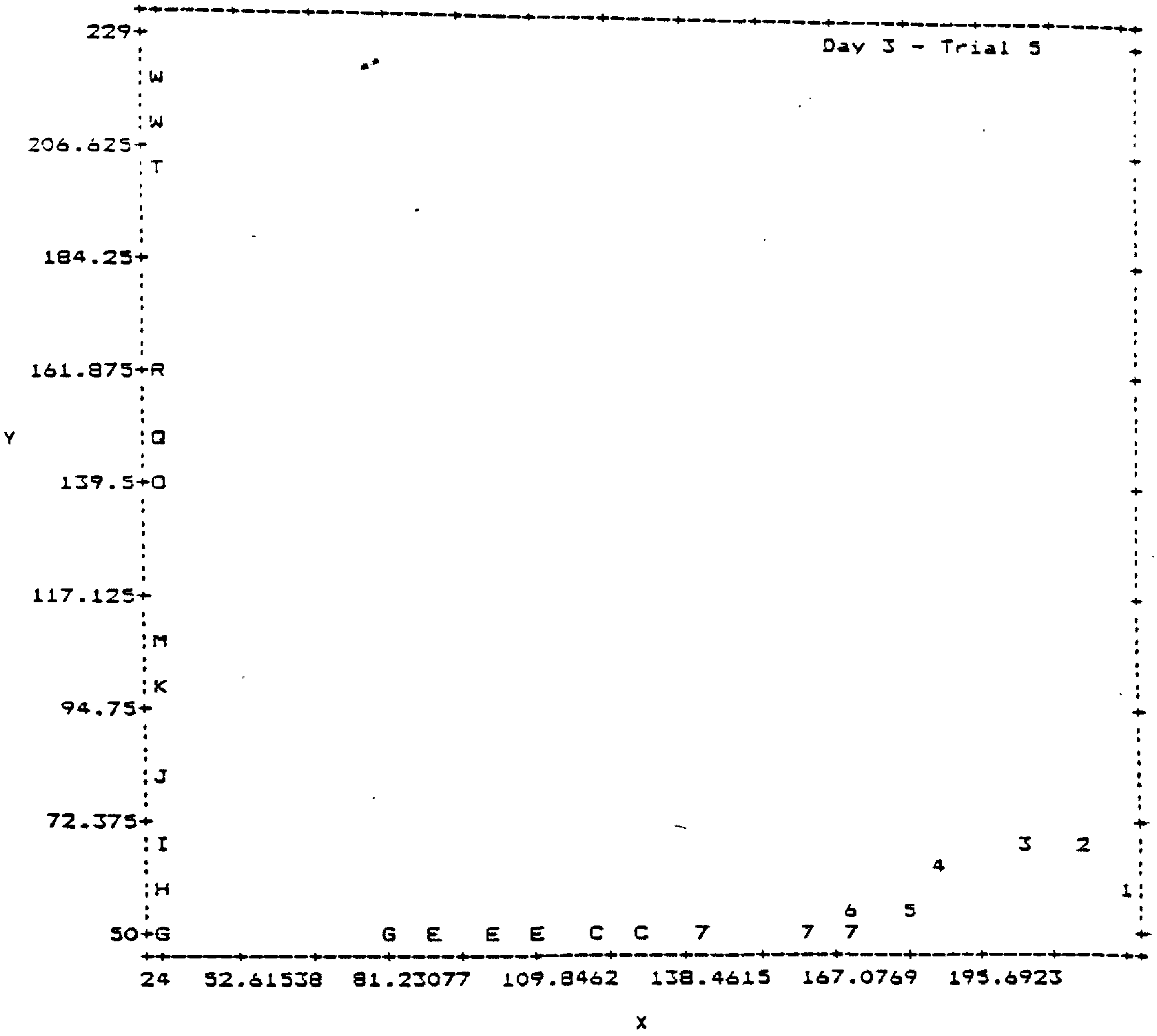
```
          43 cases plotted. The bounds of TIME are defined as follows:
 1:    2.000-    4.719  2:    4.719-    7.438  3:    7.438-   10.156
 4:   10.156-   12.875  5:   12.875-   15.594  6:   15.594-   18.313
 7:   18.313-   21.031  8:   21.031-   23.750  9:   23.750-   26.469
 A:   26.469-   29.188  B:   29.188-   31.906  C:   31.906-   34.625
 D:   34.625-   37.344  E:   37.344-   40.063  F:   40.063-   42.781
 G:   42.781-   45.500  H:   45.500-   48.219  I:   48.219-   50.938
 J:   50.938-   53.656  K:   53.656-   56.375  L:   56.375-   59.094
 M:   59.094-   61.813  N:   61.813-   64.531  O:   64.531-   67.250
 P:   67.250-   69.969  Q:   69.969-   72.688  R:   72.688-   75.406
 S:   75.406-   78.125  T:   78.125-   80.844  U:   80.844-   83.563
                 V:   83.563-   86.281  W:   86.281-   89.000
```

Figure 5: Monkey A - Ratio 60/9 pps representative day.



```
     32 cases plotted.  The bounds of TIME are defined as follows:
1:     .000-    1.469  2:    1.469-    2.938  3:    2.938-   4.406
4:    4.406-    5.875  5:    5.875-    7.344  6:    7.344-   8.813
7:    8.813-   10.281  8:   10.281-   11.750  9:   11.750-  13.219
A:   13.219-   14.688  B:   14.688-   16.156  C:   16.156-  17.625
D:   17.625-   19.094  E:   19.094-   20.563  F:   20.563-  22.031
G:   22.031-   23.500  H:   23.500-   24.969  I:   24.969-  26.438
J:   26.438-   27.906  K:   27.906-   29.375  L:   29.375-  30.844
M:   30.844-   32.313  N:   32.313-   33.781  O:   33.781-  35.250
P:   35.250-   36.719  Q:   36.719-   38.188  R:   38.188-  39.656
S:   39.656-   41.125  T:   41.125-   42.594  U:   42.594-  44.063
               V:   44.063-   45.531  W:   45.531-   47.000
```

Figure 6: Monkey A — Ratio 60/9 pps representative day.



```
        41 cases plotted. The bounds of TIME are defined as follows:
 1:     .000-    1.656  2:    1.656-    3.313  3:    3.313-    4.969
 4:    4.969-    6.625  5:    6.625-    8.281  6:    8.281-    9.938
 7:    9.938-   11.594  8:   11.594-   13.250  9:   13.250-   14.906
 A:   14.906-   16.563  B:   16.563-   18.219  C:   18.219-   19.875
 D:   19.875-   21.531  E:   21.531-   23.188  F:   23.188-   24.844
 G:   24.844-   26.500  H:   26.500-   28.156  I:   28.156-   29.813
 J:   29.813-   31.469  K:   31.469-   33.125  L:   33.125-   34.781
 M:   34.781-   36.438  N:   36.438-   38.094  O:   38.094-   39.750
 P:   39.750-   41.406  Q:   41.406-   43.063  R:   43.063-   44.719
 S:   44.719-   46.375  T:   46.375-   48.031  U:   48.031-   49.688
                  V:   49.688-   51.344  W:   51.344-   53.000
```

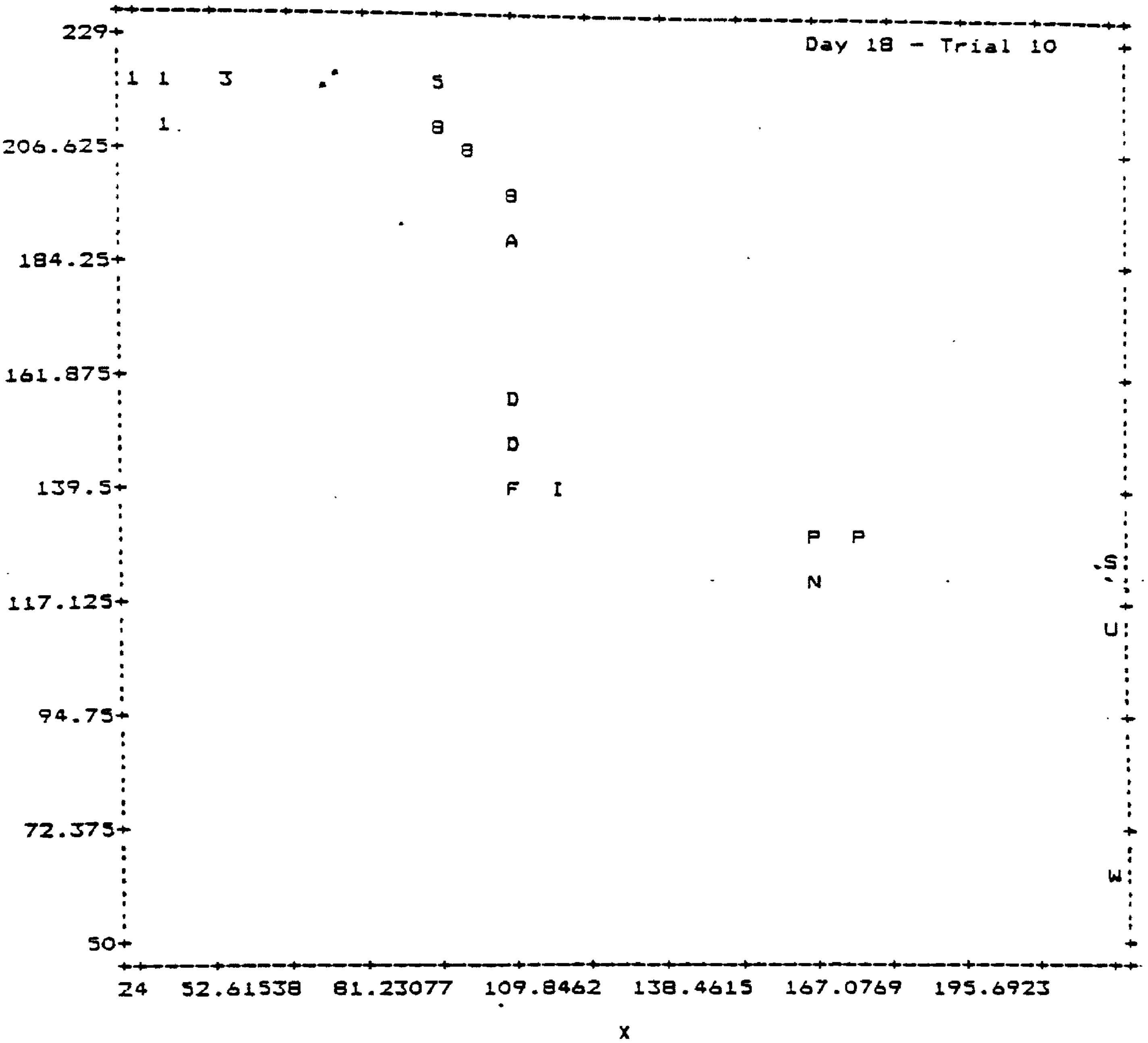
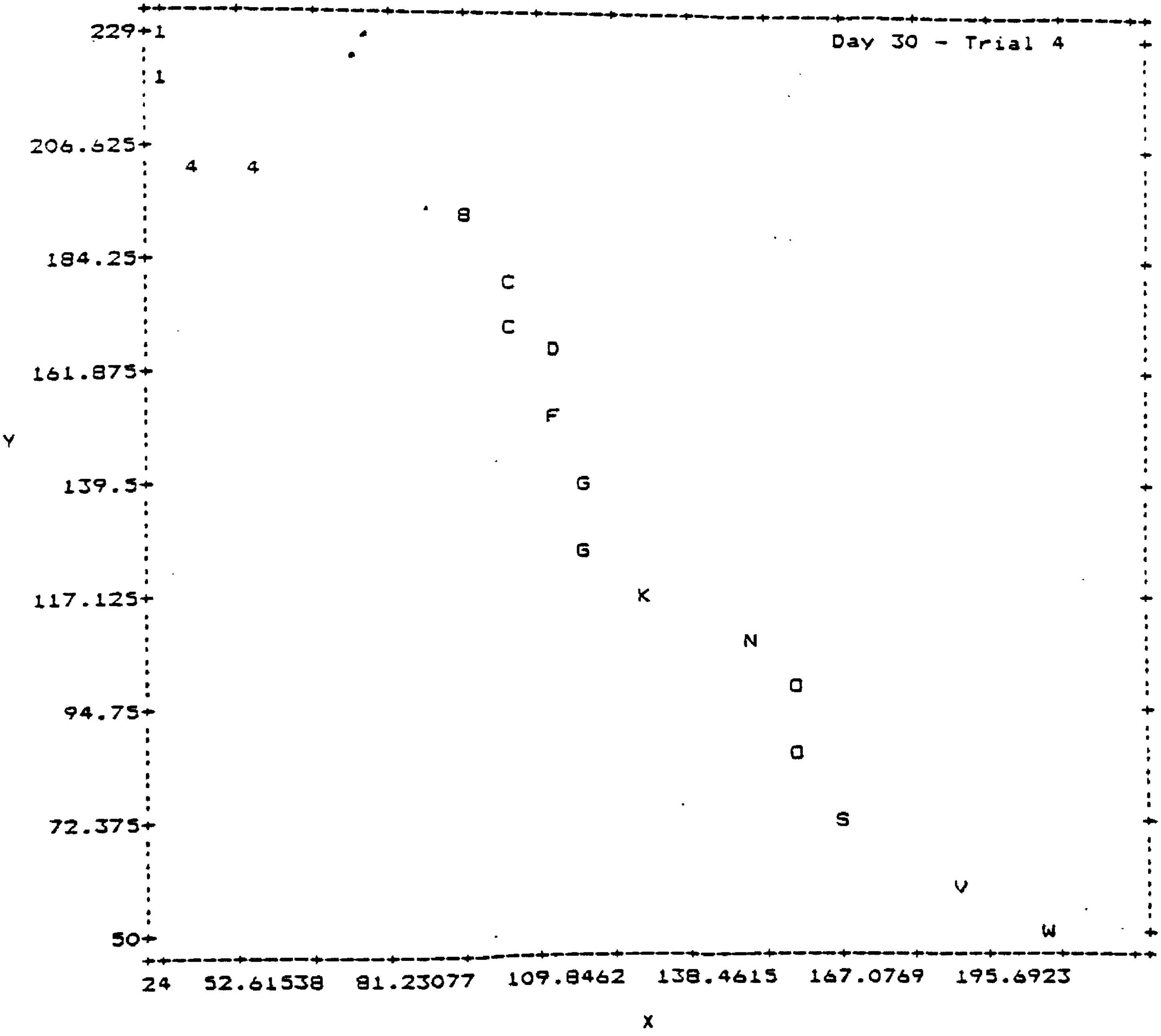


Figure 7: Monkey A - Ratio 60/25 pps representative day.

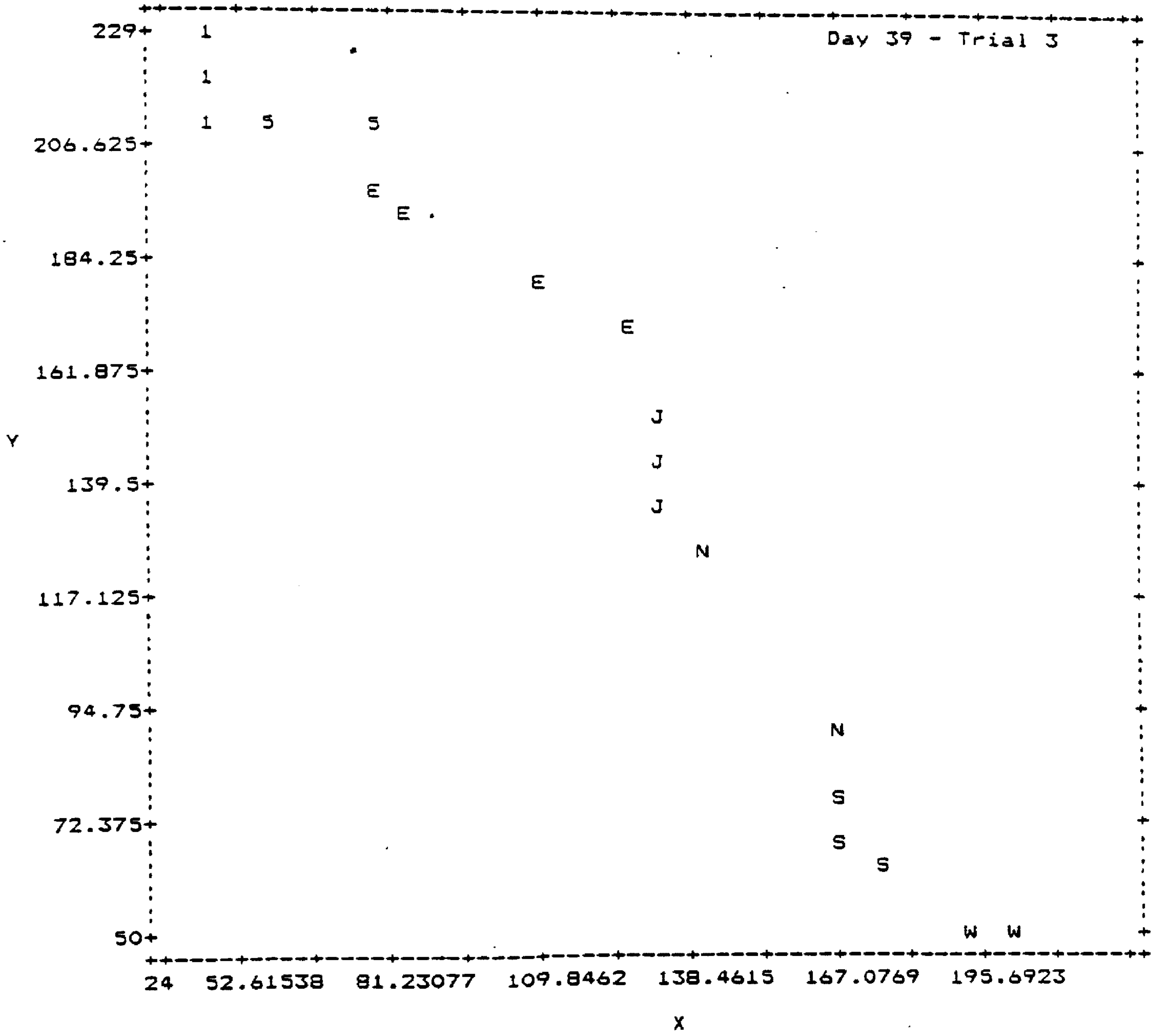
```
          27 cases plotted. The bounds of TIME are defined as follows:
   1:   4.000-   4.406  2:   4.406-   4.813  3:   4.813-   5.219
   4:   5.219-   5.625  5:   5.625-   6.031  6:   6.031-   6.438
   7:   6.438-   6.844  8:   6.844-   7.250  9:   7.250-   7.656
   A:   7.656-   8.063  B:   8.063-   8.469  C:   8.469-   8.875
   D:   8.875-   9.281  E:   9.281-   9.688  F:   9.688-  10.094
   G:  10.094-  10.500  H:  10.500-  10.906  I:  10.906-  11.313
   J:  11.313-  11.719  K:  11.719-  12.125  L:  12.125-  12.531
   M:  12.531-  12.938  N:  12.938-  13.344  O:  13.344-  13.750
   P:  13.750-  14.156  Q:  14.156-  14.563  R:  14.563-  14.969
   S:  14.969-  15.375  T:  15.375-  15.781  U:  15.781-  16.188
                 V:  16.188-  16.594  W:  16.594-  17.000
```

Figure 8: Monkey A - Ratio 90/18 pps representative day.



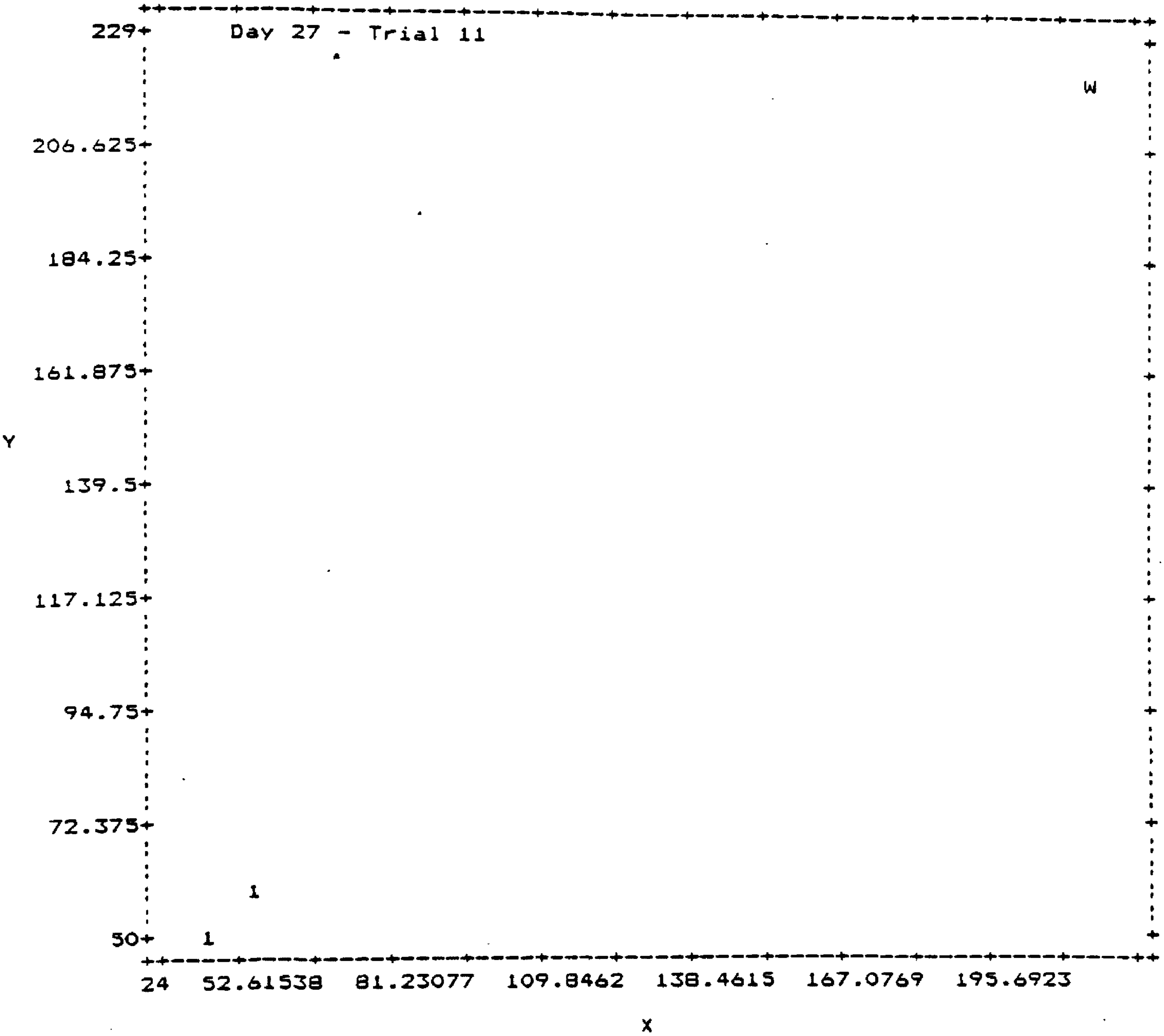
```
      22 cases plotted. The bounds of TIME are defined as follows:
1:    1.000-    1.625  2:    1.625-    2.250  3:    2.250-    2.875
4:    2.875-    3.500  5:    3.500-    4.125  6:    4.125-    4.750
7:    4.750-    5.375  8:    5.375-    6.000  9:    6.000-    6.625
A:    6.625-    7.250  B:    7.250-    7.875  C:    7.875-    8.500
D:    8.500-    9.125  E:    9.125-    9.750  F:    9.750-   10.375
G:   10.375-   11.000  H:   11.000-   11.625  I:   11.625-   12.250
J:   12.250-   12.875  K:   12.875-   13.500  L:   13.500-   14.125
M:   14.125-   14.750  N:   14.750-   15.375  O:   15.375-   16.000
P:   16.000-   16.625  Q:   16.625-   17.250  R:   17.250-   17.875
S:   17.875-   18.500  T:   18.500-   19.125  U:   19.125-   19.750
              V:   19.750-   20.375  W:   20.375-   21.000
```

Figure 9: Monkey A - Ratio 90/60 pps representative day.



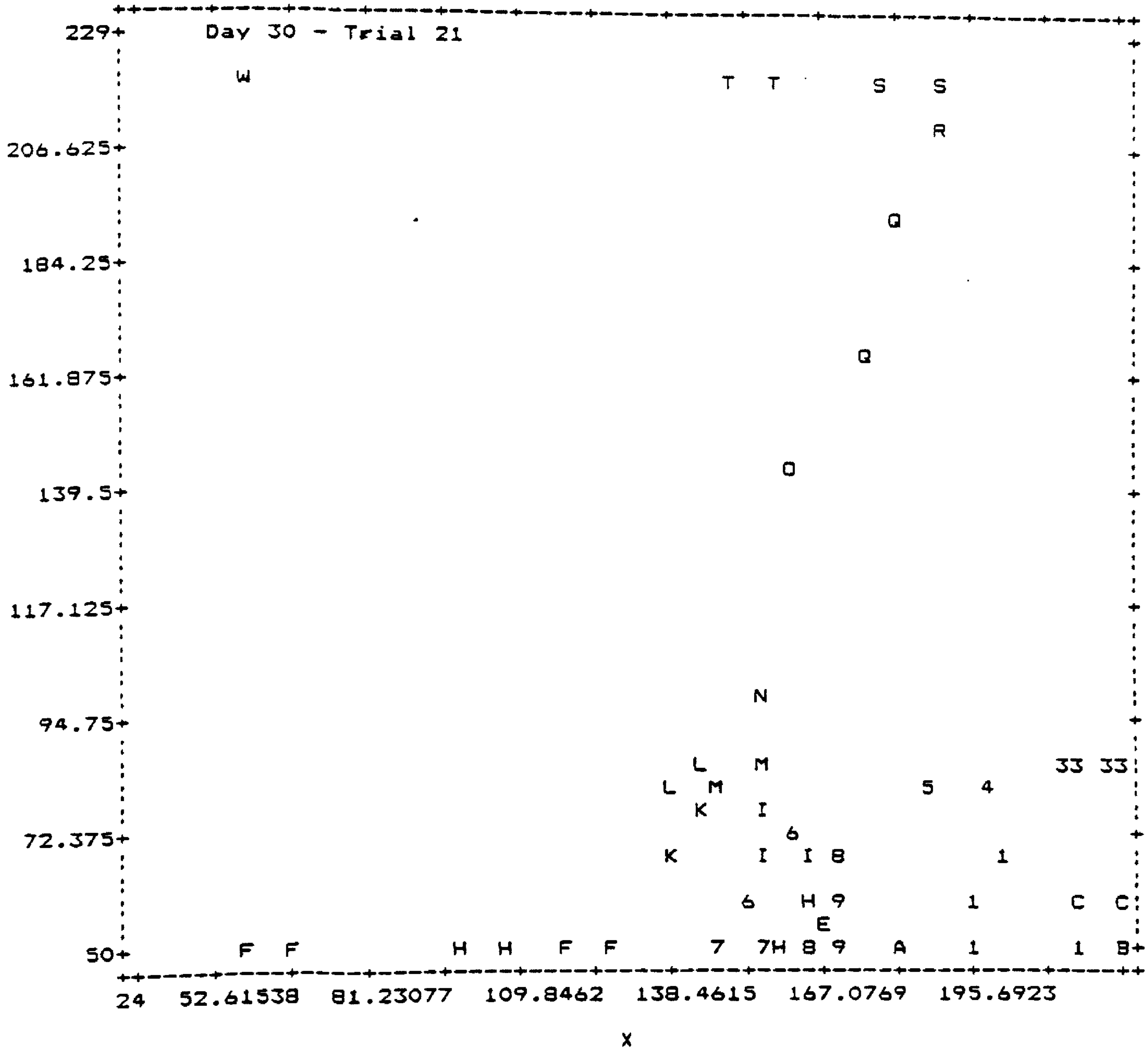
```
          21 cases plotted. The bounds of TIME are defined as follows:
  1:    3.000-    3.219  2:    3.219-    3.438  3:    3.438-    3.656
  4:    3.656-    3.875  5:    3.875-    4.094  6:    4.094-    4.313
  7:    4.313-    4.531  8:    4.531-    4.750  9:    4.750-    4.969
  A:    4.969-    5.188  B:    5.188-    5.406  C:    5.406-    5.625
  D:    5.625-    5.844  E:    5.844-    6.063  F:    6.063-    6.281
  G:    6.281-    6.500  H:    6.500-    6.719  I:    6.719-    6.938
  J:    6.938-    7.156  K:    7.156-    7.375  L:    7.375-    7.594
  M:    7.594-    7.813  N:    7.813-    8.031  O:    8.031-    8.250
  P:    8.250-    8.469  Q:    8.469-    8.688  R:    8.688-    8.906
  S:    8.906-    9.125  T:    9.125-    9.344  U:    9.344-    9.563
                V:    9.563-    9.781  W:    9.781-   10.000
```

Figure 10: Monkey B - Ratio 60/25 pps best day.



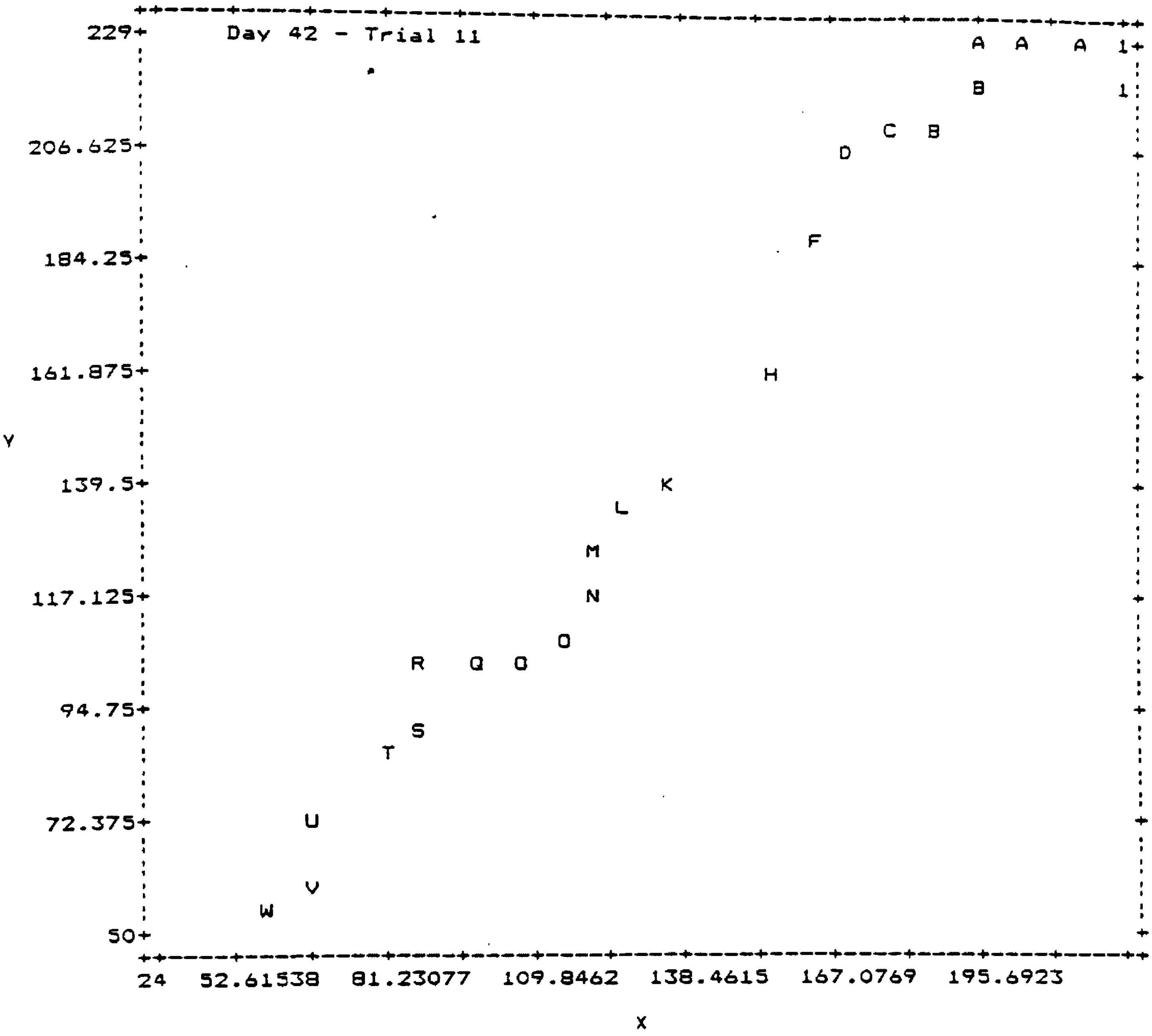
```
         5 cases plotted. The bounds of TIME are defined as follows:
1:    3.000-    3.219  2:    3.219-    3.438  3:    3.438-    3.656
4:    3.656-    3.875  5:    3.875-    4.094  6:    4.094-    4.313
7:    4.313-    4.531  8:    4.531-    4.750  9:    4.750-    4.969
A:    4.969-    5.188  B:    5.188-    5.406  C:    5.406-    5.625
D:    5.625-    5.844  E:    5.844-    6.063  F:    6.063-    6.281
G:    6.281-    6.500  H:    6.500-    6.719  I:    6.719-    6.938
J:    6.938-    7.156  K:    7.156-    7.375  L:    7.375-    7.594
M:    7.594-    7.813  N:    7.813-    8.031  O:    8.031-    8.250
P:    8.250-    8.469  Q:    8.469-    8.688  R:    8.688-    8.906
S:    8.906-    9.125  T:    9.125-    9.344  U:    9.344-    9.563
                V:    9.563-    9.781  W:    9.781-   10.000
```

Figure 11: Monkey B - Ratio 60/9 pps worst day.



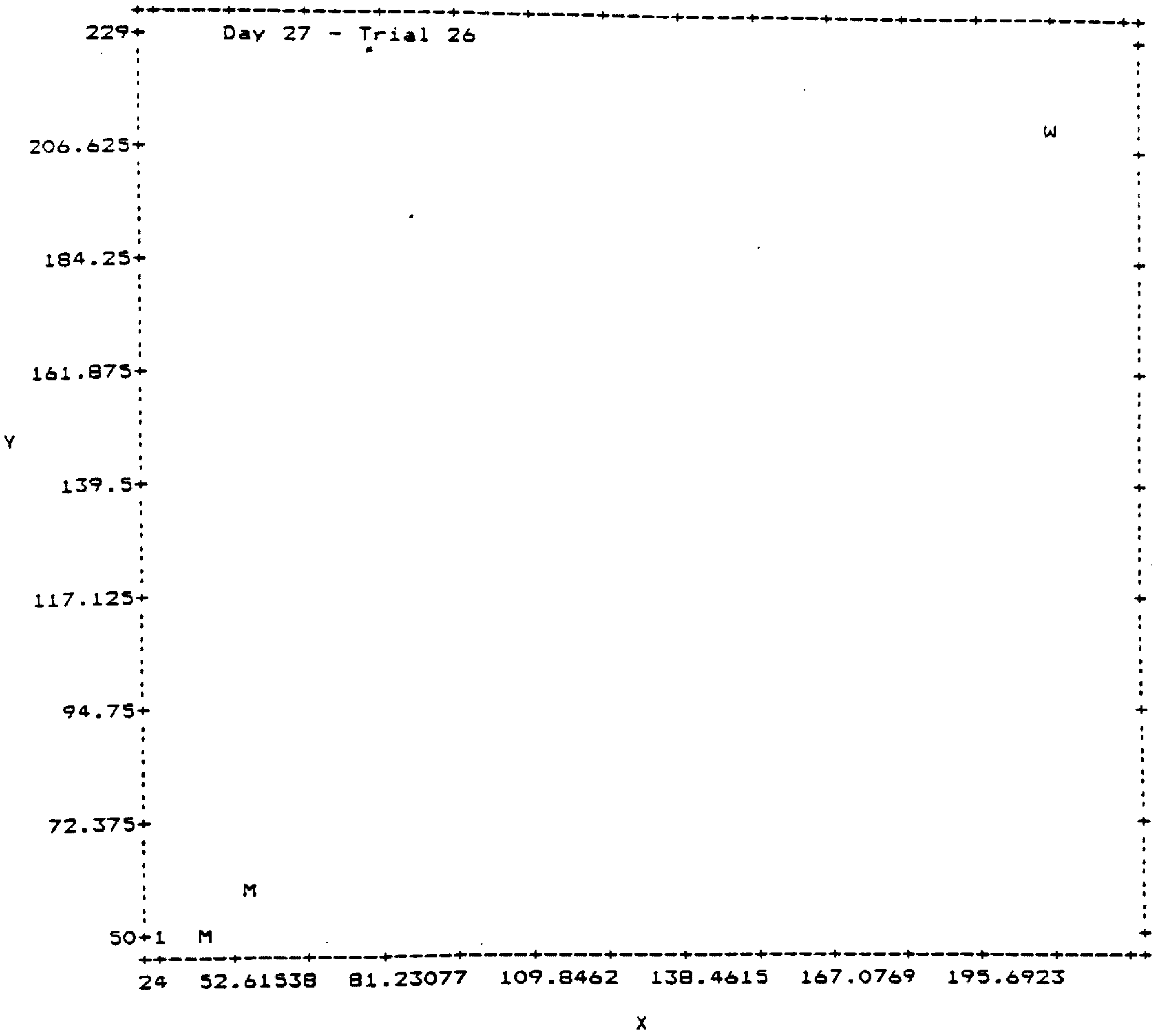
```
        100 cases plotted.  The bounds of TIME are defined as follows:
 1:    7.000-   10.438  2:   10.438-   13.875  3:   13.875-   17.313
 4:   17.313-   20.750  5:   20.750-   24.188  6:   24.188-   27.625
 7:   27.625-   31.063  8:   31.063-   34.500  9:   34.500-   37.938
 A:   37.938-   41.375  B:   41.375-   44.813  C:   44.813-   48.250
 D:   48.250-   51.688  E:   51.688-   55.125  F:   55.125-   58.563
 G:   58.563-   62.000  H:   62.000-   65.438  I:   65.438-   68.875
 J:   68.875-   72.313  K:   72.313-   75.750  L:   75.750-   79.188
 M:   79.188-   82.625  N:   82.625-   86.063  O:   86.063-   89.500
 P:   89.500-   92.938  Q:   92.938-   96.375  R:   96.375-   99.813
 S:   99.813-  103.250  T:  103.250-  106.688  U:  106.688-  110.125
             V:  110.125-  113.563  W:  113.563-  117.000
```

Figure 12: Monkey B - Ratio 60/9 pps representative day.



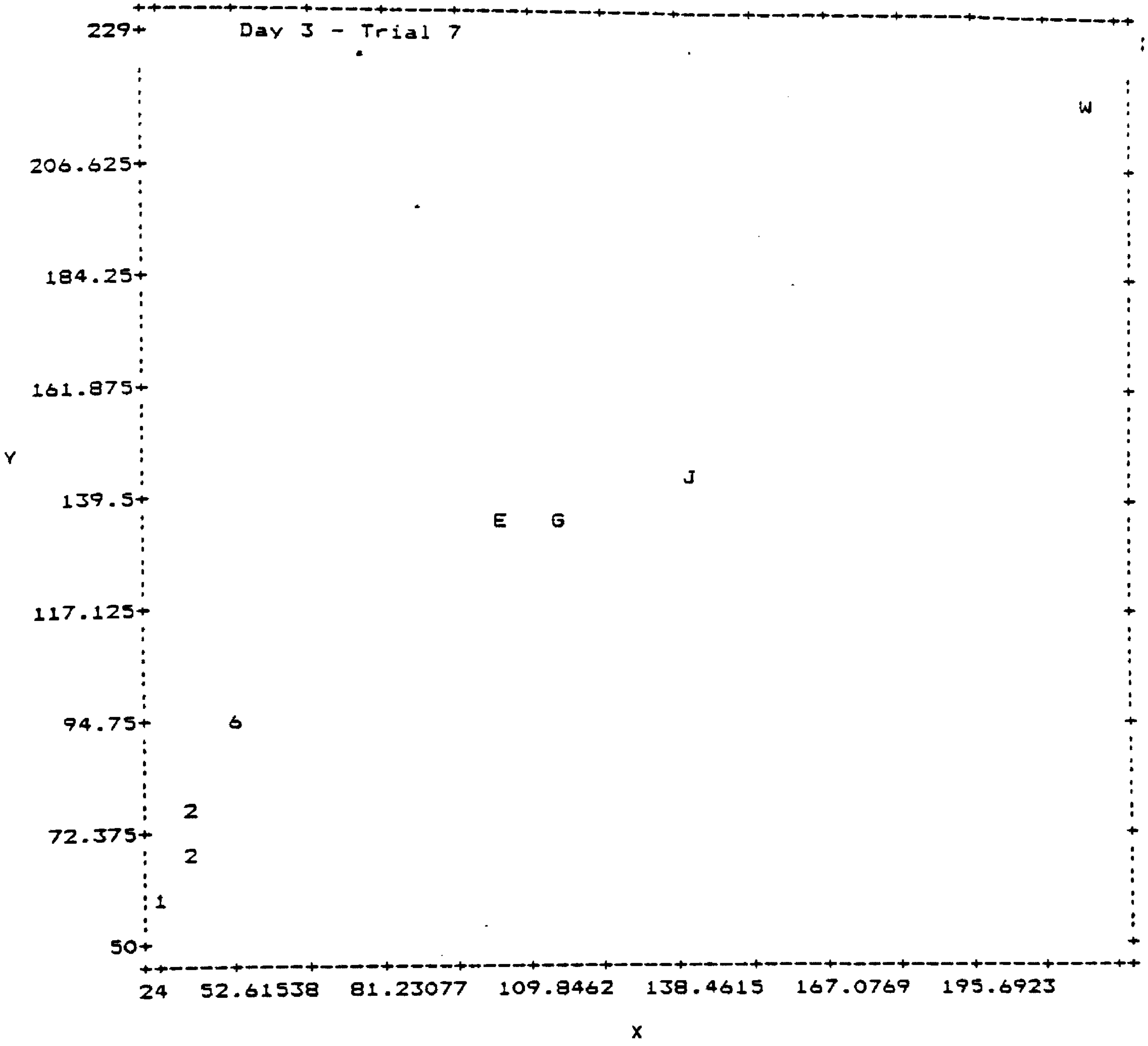
```
          31 cases plotted. The bounds of TIME are defined as follows:
1:    4.000-    5.375  2:    5.375-    6.750  3:    6.750-    8.125
4:    8.125-    9.500  5:    9.500-   10.875  6:   10.875-   12.250
7:   12.250-   13.625  8:   13.625-   15.000  9:   15.000-   16.375
A:   16.375-   17.750  B:   17.750-   19.125  C:   19.125-   20.500
D:   20.500-   21.875  E:   21.875-   23.250  F:   23.250-   24.625
G:   24.625-   26.000  H:   26.000-   27.375  I:   27.375-   28.750
J:   28.750-   30.125  K:   30.125-   31.500  L:   31.500-   32.875
M:   32.875-   34.250  N:   34.250-   35.625  O:   35.625-   37.000
P:   37.000-   38.375  Q:   38.375-   39.750  R:   39.750-   41.125
S:   41.125-   42.500  T:   42.500-   43.875  U:   43.875-   45.250
                V:   45.250-   46.625  W:   46.625-   48.000
```

Figure 13: Monkey B - Ratio 60/25 pps representative day.



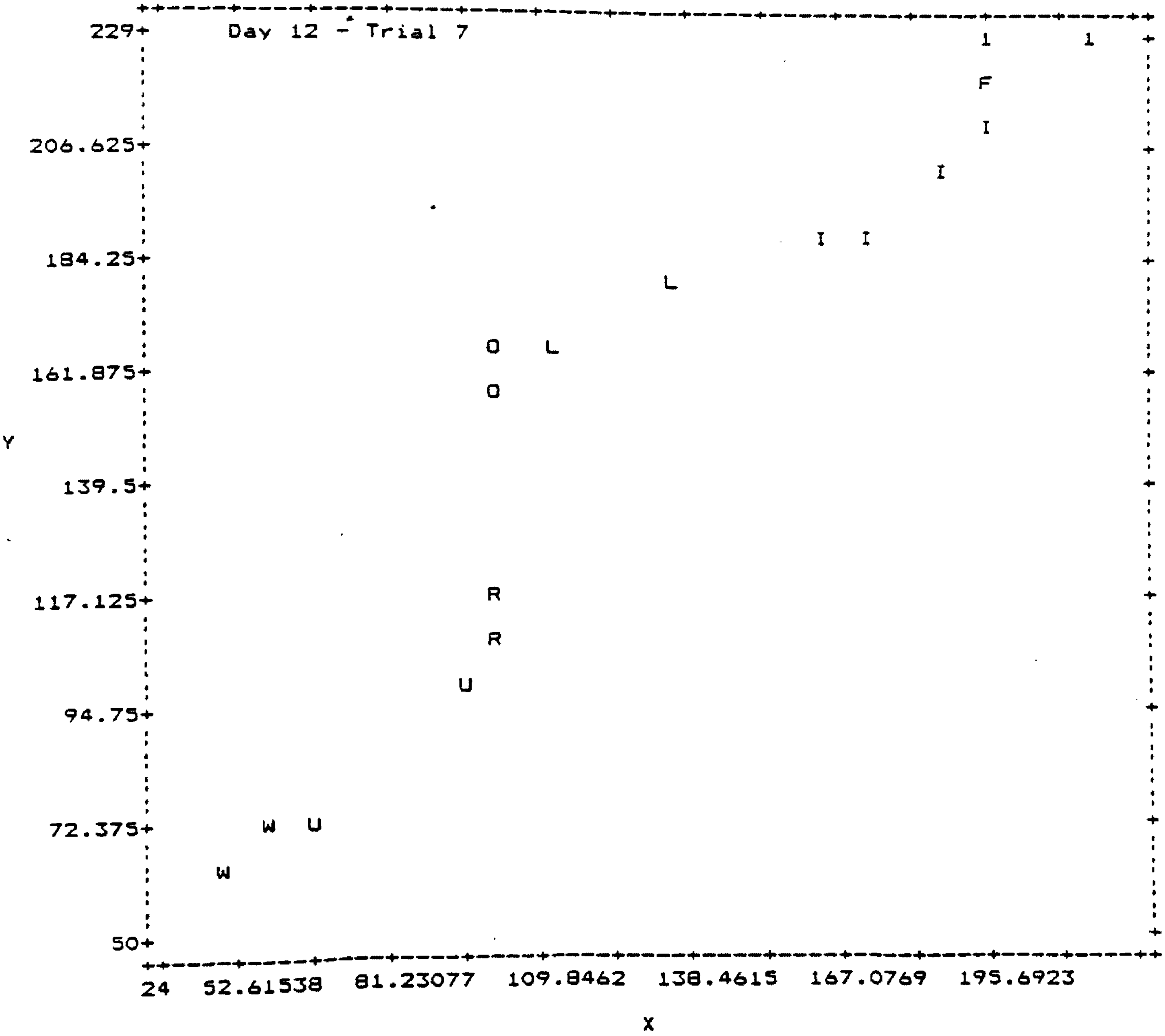
```
         5 cases plotted. The bounds of TIME are defined as follows:
1:     .000-     .594  2:     .594-    1.188  3:    1.188-    1.781
4:    1.781-    2.375  5:    2.375-    2.969  6:    2.969-    3.563
7:    3.563-    4.156  8:    4.156-    4.750  9:    4.750-    5.344
A:    5.344-    5.938  B:    5.938-    6.531  C:    6.531-    7.125
D:    7.125-    7.719  E:    7.719-    8.313  F:    8.313-    8.906
G:    8.906-    9.500  H:    9.500-   10.094  I:   10.094-   10.688
J:   10.688-   11.281  K:   11.281-   11.875  L:   11.875-   12.469
M:   12.469-   13.063  N:   13.063-   13.656  O:   13.656-   14.250
P:   14.250-   14.844  Q:   14.844-   15.438  R:   15.438-   16.031
S:   16.031-   16.625  T:   16.625-   17.219  U:   17.219-   17.813
               V:   17.813-   18.406  W:   18.406-   19.000
```

Figure 14: Monkey B - Ratio 90/18 pps representative day.



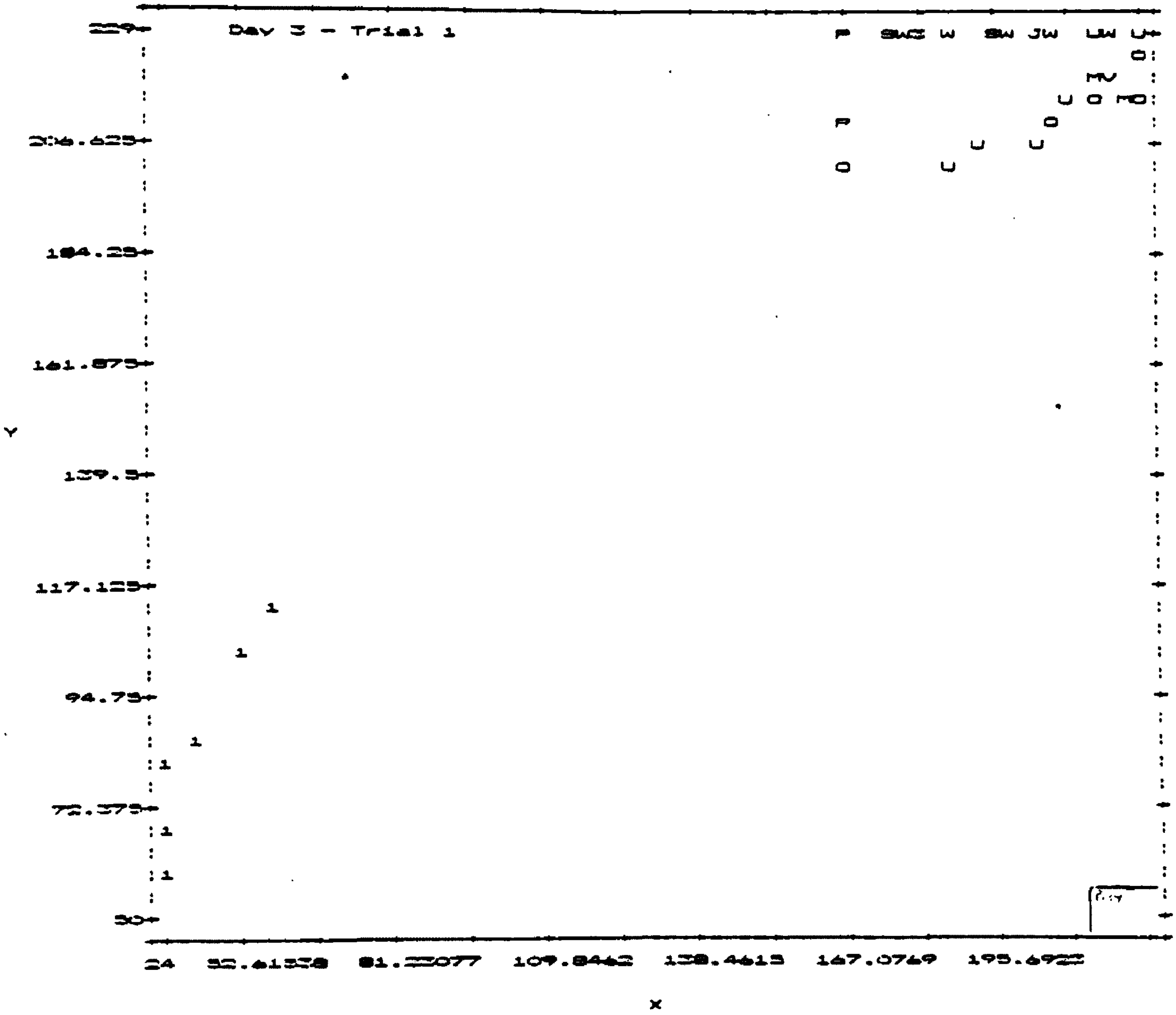
```
             9 cases plotted. The bounds of TIME are defined as follows:
1:      5.000-     5.531  2:     5.531-     6.063  3:     6.063-     6.594
4:      6.594-     7.125  5:     7.125-     7.656  6:     7.656-     8.188
7:      8.188-     8.719  8:     8.719-     9.250  9:     9.250-     9.781
A:      9.781-    10.313  B:    10.313-    10.844  C:    10.844-    11.375
D:     11.375-    11.906  E:    11.906-    12.438  F:    12.438-    12.969
G:     12.969-    13.500  H:    13.500-    14.031  I:    14.031-    14.563
J:     14.563-    15.094  K:    15.094-    15.625  L:    15.625-    16.156
M:     16.156-    16.688  N:    16.688-    17.219  O:    17.219-    17.750
P:     17.750-    18.281  Q:    18.281-    18.813  R:    18.813-    19.344
S:     19.344-    19.875  T:    19.875-    20.406  U:    20.406-    20.938
                  V:    20.938-    21.469  W:    21.469-    22.000
```

Figure 15: Monkey B - Ratio 90/60 pps representative day.



```
      19 cases plotted. The bounds of TIME are defined as follows:
1:     .000-    .344  2:    .344-    .688  3:    .688-   1.031
4:    1.031-   1.375  5:   1.375-   1.719  6:   1.719-   2.063
7:    2.063-   2.406  8:   2.406-   2.750  9:   2.750-   3.094
A:    3.094-   3.438  B:   3.438-   3.781  C:   3.781-   4.125
D:    4.125-   4.469  E:   4.469-   4.813  F:   4.813-   5.156
G:    5.156-   5.500  H:   5.500-   5.844  I:   5.844-   6.188
J:    6.188-   6.531  K:   6.531-   6.875  L:   6.875-   7.219
M:    7.219-   7.563  N:   7.563-   7.906  O:   7.906-   8.250
P:    8.250-   8.594  Q:   8.594-   8.938  R:   8.938-   9.281
S:    9.281-   9.625  T:   9.625-   9.969  U:   9.969-  10.313
          V:  10.313-  10.656  W:  10.656-  11.000
```

Figure 16: Monkey B - Ratio 90/18 ops missed pretest trial.



```
          119 cases plotted. The bounds of TIME are defined as follows:
   1:    6.000-  17.563  2:  17.563-  29.125  3:  29.125-  40.688
   4:   40.688-  52.250  5:  52.250-  63.813  6:  63.813-  75.375
   7:   75.375-  86.938  8:  86.938-  98.500  9:  98.500- 110.063
   A:  110.063- 121.625  B: 121.625- 133.188  C: 133.188- 144.750
   D:  144.750- 156.313  E: 156.313- 167.875  F: 167.875- 179.438
   G:  179.438- 191.000  H: 191.000- 202.563  I: 202.563- 214.125
   J:  214.125- 225.688  K: 225.688- 237.250  L: 237.250- 248.813
   M:  248.813- 260.375  N: 260.375- 271.938  O: 271.938- 283.500
   P:  283.500- 295.063  Q: 295.063- 306.625  R: 306.625- 318.188
   S:  318.188- 329.750  T: 329.750- 341.313  U: 341.313- 352.875
                  V: 352.875- 364.438  W: 364.438- 376.000
```