

THE UNIVERSITY OF CALGARY

NON-SPATIAL HABIT REVERSAL LEARNING
IN RATS, SQUIRRELS AND CHIPMUNKS

by

Bryan E. Kolb

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF PSYCHOLOGY

CALGARY, ALBERTA

March 24, 1970

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THE UNIVERSITY OF CALGARY
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Non-Spatial Habit Reversal Learning in Rats, Squirrels and Chipmunks" submitted by Bryan E. Kolb in partial fulfillment of the requirements for the degree of Master of Science.

R. E. Franken

Supervisor

R. Schaub

E. Rowland

N. Gust

DATE March 24, 1970

ABSTRACT

The development of nonspatial reversal learning sets was studied in three problems in each of 3 species of rodents (Rattus, Sciurus and Tamias). On initial learning one group from each species was trained to approach a black and white checkered stimulus (C) instead of a black and white vertically striped stimulus (S), while a second group was trained to approach "S" instead of a half-white and half-black vertically divided stimulus (H) and a third group was trained to approach "H" instead of "S". Each group was then trained on 10 reversals of their respective discrimination. Within each training group, all three species improved over the reversals. When the results for the first five reversals for Groups 2 and 3 were pooled there was a significant Species effect ($p < .05$) as well as a significant Species X Group interaction ($p < .05$). The implications of this research on interspecies comparisons was discussed.

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ACKNOWLEDGEMENTS

I would like to express my gratitude to my thesis supervisor Dr. R. E. Franken for his guidance and encouragement throughout my entire Masters program and particularly in the preparation of this thesis.

I would also like to extend my thanks to Dr. G. L. Rowland for his very helpful advice on the handling of the animal colony, the experimental procedure and the statistics used for this thesis.

I must also express my gratitude to Dr. R. S. Sainsbury for his advice, criticisms and encouragement.

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I. INTRODUCTION AND HISTORICAL REVIEW

Although Darwin (1871) suggested that animals differed only in "degree" of learning ability, many researchers have since taken the position that through evolution all animals developed a similar learning "mechanism" (or process) with more developed animals having a more developed or refined mechanism. Others, however, hold that as the different species evolved they developed distinctly different learning "mechanisms".

Thorndike, in his book Animal Intelligence, accepted Darwin's position:

Experiments have been made on fishes, reptiles, birds and various mammals, notably dogs, cats, mice and monkeys, to see how they learned to do simple things in order to get food. All these animals manifest fundamentally the same sort of intellectual life. Their learning is of the same type. (Thorndike, 1911, pp. 282-283).

To Thorndike, animals might differ in "what" they learned or in the "degree" of their learning ability, but the principles which governed their learning ability were identical. Such a view also receives some support from contemporary evolutionary theorists. For example, Simpson (1949) has pointed out that the difference from class to class and order to order are small and gradual. On this basis, it is reasonable to speculate that differences in learning ability would reflect differences of degree rather than of kind.

Harlow (1959) accepted a position similar to Thorndike's. Harlow suggested that the degree to which an animal can benefit from prior experience may reflect his general learning ability.

Harlow found that after learning a number of two-choice object discrimination problems, a monkey's ability to solve similar problems improved. (That is, the monkey had developed a win-stay, lose-shift approach to the problem.) Harlow attributed this improved performance to interproblem learning, and described this phenomenon as a discrimination learning set.

On the basis of both primate and nonprimate discrimination learning set data, Harlow (1959) has concluded that:

By and large, the phylogenetic data demonstrate that LS [learning set] formation is closely related to evolutionary position, as conventionally described, and to cortical complexity in so far as this characteristic has been effectively measured. (Harlow, 1959, p. 508)

Harlow (1958) concluded that essentially there is no evidence to suggest that any sharp break occurred in the evolution of the learning process. Harlow suggested that such a conclusion is reasonable if one considers modern evolutionary concepts:

The fundamental unity of learning and the continuity of its developing complexity throughout phylogenesis or at the least within the phylogenetic tree, would seem in keeping with modern genetic theory. (Harlow, 1958, p. 288)

Harlow made two main points: 1) that differences in learning set performance are of degree; 2) that the differences are related to cortical complexity. The notion that the cortical complexity of an animal is a good predictor of performance on discrimination tasks has been supported by various other authors [e.g., Rensch (1959)]. However, Stettner and Matyniak (1968) questioned such conclusions.

Stettner and Matyniak (1968) tested various species of birds on discrimination tasks. They reported that some birds can master very complex problems such as oddity problems while many mammals cannot. (The oddity problem requires an animal to approach one of three patterns or objects. The correct one is the one which differs from the other two.)

They concluded that:

...birds are capable of intelligent achievements equalling or even exceeding those of many mammals. Even if future studies should reestablish mammalian superiority, it cannot be denied that birds show some mental capacities that have long been thought to belong solely to animals with a well developed cerebral cortex. (Stettner & Matyniak, 1968, p.71)

Stettner and Matyniak's findings are particularly important since birds have little neocortex. They propose that although cortical complexity might correlate with learning ability in mammals, the development of the hyperstriatum appears to correlate with learning ability in birds. Since there appears to be a different brain structure involved in avian learning, Stettner and Matyniak's conclusions do not support Harlow's thesis that differences in learning ability are related to cortical complexity.

Bitterman (1965) has also taken a view quite different from that of Harlow. Bitterman trained animals on two different types of tasks - a habit reversal task and a probability learning task. In the habit reversal task an animal first learns that a particular stimulus is associated with reward and a second stimulus with non-reward. Either after reaching some performance criterion or after some fixed number of trials the reward contingencies are reversed.

Gonzalez, Roberts and Bitterman (1964) reported spatial habit reversal data for rats. The rats improved over time. That is, the rats made fewer errors to criterion after 10 reversals than after 1 or 2. Such results would be expected from Harlow's learning set research. However, Bitterman, Wodinsky and Candland (1958) found no progressive improvement in fish over a similar number of reversals. In later experiments Bitterman has presented fish up to 150 reversals with no sign of improvement. The rats and fish also differed on probability learning tasks (Bitterman, Wodinsky & Candland, 1968).

In the probability learning task, an animal must learn a discrimination in which one stimulus is randomly rewarded a given percentage of the time (say 70 percent) and the other stimulus the remainder. Figure 1 shows the basic difference between rats and fish on such tasks (Bitterman, Wodinsky & Candland, 1958). The rats tended to maximize on this problem. That is, they tended to approach the most frequently reinforced stimulus 100 percent of the time. Fish, however, tended to probability match. They approached the stimulus that was rewarded 70 percent of the time on about 70 percent of the trials and the stimulus that was rewarded 30 percent of the time on 30 percent of the trials.

Other species have been studied on similar tasks. Bitterman has classified the results as reflecting either "ratlike" or "fishlike" behavior (see Figure 2). From this data Bitterman (1965) has suggested that the results for reversal learning reflect one qualitative difference and the probability learning

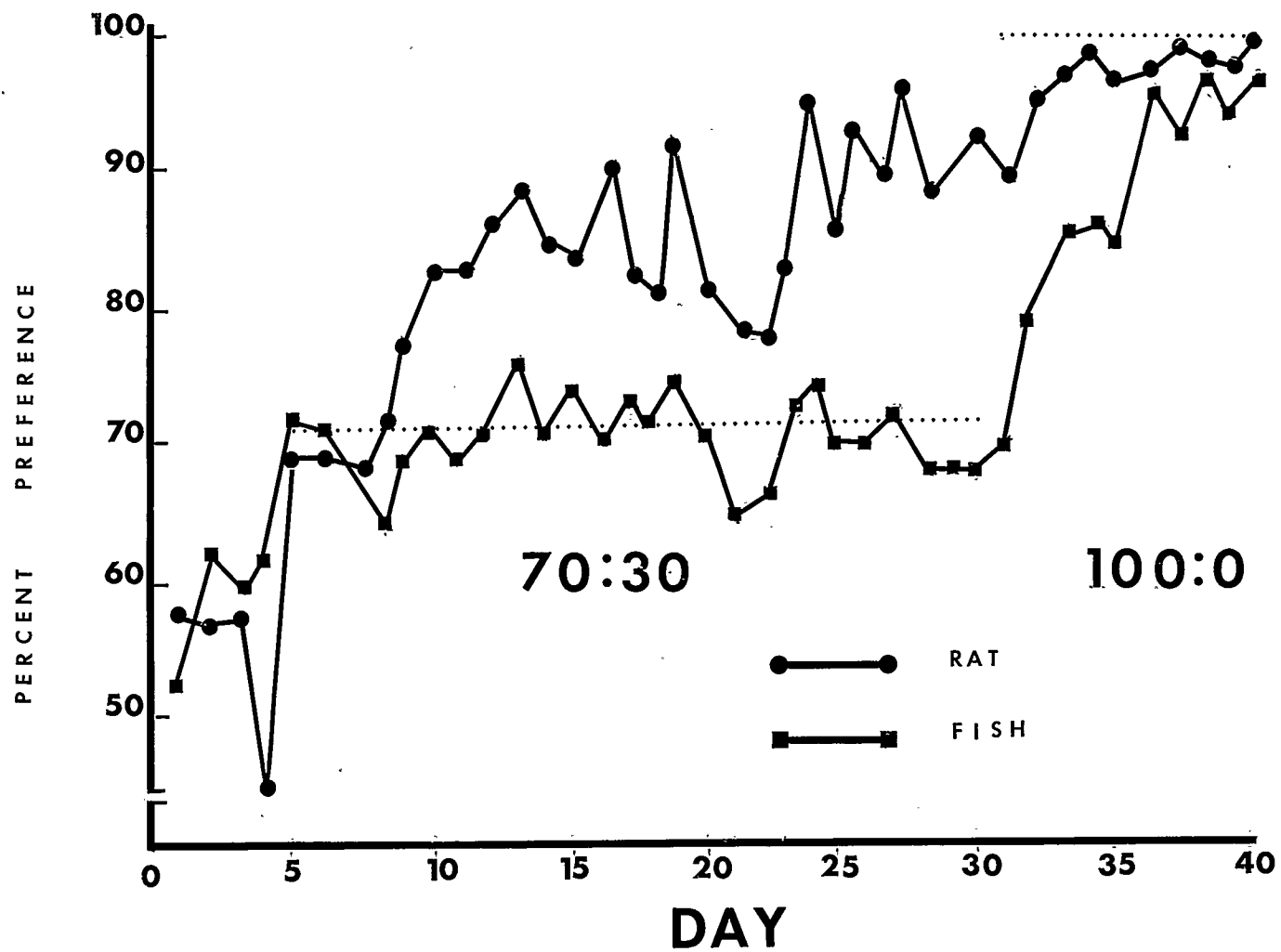


Figure 1. Visual probability learning in fish and rat (from Bitterman, Wodinsky & Candland, 1958).

Animal	Spatial Problems		Visual Problems	
	Reversal	Probability	Reversal	Probability
Monkey	R	R	R	R
Rat	R	R	R	R
Pigeon	R	R	R	F
Turtle	R	R	F	F
Decorticated Rat	R	R	F	F
Fish	F	F	F	F
Cockroach	F	F	-	-
Earthworm	F	-	-	-

Figure 2. Behavior of a variety of animals in four classes of problems which differentiate rat and fish expressed in terms of similarity to the behavior of one or the other of these two reference animals (from Bitterman, 1965).

Note: F means behavior like that of the fish (random probability matching and failure of progressive improvement in habit reversal). R means behavior like that of the rat (maximizing or nonrandom probability matching and progressive improvement in habit reversal). Transitional regions are connected by the stepped line. The brackets group animals which have not yet been differentiated by these problems.

results another.

However, Bitterman's classifications as "fishlike" and "ratlike" behavior could be somewhat premature. Bitterman's results certainly do not allow him to make generalizations about the evolution of intelligence since the species studied do not represent any common evolutionary lineage. Figure 3 demonstrates this point. The rat evolved at a different time during the mammalian development than the monkey. Bitterman has attributed "ratlike" behavior to both the rat and the monkey but Hodos and Campbell (1969) have pointed out that:

Since no rat was ever an ancestor of any monkey, it is not clear whether the rat and monkey independently evolved the "ratlike" pattern or whether it was inherited from a common reptilian ancestor. (Hodos and Campbell, 1969, p. 345)

This argument also receives support from modern evolutionary theory. As Simpson has pointed out:

A typical mammalian level of intelligence is not an original or early characteristic of the Mammalia, but has developed independently and rather differently in each of the different groups of mammals that show it. (Simpson, 1949, p. 79)

If one keeps these arguments in mind it is quite conceivable that there are also differences between the rat and the monkey but the tasks that Bitterman has used are not sensitive enough to detect them. If a task were so difficult that only monkeys could solve it, then both rats and fish might be classed together. Should this be the case, animals could be classified as responding in a "ratlike" manner or in a "monkeylike" manner.

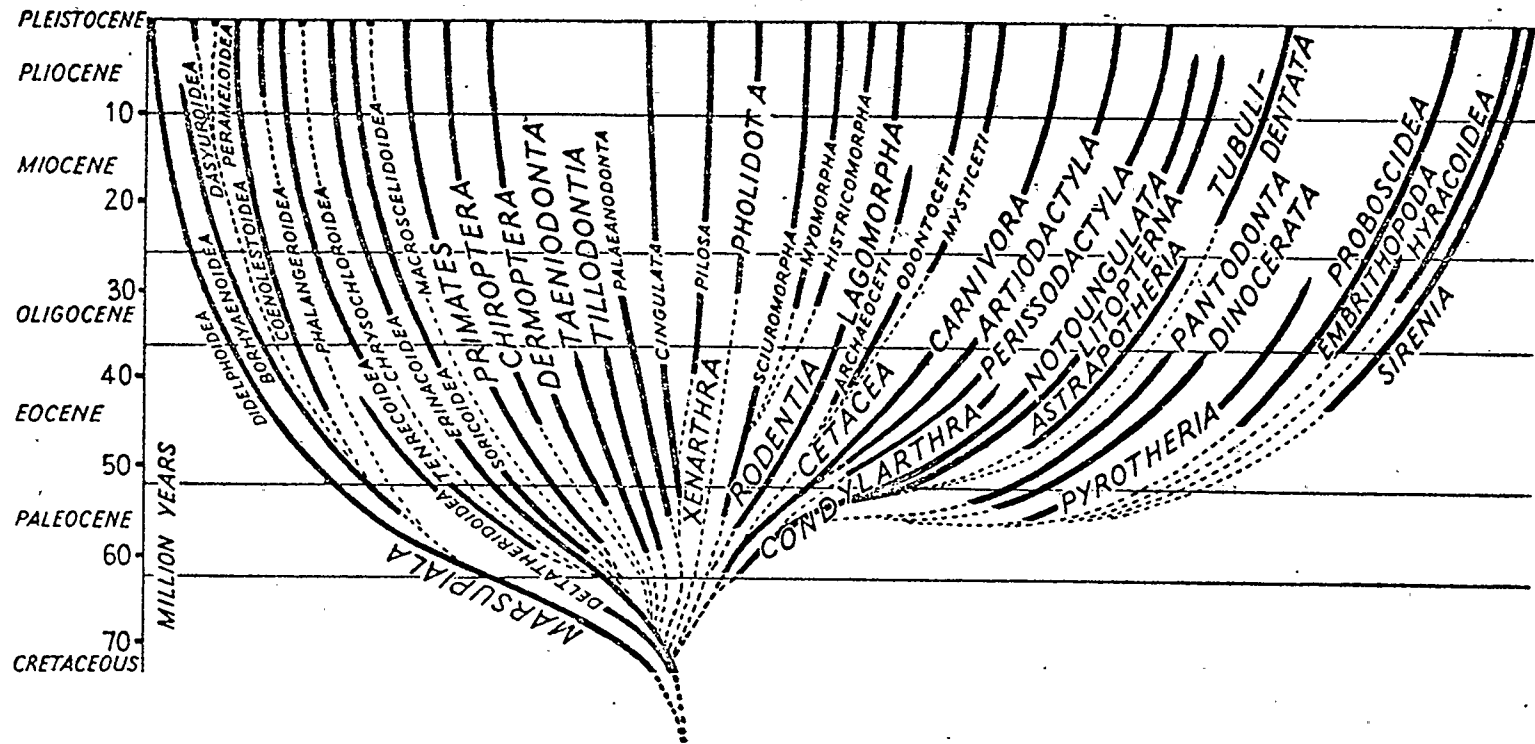


Figure 3. Chart showing the probable affinities of the orders of Mammals (from Young, 1962, p. 579).

On the other hand, to suggest that there is an abrupt shift from "fishlike" behavior to "ratlike" or from "ratlike" behavior to "monkeylike" behavior may be equally premature. Just because the difference between two evolutionarily widely separated species such as the fish and rat appears to be quite distinct does not necessarily imply a different learning mechanism. A picture of gradual change in performance may develop with further study of many animals which are evolutionarily between the rat and the fish. After reviewing learning set data, Warren (1965) comes to a similar conclusion:

In general the available data suggest that the phylogenetic development of capacity for learning set formation in mammals is best described as a continuous S-function with no sharp discontinuities between adjacent taxa but with marked quantitative differences between the extremes of the distribution. (Warren, 1965, pp. 262-263)

Bitterman's data from the turtle in Figure 2 could be interpreted as support for such a conclusion. It is possible that this data represents part of a transition from fish to rat. If data were collected on many more species between the fish and the rat it is possible that a similar table would show a gradual transition from "fishlike" to "ratlike" behavior.

A second possible problem with Bitterman's conclusions is that they are based on both too few species and too few tasks. Bitterman's table might look different if he examined more species on more tasks. Ethologists, for example, have found differences in the behaviors of painted and snapping turtles. Bitterman has examined only one type of turtle on one type of task and from these results has been quick to draw

conclusions about all turtles. Had he used snapping turtles, Bitterman might have found improvement on visual reversal tasks. Furthermore, it is also possible that painted turtles might improve on a different habit reversal task.

Bitterman has also suggested that the differences between rats and fish may be related to differences in brain structure. This notion is not unlike Harlow's conclusion that intelligence is related to cortical complexity. Gonzalez, Roberts and Bitterman (1964) reported data which Bitterman suggested supports such an hypothesis. Decorticated rats behaved like normal rats in experiments requiring more spatial learning but in experiments requiring visual discriminations they behaved like fish. Bitterman (1965) stated that:

These results are compatible with the hypothesis that the cortex of the rat is responsible in some measures for its progressive improvement in habit reversal and for its failure to random probability matching, at least in visual problems. (Bitterman, 1965, p. 404)

Both Harlow and Bitterman appear to have assumed that the brains of more developed animals feature increased amounts of cortex and that this cortex has merely been added through evolution to improve "higher" intellectual functions. Pribram (1958) suggested that such a conclusion may be faulty:

The brain has not evolved by simple accretion but by general remodeling, a conclusion that is even a priori, practically inescapable. It is simply incredible that so complex an organ could continue to function so smoothly as it does by, so to speak, simply plugging in new parts on an old chassis. (Pribram, 1958, p. 512)

If the mammalian brain has been remodeled as each new order has evolved, the function of the brain components could be somewhat different. If this were true, it is possible that either anatomically different areas, or a different mechanism (or process), is involved in the learning of similar tasks by different species.

The research reviewed here indicates that there is considerable controversy about the evolution of learning ability. However, there may be indications that differences in learning from species to species might not be simple differences of "degree" as Darwin had suggested. It might be possible to make more definite conclusions if more species, particularly from within common evolutionary lineages, are tested on many tasks. Consequently, the first purpose of this research is to extend the habit reversal data to the family Sciuridae (Sciurus and Tamias) and to replicate data from the family Muridae (Rattus) both of which are from the order Rodentia.

Since Bitterman (1965) found that habit reversals on visual discriminations produced quantitative (and perhaps qualitative) differences among some species studied, the present research has used visual pattern discriminations. However, the effect of the physical properties of the stimuli on the ease or difficulty of learning the discriminations is considered. Although most researchers have ignored this problem, there are some data to suggest that this might be an important variable to consider.

Franken, Kolb and Wenger (1969) demonstrated that for some pairs of stimuli, the speed of learning (as measured by both errors

and trials to criterion) depended upon which of the stimuli was reinforced. When approaches to a half black and half white, vertically divided stimulus were reinforced, and approaches to a vertical black and white striped stimulus were not reinforced, learning was significantly faster than when approaches to the striped stimulus were reinforced and approaches to the vertically divided stimulus were not. Similar results have been shown for a wide variety of stimulus pairs including solid white versus solid black (e.g., Franken & Kolb, 1969b). Moreover, Franken and Kolb (1969a) and Franken, Kolb and Wenger (1969) have shown that the initial ease or difficulty of the learning of a discrimination can effect reversal performance on that discrimination. For example, if subjects learned a discrimination quickly, they reversed quickly, whereas if they learned slowly, they reversed slowly. From these studies it would seem that both the nature of the stimuli themselves and the order of presentation of the two stimuli are important variables in visual discrimination tasks.

Many researchers have failed to consider findings such as these. For example, Foley (1968) examined cued and non-cued reversal shifts in primates and non-primates by using a horizontal-vertical stripe discrimination. Unfortunately, Foley failed to consider the physical stimulus properties which is reflected by the fact that he neglected to report which stimulus was positive first. From both Franken and Kolb's (1969a) data and Franken, Kolb and Wenger's (1969) data it is reasonable to suspect that Foley's results may have been different had he chosen either a

different set of stimuli or had he reversed the reward properties of the stimuli he chose for initial learning.

This problem is not peculiar to Foley's research. Bitterman has also failed to consider this problem. Some of the discrimination tasks used by Bitterman may have provided an initial advantage for some species. Bitterman's results could be somewhat different (or at least somewhat clearer) if he had considered that the performance of the various species might have been stimulus specific.

Although Franken, Kolb and Wenger (1969) have demonstrated differences in one reversal after initial learning, the effect on more than one reversal has not been demonstrated. The second purpose of this research is to see if the effects found by Franken et al. for one reversal persist through any or all of 9 additional reversals.

Since the procedure varied somewhat from species to species, the procedure used for each species is described as a separate experiment. The rats were run in Experiment 1A, the squirrels in Experiment 1B and the chipmunks in Experiment 1C. However, since the main purpose of this thesis was to make interspecies comparisons, the results were examined both statistically and graphically in a single "Results" section.

II. EXPERIMENT 1A

METHOD

Subjects

Twelve male Long-Evans black-hooded rats (Rattus), aged 80 to 90 days at the beginning of pretraining, were divided into three groups. Each group was presented with a different visual pattern discrimination (see Figure 4).

All animals were individually housed in 18 X 18 X 18 inch cages constructed from 1 inch X 1 inch X 16 gauge galvanized cage wire. The cages were set on cedar wood chips in galvanized metal trays and each cage had a water bottle and an aluminum feed dish located 8 inches above the floor of the cage.

The animals were maintained on a diet of Purina Rat Chow. The lighting in the animal quarters was programmed to produce a light-dark cycle of 14 hours of light and 10 hours of darkness.

Apparatus

The apparatus was a standard Wisconsin General Test Apparatus (see Figure 5). In order to avoid handling the animals during testing, each animals' cage was transported to the test room and placed in the apparatus so that each animal could be tested in its home cage.

The test area was illuminated by an 8 watt strip light while a 150 watt drafting lamp located directly above the front screen illuminated both the cage and test area (see Figure 5).

The foodwells on the 13 inch X 15 inch formboard were 1 inch in diameter and $4\frac{1}{2}$ inches from center to center.

The discriminanda were constructed from 3 inch X 7 inch X 28 gauge

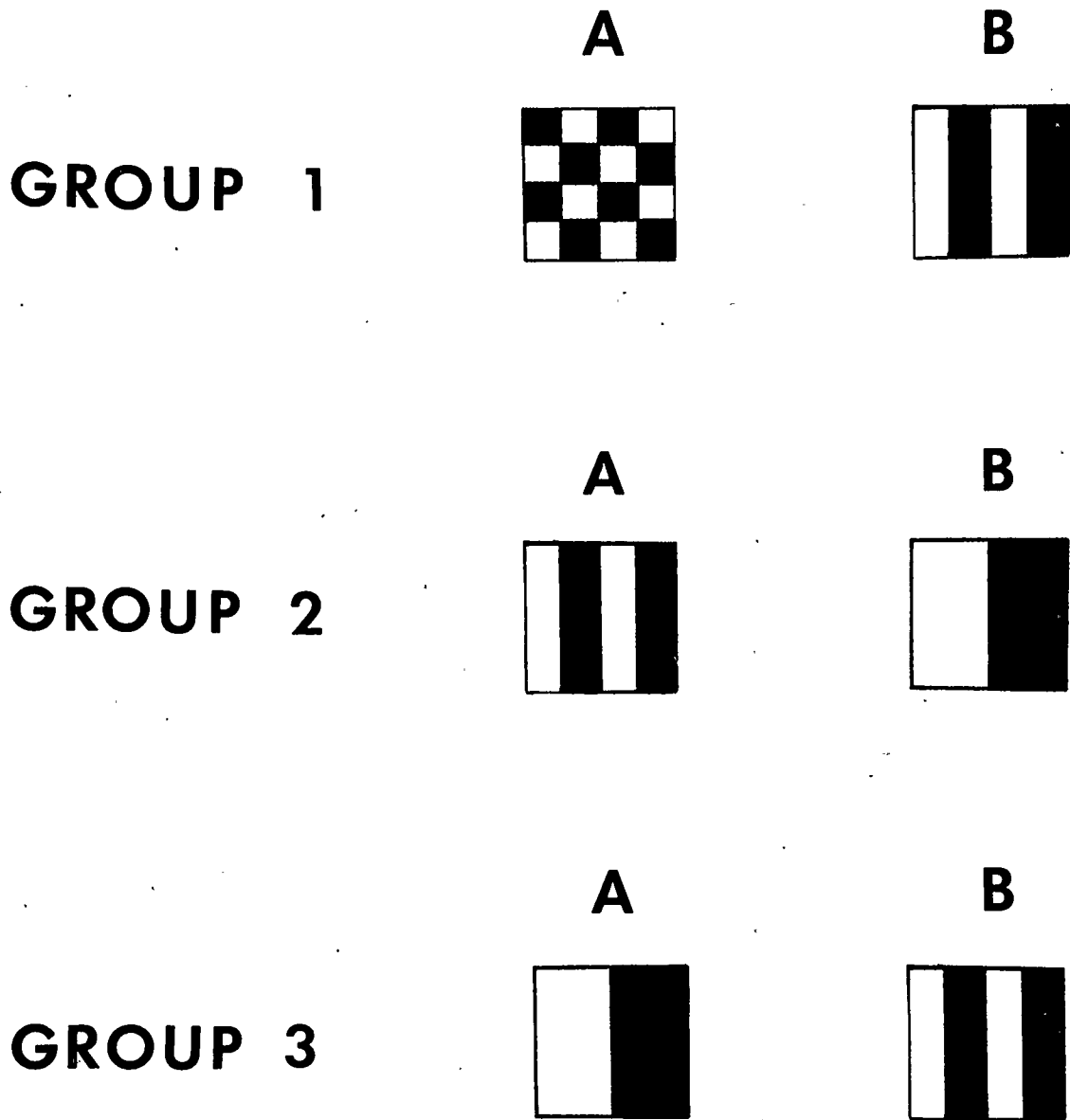


Figure 4. The three discrimination groups (On initial learning the reward was under stimulus A).

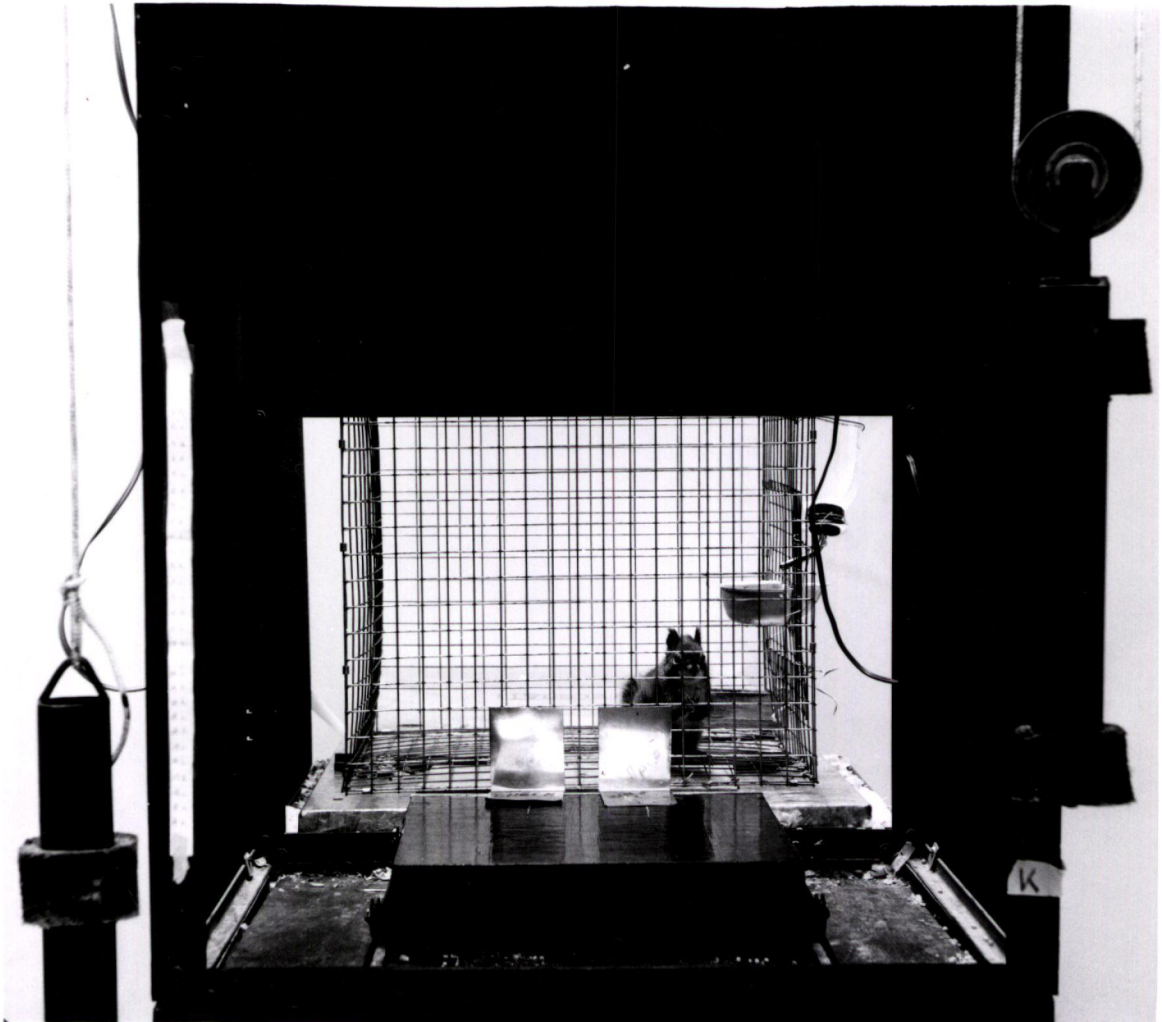


FIGURE 5: The Wisconsin General Test Apparatus

tin plates which were bent in the middle at right angles to produce a 3 inch X 3½ inch pattern display area and a similar sized base. The patterns were made by fixing white "counter-top" material to the tin and then overlaying the white with black plastic tape to form the three patterns. Two additional plain white displays were made for pretraining. The patterns are shown in Figure 4.

The reward was four 45 mg Noyes food pellets. In order to allow the Ss complete access to the reward, one vertical bar was cut out of each cage in front of each foodwell to allow each subject a 1 inch X 2 inch rectangular hole from which he could remove the food.

All subjects had free access to water throughout the entire testing period.

Procedure

Adaptation. All animals were placed in cages at least two weeks prior to testing and were immediately placed on a 22 hour food deprivation schedule.

Pretraining. When first placed in the apparatus, subjects were allowed free access to a reward from either foodwell. After an animal had taken a reward fifteen times (with a maximum of 5 times per day) from each foodwell, the two white pretraining discriminanda were introduced about 1 inch behind the foodwells. They were gradually moved forward until the subjects were displacing the discriminanda to obtain the rewards. Discrimination training began when subjects had completely displaced both pretraining discriminanda five times.

Training. Each group of animals was trained for 20 trials per day. The presentation sequence was a 30 trial Gellerman series using a modified

correction procedure. If an animal made an error (that is, the negative or unrewarded stimulus was displaced) the formboard was pulled back, the displaced card was again placed over the foodwell and the formboard was moved forward. In this way a trial was completed only after a subject made a correct choice. An 8½ inch X 11 inch piece of cardboard was used to block the subjects' vision of the formboard between trials.

Training was completed on each task when a subject reached the probability criterion outlined by Grant (1946). Since the probability of a subject reaching any criterion by chance increases with time, Grant (1946) developed a probability criterion to contend with this problem. The criterion used was: Trials 0-45, 5 correct trials in a row followed by 12 correct out of 15; Trials 46-95, 6 correct trials in a row followed by 12 correct out of 15; Trials 96-145, 7 correct trials in a row followed by 12 correct out of 15; Trials 146-195, 8 correct trials in a row followed by 12 correct out of 15. By using this criterion, the probability of an animal reaching criterion by chance is less than .01 (Grant, 1946).

Following training on the initial task all animals were reversed ten times. Any animal that failed to reach criterion by 160 trials was shifted to the next reversal.

III. EXPERIMENT 1B

INTRODUCTION

Virtually no research has been done on the learning capacity of animals from the Suborder Sciuromorpha. This group includes such families as beavers (Castoridae and Aplodontidae), squirrels (Sciuridae) and gophers (Geomidae). Dodwell and Bessant (1961) did some preliminary work on pattern discriminations in squirrels in which they demonstrated that squirrels tend to have strong natural preference for some visual patterns. Since the consequences of such preferences on visual learning set performance is of prime importance in this thesis, it was decided that squirrels (Sciurus) and chipmunks (Tamias), which are both from the Family Sciuridae, would be tested. Sciurus were tested in Experiment 1B and Tamias in Experiment 1C.

METHOD

Subjects

Twelve red squirrels (Tamiasciurus hudsonicus), which were trapped in the vicinity of the Kananaskis Environmental Sciences Centre, were divided into three groups. Each group was presented with a different visual pattern discrimination (see Figure 4).

The cages were identical to those in Experiment 1A with the exception that there was an additional food dish. It was a wooden box, roughly 5 inches long X 2 inches wide X 2 inches high and was at floor level. The second dish was added because many of the animals persisted in nesting in their aluminum dish.

All animals were maintained on a diet of unshelled sunflower seeds,

corn, wheat, oats, and other small seeds in which the ratio of sunflower seeds to the rest was about 3:1.

Apparatus and Procedure

With the exception of the reward, the apparatus and procedure were identical to those in Experiment 1A. The reward consisted of one-quarter of a salted peanut.

IV. EXPERIMENT 1C

METHOD

Subjects

Twelve yellow-bellied chipmunks (Eutamias minimus borealis) which were trapped in the vicinity of the Kananaskis Environmental Sciences Centre, were divided into three groups. Each group was presented with a different visual pattern discrimination (see Figure 4).

Due to the small size of Tamias the cages were made from 1 inch X $\frac{1}{2}$ inch cage wire but were of the same volume as those in Experiments 1A and 1B.

Apparatus

In both Experiments 1A and 1B a 1 inch X 2 inch rectangular hole was cut in front of the foodwells. Due to the size of Tamias, the size of the hole had to be modified. Since a 1 inch hole proved too large, a trapezoidal shaped hole with a 1 inch base and $\frac{1}{2}$ inch top was used. This was produced by cutting the vertical bar nearest the foodwell at its base and then bending it at a 45 degree angle towards an adjacent vertical bar.

Aside from these small modifications, the apparatus was identical to Experiment 1B.

Procedure

The 22 hour food deprivation schedule proved to be too rigorous for Tamias. It was discovered that E could produce convulsions involving the legs and/or trunk of the animals simply by entering the animal quarters to remove the food. This behavior appeared to be linked to the continual

hoarding behavior of Tamias. That is, the chipmunks appeared to spend most of the two feeding hours hoarding their food rather than eating it. The convulsions were eliminated by reducing the deprivation period to 16 hours and allowing a 24 hour feeding period every tenth day. All hoarded food was removed after the feeding period.

Although the reward was reduced to about 1/12 th of a peanut, the remainder of the pretraining and training procedures were identical to Experiment 1B.

V. RESULTS

The results were divided into two major sections entitled "Interspecies Comparisons" and "Intraspecies Comparisons". By separating the results in this way, it was possible to examine differences in initial learning and rates of improvement both within and between species. In the "Interspecies Comparisons" section there were two additional subheadings - initial learning and reversal learning. This made it possible to statistically analyse the data (errors to criterion) for initial learning separately from the data for reversal learning (errors to criterion on each reversal) so that an analysis of improvement across reversals could be made.

The data were examined for homogeneity of variance and then transformed ($X' = \sqrt{X}$) by procedures outlined by Winer (1962, p. 220).

Interspecies Comparisons

The transformed data for Groups 1, 2 and 3 are graphed in Figures 6, 7 and 8 respectively, while the graphs of the non-transformed data are presented in Appendices D, E and F respectively.

Initial learning

A one-way analysis of variance, which was performed across species on the initial learning of Group 1 showed that there was a significant difference among the species ($F = 5.16$, $df = 2/9$, $p < .05$). It appeared from Figure 6 that the squirrels learned

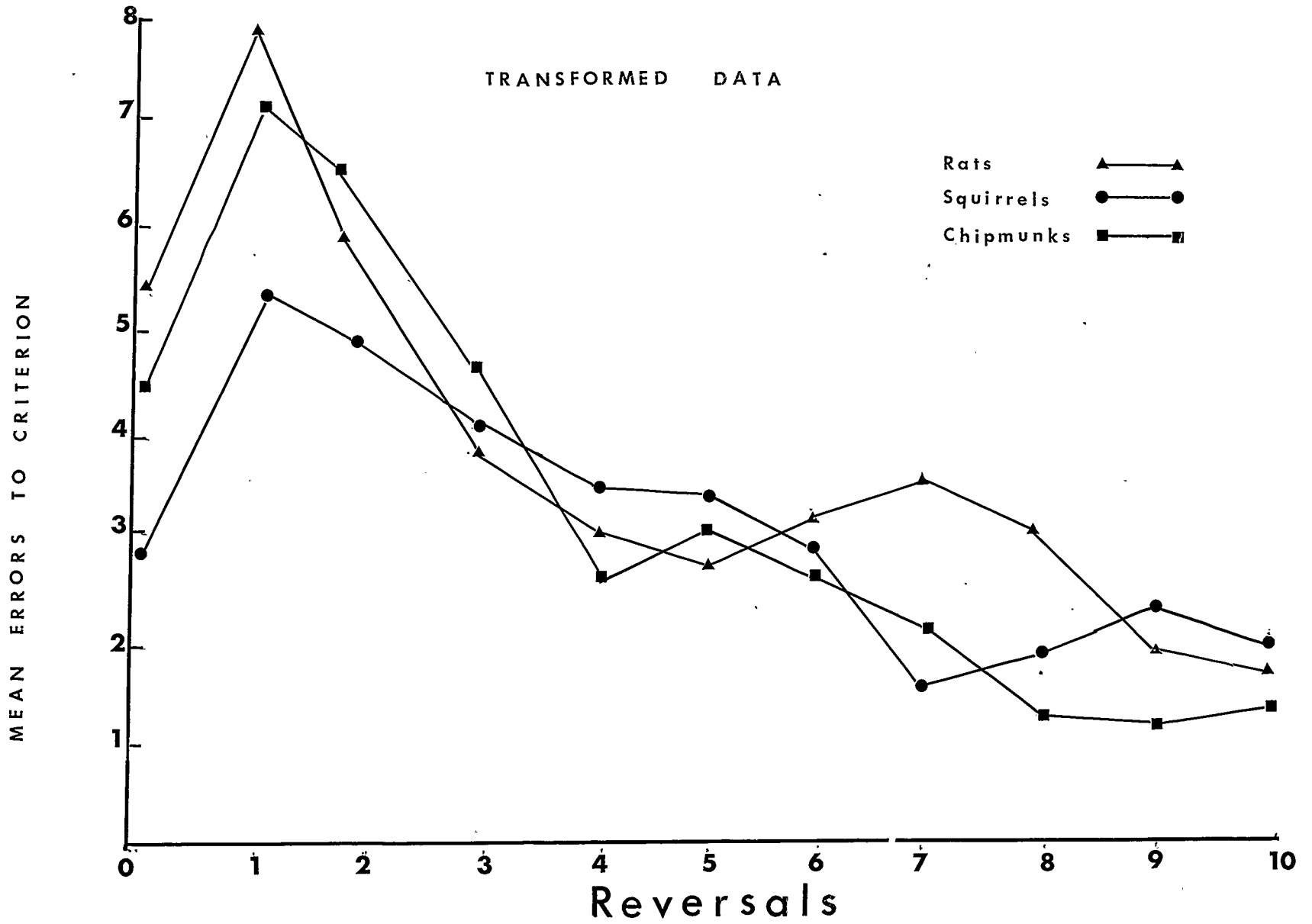


Figure 6. Group 1

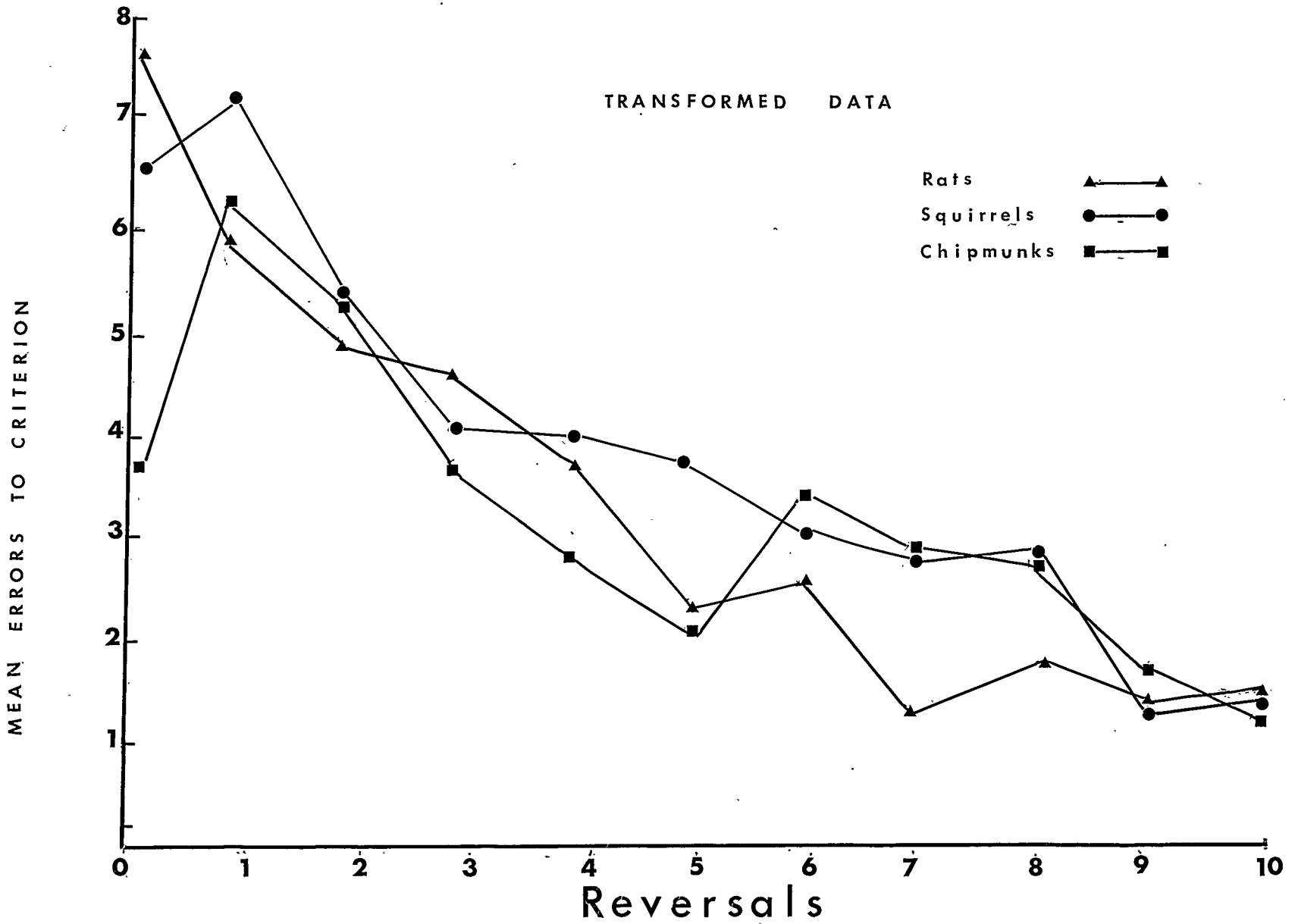


Figure 7. Group 2

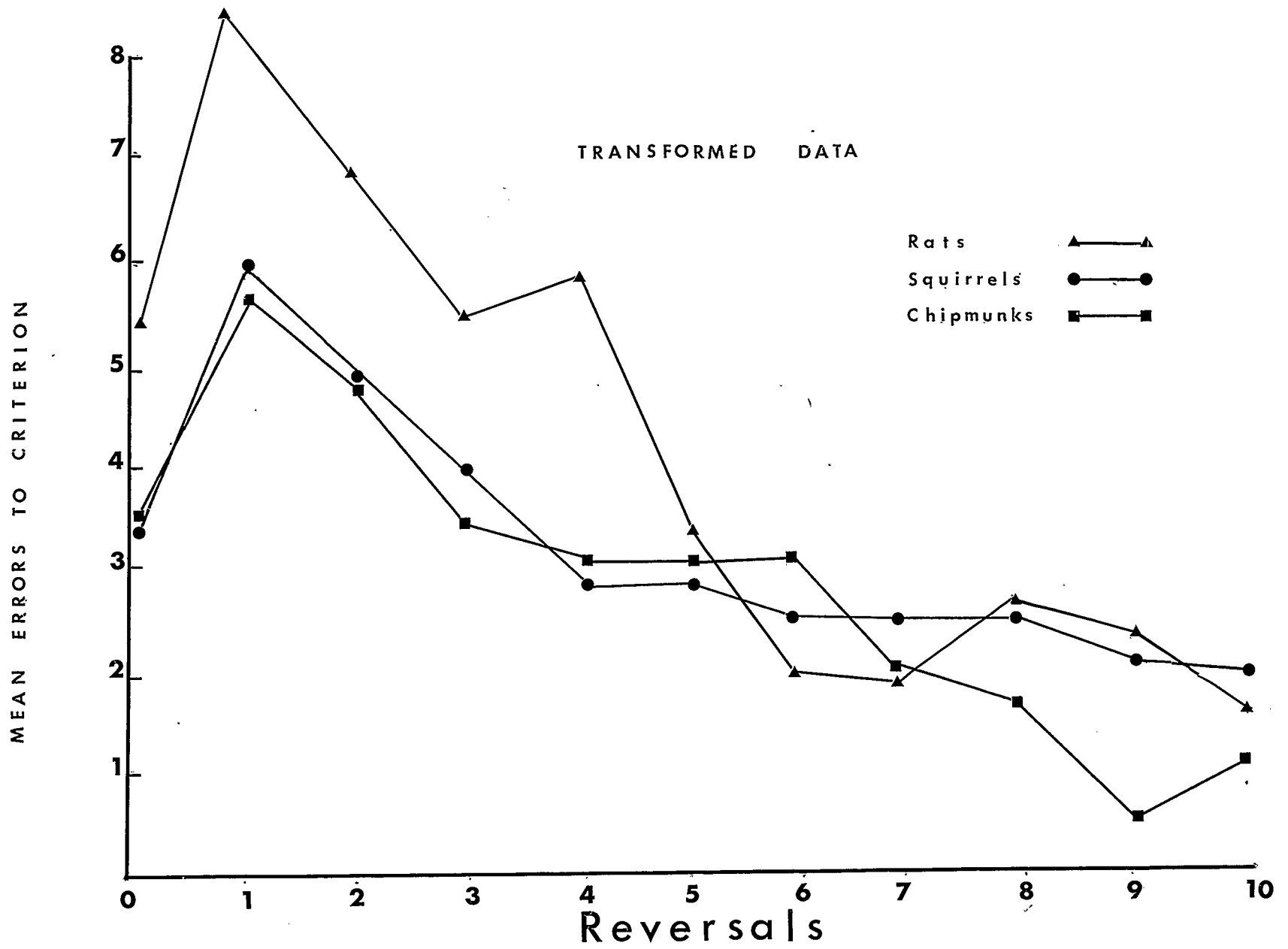


Figure 8. Group 3

more quickly than either the rats or chipmunks. This conclusion was substantiated by a Duncan Multiple Range Test ($p < .05$). In addition, this test also revealed a significant difference between the rats and chipmunks ($p < .05$). Similarly, a one-way analysis of variance on the initial learning in Group 2 also produced a significant difference among the species ($F = 6.05$, $df = 2/9$, $p < .05$). From Figure 7 it appears that the chipmunks learned the initial discrimination faster than either the rats or the squirrels. A Duncan Multiple Range Test on these data showed that the chipmunks did learn this discrimination faster than the rats and squirrels ($p < .05$) while the rats and squirrels did not differ ($p > .05$). Although the rats appeared to have learned the Group 3 discrimination more slowly than the other species, an analysis of variance revealed no significant difference ($F = 1.26$, $df = 2/9$, $p > .05$). This might be accounted for by the fact that the intersubject variability was quite large. This is reflected by the group ranges. The range in transformed error scores for the rats was from 3.00 to 7.00, the range in transformed error scores for the squirrels was from 0.00 to 4.58 while the range in scores for the chipmunks was from 1.00 to 5.91. The source tables for the one-way analyses of variance are given in Appendices J, K and L respectively.

Reversal learning

It is apparent from Figures 6, 7 and 8 that all three groups improved across the reversals and that the reversal performance curves began to asymptote after about five reversals. The

reversal performance curves appear to asymptote at about the same time for all species and on all three groups. It is interesting to note that the rats in Group 2 (Figure 7) show a decrease in errors on the first reversal. This was not typical of any of the other performance curves. This unusual decrease may be due to a very strong preference in rats for the half-white and half-black stimulus over the striped stimulus.

An overall analysis of variance was performed on the reversal data in order to examine the possibility of interspecies differences over reversals and groups. Since interspecies differences appeared to be virtually nonexistent by the fifth reversal, only the first five reversals were statistically analyzed. Since one purpose of this thesis was to examine the effect of the physical properties of the discriminative stimuli on reversal performance by counterbalancing the stimuli, it was decided to include only the counterbalanced groups (Groups 2 and 3) in this analysis. The source table is presented in Table 1. The Species and Reversal main effects were significant ($F = 4.27$, $df = 2/18$, $p < .05$; $F = 12.99$, $df = 4/72$, $p < .05$) as was the Species X Group interaction ($F = 6.03$, $df = 2/18$, $p < .05$). This significant interaction infers that counterbalancing had a differential effect across species. To understand the implications of the the Species X Group interaction, it is necessary to examine Figures 7 and 8. The performance curve for the rats in Group 2 (Figure 7) is almost identical to those of the squirrels and chipmunks but the performance curve for the rats in Group 3 is quite different than either the squirrels' or chipmunks' for

TABLE 1

Analysis of Variance: First Five Reversals

Source	df	MS	F
Specie (A)	2	12.34	4.27*
Reversal (B)	4	51.82	12.99*
Group (C)	1	4.73	1.64
AB	8	1.04	.26
AC	2	17.44	6.03*
BC	4	.26	.07
ABC	8	.96	.24
Total	119		

* $p < .05$

at least the first four reversals. When an individual degree of freedom test was performed to compare the weighted average of the chipmunks and squirrels against the rats, there was a significant difference ($F = 6.89$, $df = 1/18$, $p < .05$). A similar test showed that the squirrels and chipmunks did not differ ($F = 1.65$, $df = 1/18$, $p > .05$). However, by comparing Figures 7 and 8, it would appear that the statistical inferiority of the rats is entirely due to their comparatively poor performance in Group 3.

Intraspecies Comparisons

The performance of each of the species has been graphed separately. The rat data are graphed in Figure 9, the squirrel data in Figure 10 and the chipmunk data in Figure 11. The non-transformed data are graphed in Appendices I, J, and K. It appears from Figures 9 and 10 that neither the rats nor the squirrels prefer the striped stimulus since the initial performance on Group 2 by both species is poorer than the performance by Groups 1 and 3. The performance of both of these species is particularly interesting on the first reversal. It was noted earlier that the Group 2 rats actually improved on the first reversal. Although the Group 2 squirrels did not improve on the first reversal, the increases in errors by the squirrels in Groups 1 and 3 are considerably larger than those for Group 2. The mean for Group 1 increased from 2.79 to 5.47 (resulting in an increase of 2.36), and the mean for Group 3 increased from 3.30 to 6.04 (resulting in an increase of 2.74), while the mean for Group 2 only increased

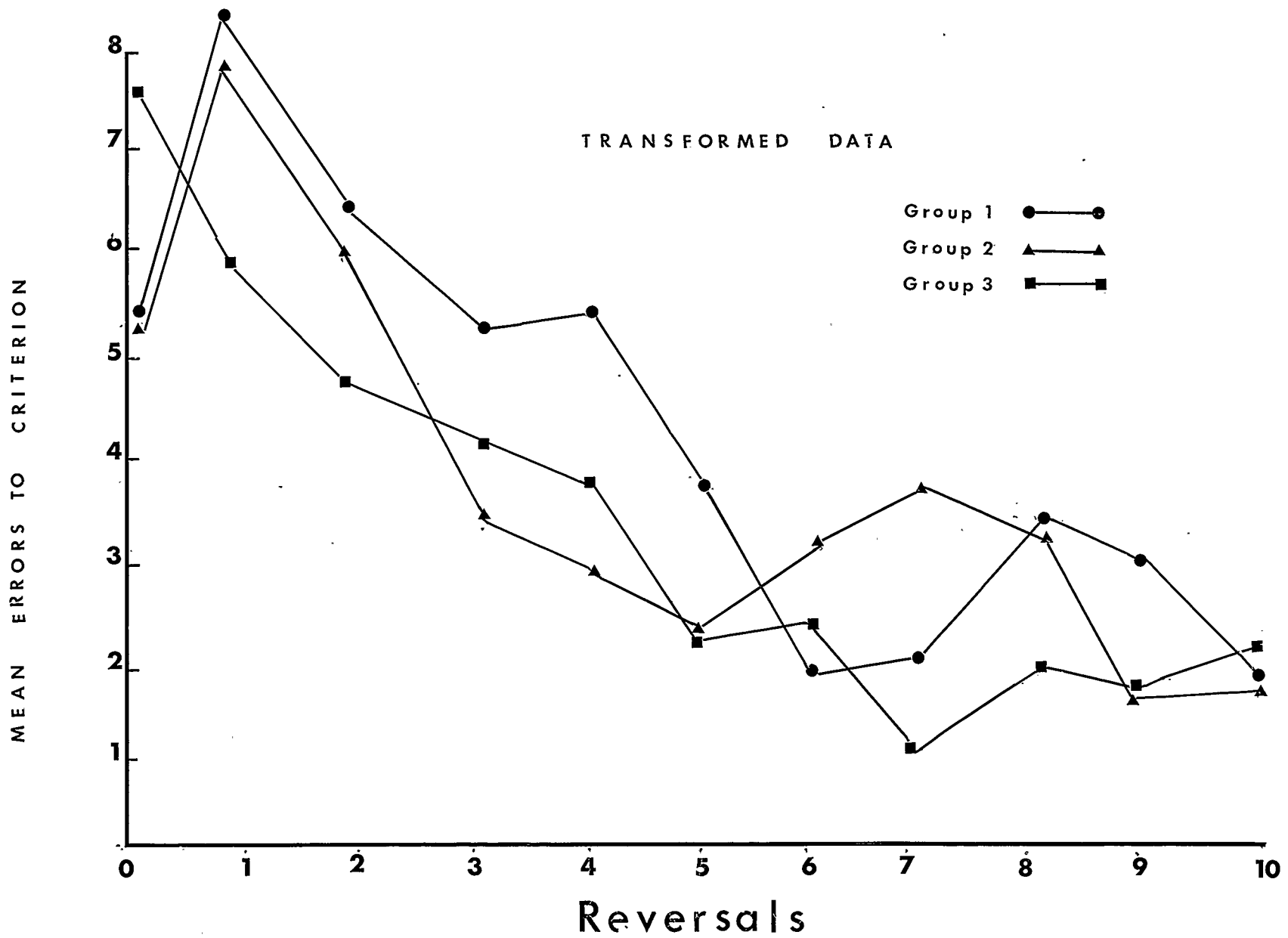


Figure 9. Rats

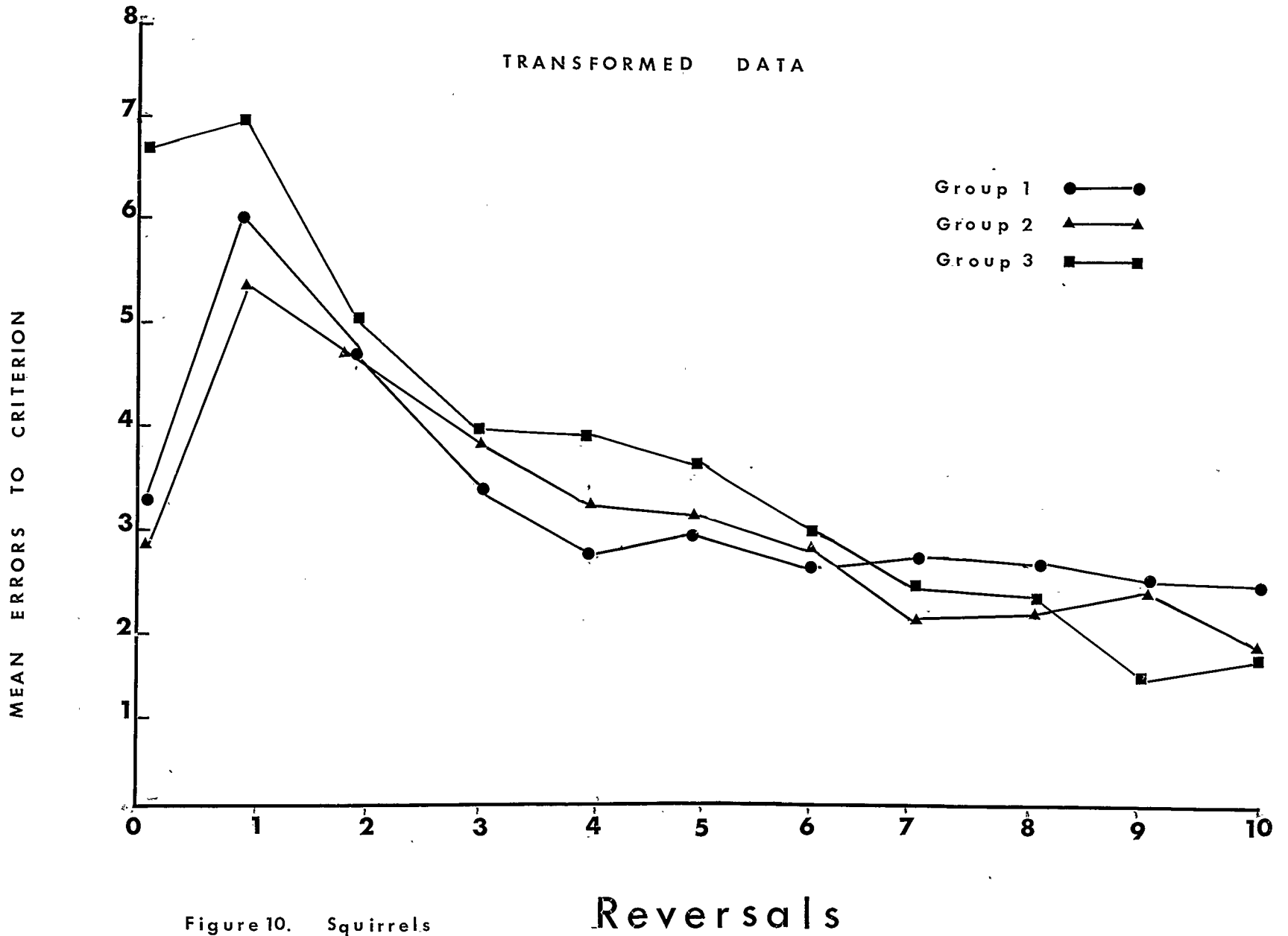


Figure 10. Squirrels

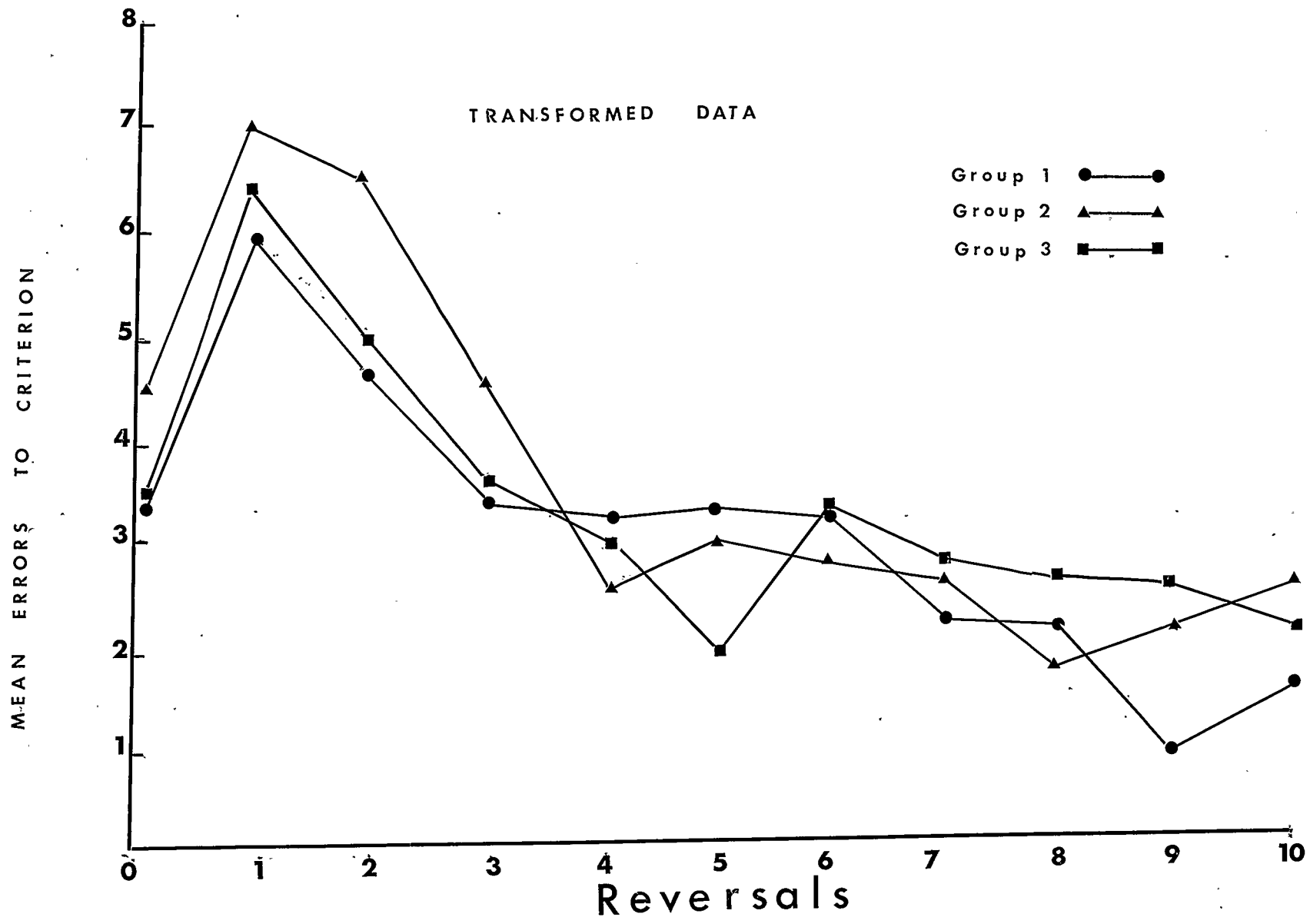


Figure 11. Chipmunks

from 6.73 to 7.04 (resulting in an increase of .31). It appears that the first reversal for both the rats and squirrels in Group 2 was easier than for Groups 1 and 3 which now had to learn to approach the striped stimulus. In Figure 11 it is evident that the presentation of the striped stimulus to the chipmunks did not produce the same effect as it did in the rats and squirrels. The chipmunks do not appear to have a preference for any of the stimuli although the checkered stimulus may have some aversive qualities to this species.

VI. DISCUSSION

All three of the species improved over the reversals. This was expected since the previous research on other rodents had produced similar results. Gonzalez, Roberts and Bitterman (1964) found improvement over reversals in rats, while Rees (1968) found improvement in both roundtailed ground squirrels and white-throated woodrats, and King (1965) found similar improvement in rock squirrels. King ran his animals for a fixed number of trials before each reversal while in the present experiments, all animals were run to a performance criterion. Improvement in rodents on visual habit reversals is a reliable phenomenon as it occurs in many species and under different experimental conditions.

Franken, Kolb and Wenger (1969) found that rats had more difficulty learning a discrimination when a striped stimulus was positive and a half-black and half-white stimulus was negative than when the reverse was true. They proposed that one theoretical interpretation of this result was that the animals had a preference for the half-black and half-white stimulus. The data from this thesis indicated that preferences affect both initial learning and the learning of the first few reversals but do not prevent acquisition of a learning set.

The particular stimulus pairs chosen for this research produced differences in the initial learning of the rats and squirrels which were similar to those found by Franken, Kolb and Wenger (1969). On the first reversal, Franken et al. found that

when the previously rewarded striped stimulus became the non-rewarded stimulus, the reversal learning was slower than the reversal learning of the counterbalanced group. This was not the case for the rats in the present study. Those rats who now had to learn to approach the half-black and half-white stimulus actually improved, while those who now had to learn to approach the striped stimulus learned more slowly. No explanation of this difference can be offered.

The most important finding in this thesis was the significant Group X Species interaction. This interaction of the stimulus pairs and the species could have a profound effect on any conclusions about interspecies differences. Some examples should illustrate the point.

In the present experiments, if the striped stimulus was positive in initial learning the conclusion would have been that all three species improved at a similar rate. On the other hand, if only the counterbalanced group had been tested, the conclusion would have been that there was a quantitative difference between the performance of the rats and that of the squirrels and chipmunks. Since both counterbalanced groups were tested, the latter conclusion appears faulty. These data suggest that since different stimuli mean different things to different species, it is very difficult to make any generalization regarding interspecies quantitative differences.

Any suggestion as to why specific stimulus properties are so important to particular animals is purely speculation but it is

clear that the assignment of "positive" and "negative" values to the discriminanda is an important variable to consider. Any assumption that the development of a discrimination is unaffected by the assignment of "positive" and "negative" values may result in invalid conclusions.

CURRENT STATUS OF LEARNING SET RESEARCH

Even though there are variables that are neither controlled nor understood, the habit reversal learning data can make a contribution to the study of the evolution of learning ability when it is considered in the light of the other learning set data. Tables 2 through 8 briefly summarize most of the work done to date on the three most common types of learning sets - habit reversal, discrimination and oddity learning sets.

The tables are set up in a way which is analogous to Bitterman's (1965) table (see Figure 2). The difference is that animals are described as improving on the problem (I), which infers the development of a learning set, or not improving, (NI), which infers that there was a failure to demonstrate the development of a learning set. The number in parenthesis following the I or NI refers to the number of the study in the References section. For example, I (20) indicates that improvement was found in a study referenced as number 20. No indication of the rate of improvement is given.

In Table 2, the only species that does not improve on a task is the tree shrew (Tupaia glis). Unfortunately, since this animal

is difficult to test successfully, the results may be a function of this. The tree shrews excepted, all primates improve on all the problems that are tabled.

In Table 3, it is interesting that those carnivores that have been tested on oddity problems have failed to develop a learning set. The carnivore results are particularly interesting in light of the findings in Table 4 because Koronokos and Arnold (1957) reported that rats developed oddity learning sets. It may be a mistake to suggest that the carnivores cannot develop oddity learning sets, or to hypothesize why, but the evidence is against it at this point. Notice also in Table 4 that the bottlenose dolphin failed to develop a discrimination learning set. However, as the footnote implies, these results may be entirely a function of spatial discontinuity between the stimulu-cue locus and response locus which may have restricted the dolphin's performance level. Herman, Beach, Pepper and Stalling (1969) the authors of the dolphin study, are presently replicating their previous findings and predict that once their apparatus has been modified they will find improvement in dolphins.

With the exception of rats and canaries, there has been little oddity learning set research in rodents or birds. It is difficult to make predictions about the performance of the untested rodents and birds on oddity tasks. They will likely also show improvement since there is little evidence to suggest that there may be qualitative differences within any class.

Table 5 summarizes the reptile research. Although there has been too little research done to make any conclusions about the reptiles, it is likely that, in general, reptiles will show improvement on both spatial and non-spatial habit reversal learning.

The results reported in Table 6 are difficult to explain on the basis of Bitterman's (1965) fish-rat dichotomy because there are two studies in which fish show "ratlike" behavior. Even though the nonimprovement studies have been replicated many times, the fact that improvement has been found at all is very important. It is likely that the recent discovery of improvement in African Mouthbreeders by Sherrington and Bishop (1967) and in Oscars by Squier (1969) will promote much more research on fish. Any conclusions about the development or lack of development of learning sets by fishes must await this research.

Out of the many thousands of species of invertebrates only six have been tested and these represent only three phyla. The only invertebrate to show improvement is the octopus (Table 8). The improvement by the octopus was on a non-spatial habit reversal while for all the other invertebrates it was on a spatial habit reversal problem. This makes the comparison somewhat difficult. It would seem reasonable to predict improvement by the octopus on the spatial task since the spatial task is probably an easier task. It might be a mistake to suggest that most invertebrates cannot improve on spatial habit reversals, but again, the evidence is against it at this point.

Even after carefully considering Tables 2 to 8, it is difficult to make very many conclusions about the evolution of learning ability. At this point, it is important to ask the question of whether the learning set research summarized in Tables 2 to 8 adds much to our understanding of the evolution of learning ability at all. This question is important in view of the problems with habit reversal learning set data that have already been pointed out in this thesis. A question that must also be considered is whether it is reasonable to attempt to make interspecies comparisons on the basis of learning set performance when psychologists don't even understand the learning by any single species on such tasks.

It appears that many of the researchers who have made interspecies comparisons based on learning sets have assumed: 1) that all stimuli are neutral and that the stimuli themselves do not effect the learning by different species; 2) that by testing animals on one discrimination it is possible to get a more or less accurate account of a species' learning ability; and 3) that it is possible to make conclusions about both "qualitative" and "quantitative" differences on the basis of a single discrimination task. The data of this thesis questions the validity of these assumptions.

In order to make valid conclusions about interspecies learning ability, psychologists will have to consider species specific behavior. This consideration is particularly important in the light of this

thesis as it is conceivable that different learning "mechanisms" may only be as different as the stimulus characteristics and the specific experimental conditions.

TABLE 2

Summary of Learning Set Research on Primates

CLASS: MAMMALIA

Order	Family	Genus	Common Name	Habit Reversal		Discrimination Problems	Oddity Problems	
				Spatial	Non-Spatial			
Primate	Pongidae	<u>Pan</u>	Chimpanzee			I (33)	I (66)	
		<u>Gorilla</u>	Gorilla			I (15)		
		<u>Pongo</u>	Orangutan			I (55)		
	Cercopithecidae	<u>Macaca</u>	Rhesus		I (74)	I (74)	I (65)	I (66)
			Stump tailed macaque				I (56)	
			Phillipine cynomolgus				I (56)	
	Cebidae	<u>Gerocebus</u>	Mangabey				I (4)	
<u>Atetes</u>			Spider			I (59)		
<u>Cebus</u>			Capuchin	I (29)		I (59)		
Callithricidae	<u>Saimiri</u>	Squirrel		I (29)	I (28)	I (59)		
		<u>Callithrix</u>	Marmoset			I (47)		
Lemuridae	<u>Lemur</u>	Lemur				I (65)		
Tupaidea	<u>Tupaia</u>	Tree shrew				NI (44)		

Note: Primate classification is from Morris (1965). In Tables 2 to 8 "I" stands for improvement and "NI" stands for no improvement while the number in parentheses refers to the number of the study in the Reference section.

TABLE 3

Summary of Learning Set Research on Carnivores

CLASS: MAMMALIA

Order	Family	Genus	Common Name	Habit Reversal		Discrimination Problems	Oddity Problems
				Spatial	Non-Spatial		
Carnivora	Canidae	<u>Canis</u>	Beagle dog		I (21)		
	Procyonidae	<u>Procyon</u>	Raccoon	I (29)		I (58)	NI (66)
		<u>Nasua</u>	Coati-	I (29)			
		<u>Potos</u>	mundi	I (29)	I (28)		
		<u>Bassariscus</u>	Kinkajou	I (29)	I (28)		
	Mustelidae	<u>Mustela</u> <u>Mustela</u> <u>Mephitis</u>	North-	I (29)	I (28)		
			American			I (14)	
			cacomistle			I (14)	
Felidae	<u>Felis</u>	Pearl mink					
		Ferret					
		<u>Mephitis</u>	Striped skunk	I (29)	I (28)	I (14)	
			Cat	I (74)	I (74)	I (74)	NI (66)
			Burmese cat			I (65)	

Note: Carnivore classification is from Morris (1965).

TABLE 4

Summary of Learning Set Research on Rodents and Other Miscellaneous Mammals

CLASS: MAMMALIA

Order	Family	Genus	Common Name	Habit Reversal		Discrimination Problems	Oddity Problems
				Spatial	Non-Spatial		
Rodentia	Sciuridae	<u>Sciurus</u>	Red squirrel		I (+)		
		<u>Tamias</u>	Least chipmunk		I (+)		
		<u>Citellus</u>	Roundtailed ground squirrel		I (53)		
			Rock squirrel		I (42)	I (42)	
	Muridae	<u>Rattus</u>	Lab rat	I (22)	I (+)	I (40)	I (43)
Cricetidae	<u>Neotoma</u>	White-throated woodrat			I (53)		
		<u>Meriones</u>	Gerbil			I (41)	
Marsupialia	Didelphidae	<u>Didelphis</u>	Virginia opossum	I (20)			
	Macropodidae	<u>Macropus</u>	Grey kangaroo		NI (49)		
Perissodactyla	Equidae	<u>Equus</u>	Domestic horse	I (73)			
Pinnipedia	Otariidae	<u>Zalophus</u>	Calif. sea lion		I (57)		
Cetacea	Delphinidae	<u>Tursiops</u>	Bottlenose dolphin			NI (35)*	

Note: All classification is from Morris (1965)

* These results are controversial since spatial discontinuity between stimulus-cue locus and response locus may have restricted the dolphin's performance level. + Data from this thesis.

TABLE 5

Summary of Learning Set Research on Birds

CLASS: AVES

Order	Family	Genus	Common Name	Habit Reversal		Discrimination Problems	Oddity Problems
				Spatial	Non-Spatial		
Anseriformes	Anatidae	<u>Cygnus</u>	Trumpeter swan	I (24)			
Calliformes	Phasianidae	<u>Colinus</u>	Bob white quail	I (26)	NI (64)		
		<u>Perdix</u>	Chukar partridge	I (24)			
		<u>Gallus</u>	Domestic chicken	I (26)	I (23)	I (51)	
	Numidae		Guinea fowl	I (24)			
Columbiformes	Columbidae	<u>Columba</u>	Ring neck dove	I (24)			
			Pigeon	I (24)	I (10)	I (77)	
Psittaciformes	Psittacidae	<u>Amazona</u>	Yellow Head parrott	I (26)	I (23)		
Passeriformes	Corvidae	<u>Corvus</u>	Crow		I (63)		
		<u>Urocissa</u>	Himalayan magpie	I (24)			
			Red billed blue magpie	I (26)	I (23)		
	Gracula	<u>Sturnidae</u>	Greater hill myra	I (25)	I (23)		
	Placeidae	<u>Serinus</u>	Canary				I (50)

Note: All bird classification is from Austin (1961) and the American Ornithologist's Union (1957).

TABLE 6

Summary of Learning Set Research on Reptiles

CLASS: REPTILIA

Order	Family	Genus	Common Name	Habit Reversal		Discrimination Problems	Oddity Problems
				Spatial	Non-Spatial		
Squamata	Iguanidae	<u>Iguana</u>	Iguana	I (1)			
Chelonia	Emydidae	<u>Chrysemys</u>	Painted turtle	I (37)	I (37)		
Crocodilia	Crocodylidae	<u>Alligator</u>	Alligator	I (27)			
		<u>Crocodylus</u>	Crocodile	I (27)			
		<u>Gaiman</u>	Spectacled caimon	I (75)			

Note: All reptile classification from Terent'ev (1965)

TABLE 7

Summary of Learning Set Research on Fish

CLASS: PISCES

Order	Family	Genus	Common Name	Habit Reversal		Discrimination Problems	Oddity Problems
				Spatial	Non-Spatial		
Labyrinthici	Osphronomidae	<u>Macropodus</u>	Paradise Fish	NI (72)			
Chromides	Cichlidae	<u>Tilapia</u>	African mouthbreeder	NI (5) I (60)			
		<u>Astronotus</u>	Oscar fish		I (67)		
Ostariophysi	Cyprinidae	<u>Cyprinus</u>	Goldfish	NI (6)	NI (6)		

Note: All fish classification from Jordan (1963).

TABLE 8

Summary of Learning Set Research on Invertebrates

INVERTEBRATA

Class	Genus	Common Name	Habit Reversal		Discrimination Problems	Oddity Problems
			Spatial	Non-Spatial		
Cephalapoda	<u>Octopus</u>	Octopus		I (46)		
Crustacea	<u>Orconectes</u>	Crayfish	NI (11)			
	<u>Genecarcinus</u>	Bermuda land crab	NI (13)			
Oligochaeta	<u>Lumbricus</u>	Earthworm	NI (12)			
Insecta	<u>Nauphoeta</u>	Cochroach	NI (45)			
	<u>Armadillidium</u>	Sowbug	NI (69)			

Note: All invertebrate classification from Hegner and Engemann (1968).

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VIII. APPENDICES

APPENDIX A

Error Scores for Rats on All Three Groups

<u>Group 1</u>												<u>Group 2</u>												<u>Group 3</u>											
<u>No.</u>	<u>Reversal</u>											<u>No.</u>	<u>Reversal</u>											<u>No.</u>	<u>Reversal</u>										
	0	1	2	3	4	5	6	7	8	9	10		0	1	2	3	4	5	6	7	8	9	10		0	1	2	3	4	5	6	7	8	9	10
1	43	63	22	7	6	3	21	26	7	4	5	2	62	25	23	11	5	8	3	2	3	2	4	3	49	90	35	49	26	23	5	2	10	1	3
6	26	79	50	22	5	3	3	2	4	2	3	5	94	29	28	59	45	10	5	1	5	3	6	4	38	66	92	31	82	29	6	5	31	13	2
7	36	41	21	10	3	3	2	21	9	1	0	8	39	68	38	6	1	1	3	0	5	2	1	10	9	61	40	5	2	8	2	4	1	7	2
12	12	71	53	11	22	13	16	15	10	3	3	11	45	26	7	12	15	1	10	6	3	3	3	9	32	67	21	39	22	3	2	3	4	7	2

APPENDIX B

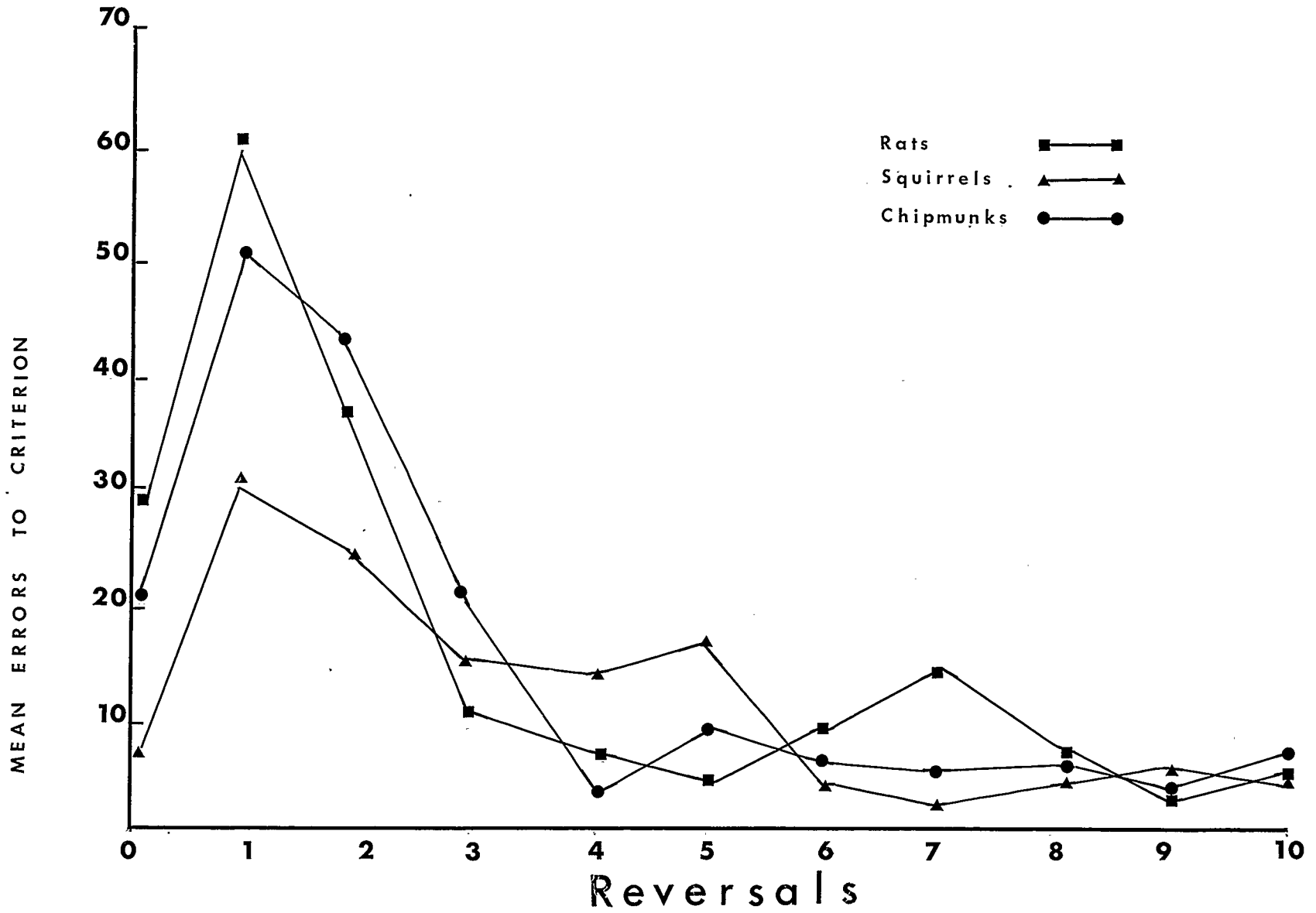
Error Scores for Squirrels on All Three Groups

<u>Group 1</u>											<u>Group 2</u>											<u>Group 3</u>													
<u>No.</u>	<u>Reversal</u>										<u>No.</u>	<u>Reversal</u>										<u>No.</u>	<u>Reversal</u>												
	0	1	2	3	4	5	6	7	8	9	10	0	1	2	3	4	5	6	7	8	9	10	0	1	2	3	4	5	6	7	8	9	10		
3.	19	48	19	5	4	6	7	1	2	3	2	5	56	48	20	26	29	21	21	15	4	4	7	7	21	55	31	33	5	12	9	7	9	12	9
8	8	39	16	31	34	42	23	6	4	10	3	F	57	59	48	29	18	14	6	2	5	2	1	6	0	21	14	3	4	3	3	15	11	2	4
S	4	37	43	8	4	3	1	3	3	2	4	4	33	45	18	7	8	4	1	1	2	0	2	1	14	34	48	16	16	7	3	2	4	2	5
D	4	7	20	23	14	3	3	1	5	3	2	2	38	47	24	8	9	19	7	5	9	6	2	R	24	40	9	16	6	13	11	3	9	8	3

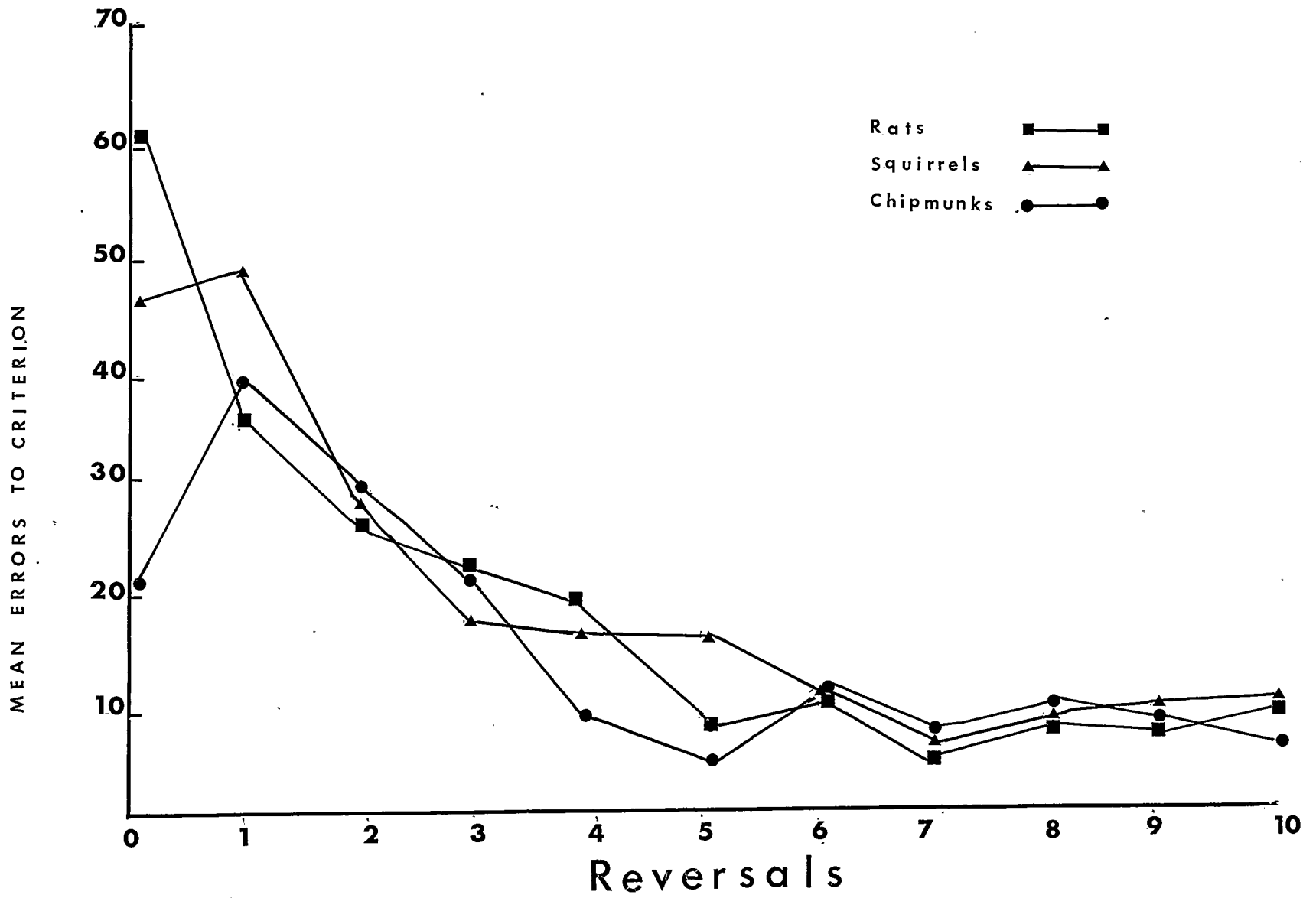
APPENDIX C

Error Scores for Chipmunks on All Three Groups

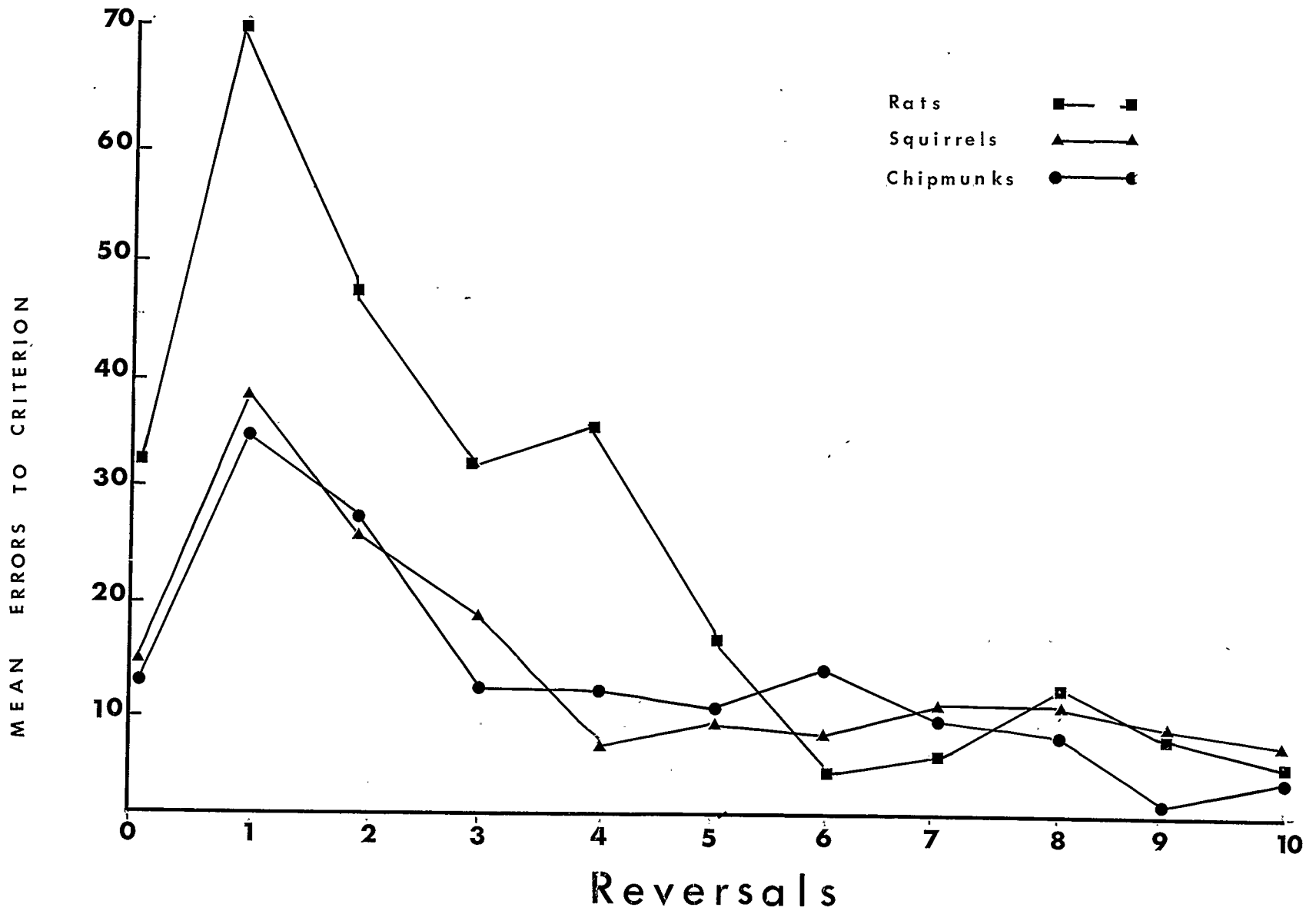
<u>Group 1</u>											<u>Group 2</u>											<u>Group 3</u>													
<u>No.</u>	<u>Reversal</u>										<u>No.</u>	<u>Reversal</u>										<u>No.</u>	<u>Reversal</u>												
	0	1	2	3	4	5	6	7	8	9	10		0	1	2	3	4	5	6	7	8	9	10		0	1	2	3	4	5	6	7	8	9	10
15	26	72	71	22	6	6	14	14	3	4	7	26	3	29	53	73	23	2	16	11	7	4	6	25	13	43	70	26	35	13	22	18	13	1	2
14	11	43	27	13	6	4	6	1	0	0	1	11	13	70	32	0	7	9	13	7	7	8	2	12	12	38	11	4	3	12	9	5	2	0	1
13	26	45	39	15	6	6	4	3	1	2	3	6	29	25	10	14	4	1	11	2	2	1	2	3	1	16	9	2	5	12	12	0	2	1	2
8	20	41	34	23	2	15	3	4	5	4	2	10	35	40	20	1	2	3	3	2	3	3	1	4	35	36	20	17	3	4	2	1	1	0	2



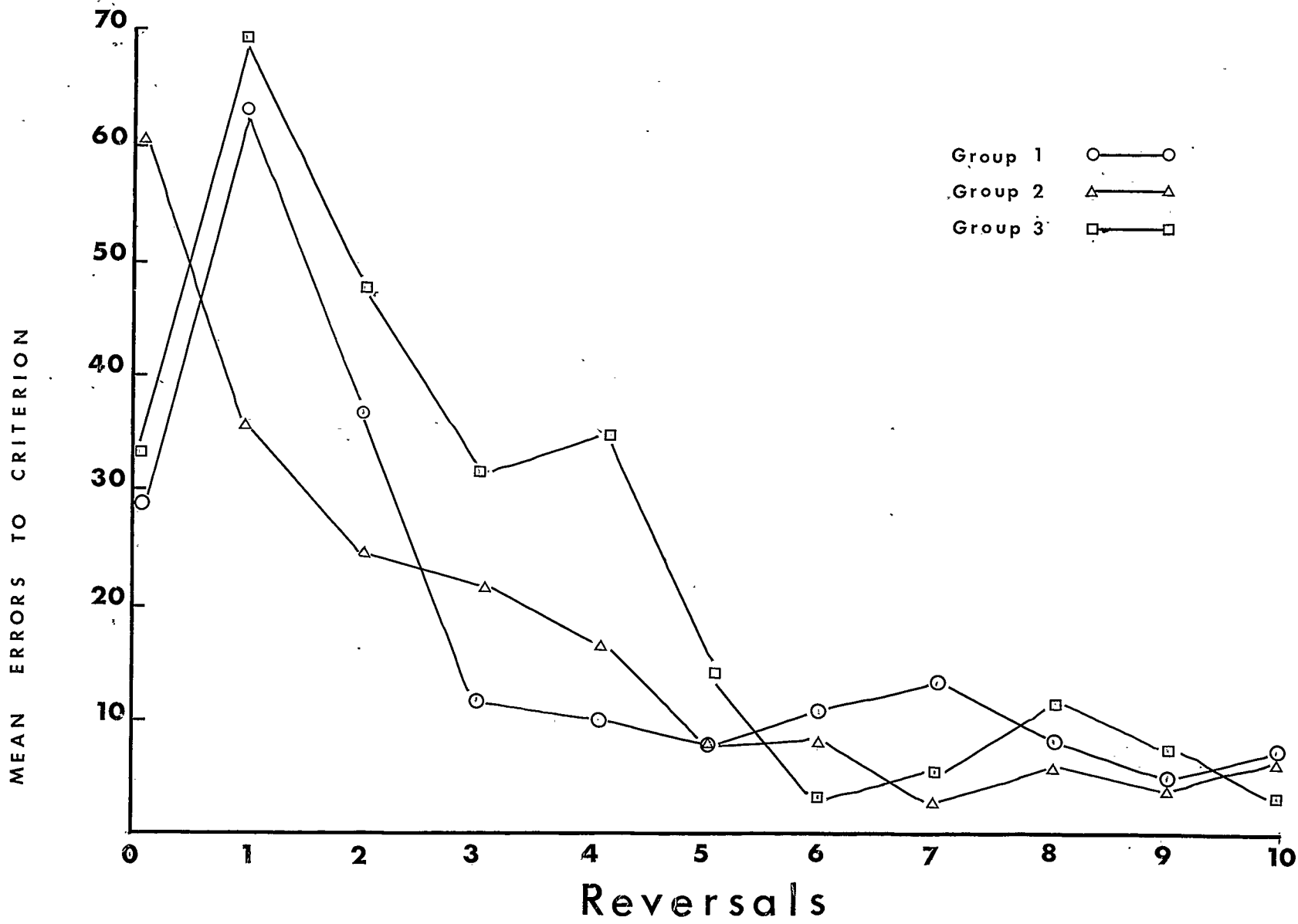
Appendix D. Group 1



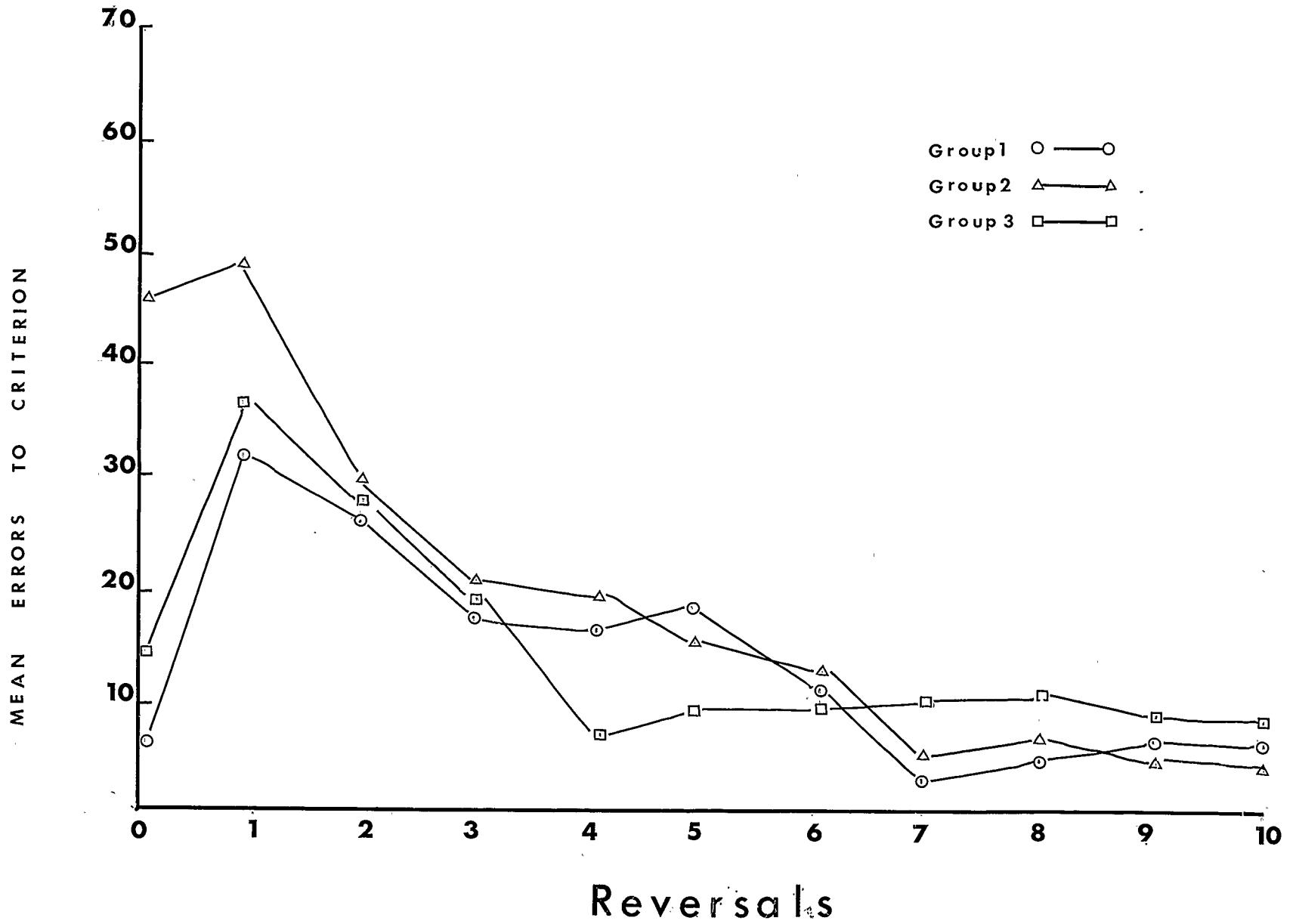
Appendix E. Group 2



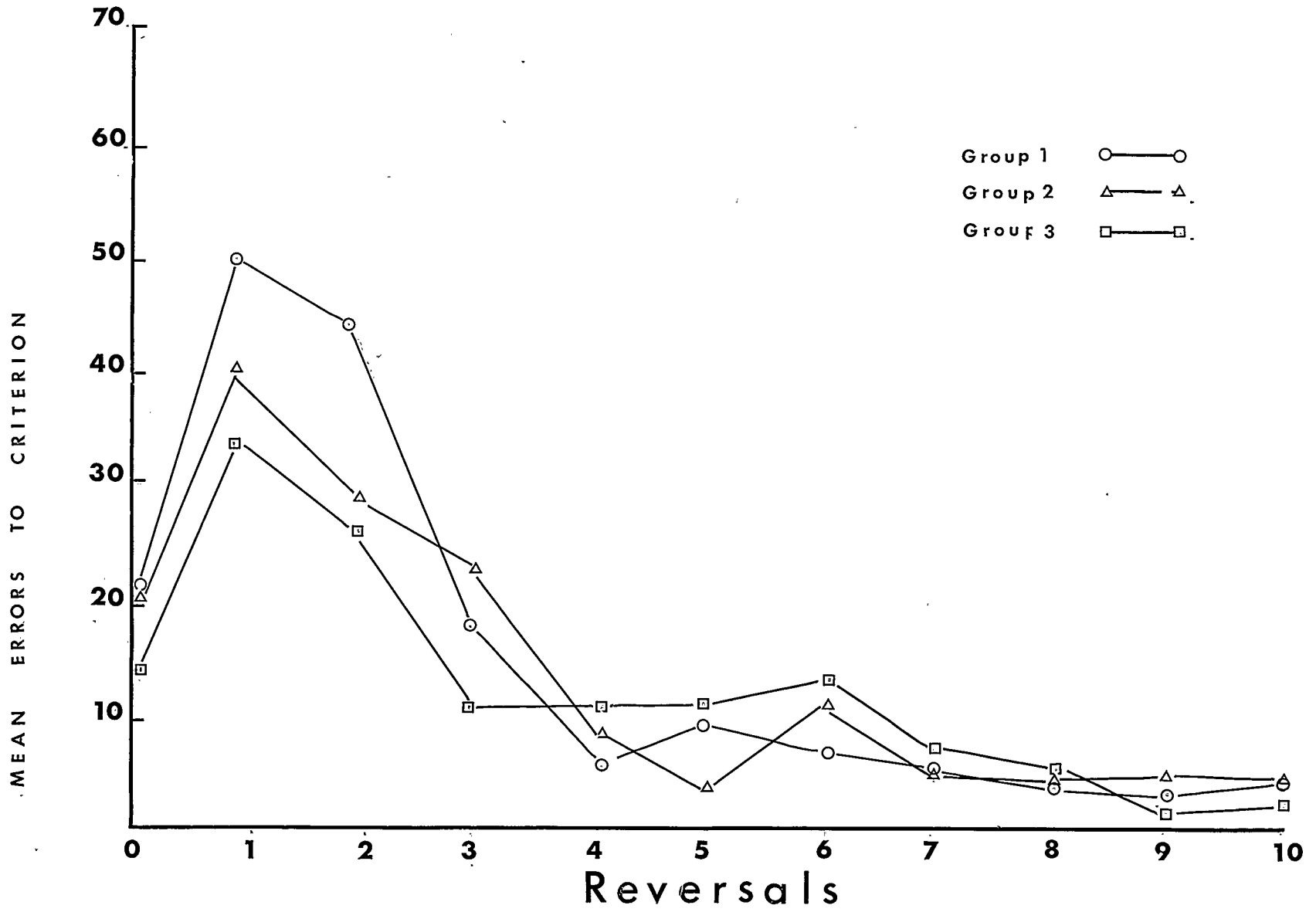
Appendix F. Group 3



Appendix G. Rats



Appendix H. Squirrels



Appendix I. Chipmunks

APPENDIX J

Analysis of Variance: Group 3 - Initial Learning

Source	df	MS	F
Between Groups	2	7.72	1.26
Within Groups	9	6.12	
Total	11		

APPENDIX K

Analysis of Variance: Group 2 - Initial Learning

Source	df	MS	F
Between Groups	2	16.69	6.05*
Within Groups	9	2.76	
Total	11		

* p < .05

APPENDIX L

Analysis of Variance: Group 1 - Initial Learning

Source	df	MS	F
Between Groups	2	6.45	5.16*
Within Groups	9	1.25	
Total	11		

* $p < .05$