THE RELATIONSHIP BETWEEN MAZE LEARNING AND HIERARCHY POSITION IN THE FISH *XIPHOPHORUS HELLERI*

Thesis for the Degree of M. S.

MICHIGAN STATE UNIVERSITY

Richard H. Gude

1962

ABSTRACT

THE RELATIONSHIP BETWEEN MAZE LEARNING AND HIERARCHY POSITION IN THE FISH XIPHOPHORUS HELLERI

By Richard H. Gude

The formation of social hierarchies and the ability to learn mazes have both been recorded separately among fishes. This study attempts to demonstrate an association between the position held in the hierarchy with the ability of individuals to learn in a measurable maze situation.

The young from breeding pairs of *Xiphophorus helleri*, purchased locally, were used as the experimental animals. Sixty-six individuals were tested individually as members of 22 monosexual three-fish hierarchies in a simple one-choice "T" maze.

The maze was constructed of opaque Plexiglas and was comprised of starting, negative choice, and goal compartments, connected by runways. The hierarchy positions were designated as: alpha, most dominant; beta, subordinate of alpha and dominant to the third; and omega, subordinate both to alpha and beta. The hierarchies were established, and

then each individual was tested in the maze. Two or more members of each of eighteen hierarchies were successful in learning the maze. In thirteen hierarchies the beta individuals were most successful. In one the beta and omega individuals had equal success. In the remaining four hierarchies two alpha and two omega fish learned the fastest. The disproportionate success of the beta individuals could not be readily attributed to chance.

The maze learning data were subjected to various statistical tests. These indicated that individuals occupying the three positions exhibited differences in learning ability. Also, there was no significant difference between sexes, and no discernable difference in the performances of the fish in the alpha and omega positions.

There was a strong correlation between the relative size of the fish and the hierarchy position held: alpha largest, beta intermediate, and omega smallest. When the actual sizes of all of the individuals in each hierarchy position were compared, however, a very definite overlap area was found among the three positions. Sixty-nine percent of all individuals tested were within this category.

After testing, individuals from several hierarchies were isolated for two weeks after which their previous heterogeneity in maze learning was lost. The beta fish showed a slight regression in ability; the alpha fish showed marked improvement; and the omega fish did not change.

The formation and maintenance of a hierarchy consisting of three members demands differing amounts of discrimination by the individuals involved. Each beta fish must be able to differentiate between an alpha and an omega fish. The alpha and omega fish need not discriminate between the other two members as far as the simple maintenance of the hierarchy is concerned. Thus, two explanations for the superiority of the beta fish in maze learning ability were possible. It was postulated that they were genetically more capable of discrimination and that this caused both the position in the hierarchy and the superior performance in the maze. This hypothesis was not supported by the results of testing after isolation. Also, there was strong correlation between relative size and hierarchy position. Thus interchanging the individuals composing hierarchies in such manner that the relative sizes would differ would cause changes in performance in the maze. This cannot be explained on a purely genetic basis. Finally, if the hierarchy affected all of its positions in the same manner, all members should have improved or regressed after isolation. This did not happen.

The second hypothesis postulates that the hierarchy situation teaches the beta individuals to discriminate, and this is the more probable explanation of the results cited above.

In nature most Xiphophorus hierarchies consist of ten to twenty individuals. Those intermediate in position between the alpha and omega fish are essentially beta individuals. If the alpha individuals alone gained the advantages offered by the hierarchy the bulk of the population would probably suffer. If, however, the beta members of the hierarchy are actually more able to discriminate as suggested by the present study this advantage will not fall to the alpha fish but instead to the beta individuals, the majority of the population. It is suggested that the importance to the population is the chief significance of the hierarchy.

THE RELATIONSHIP BETWEEN MAZE LEARNING AND HIERARCHY POSITION IN THE FISH *XIPHOPHORUS HELLERI*

By

Richard H. Gude

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology

1962

ACKNOWLEDGEMENTS

The author wishes to express his thanks to Dr. James C. Braddock, of the Department of Zoology, for suggesting this problem and also for his guidance and many helpful suggestions.

Special thanks are also extended to Dr. Philip J. Clark, of the Department of Zoology, for his assistance in the statistical analyses, Dr. Max Hensley for serving as a committee member and to Dr. John King for his critical review of this thesis.

The author would also like to express his gratitude to his wife Judith for her encouragement during this research, and for the typing of the thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The formation of social hierarchies and the ability to learn mazes have both been recorded among fishes; however, no previous attempt has been made to associate hierarchical position and learning ability. This study will attempt to demonstrate an association between the position held in the hierarchy with the ability of the individual fish to learn in a measurable learning situation.

Social hierarchies occur among both invertebrates and vertebrates. Allee and Douglis (1945), Pardi (1948), and Howard (1955) have all made reference to hierarchies among invertebrates, more specifically within the phylum Arthropoda. Social hierarchies have been described more extensively among the vertebrates. The first mention of such social hierarchies was that of Schelderup-Ebbe (1922). He described the "pecking order" of chickens. Noble and Borne (1938), without publishing their data, reported social hierarchies in Xiphophorus helleri and several other fishes. Their work indicated that hierarchies were established on the basis of such factors as, greater weight, greater color display, belligerency, and prior residence. Braddock (1945) reported similar relationships in his statistical study of hierarchy formation in *Platypoecilus maculatus*.[1] This study was expanded by describing the effect of prior residence upon such hierarchies (Braddock, 1949). Greenberg (1947) reported both hierarchy formation and territoriality in the green sunfish *Lepomis cyanellus*. He stated that hierarchies were formed among individuals of varying aggressiveness while territory formation occurred among those of more or less equal aggressiveness. Transitional stages between hierarchy formation and territoriality occurred when subordinates defended territories from all but the most dominant individual.

Studies of maze learning are quite common among many of the animal phyla; again, more so among vertebrates than invertebrates. Arbit (1957) recorded maze learning in certain species of annelids, while Hullo (1948) reported learning in the cockroach. While the classical experimental vertebrate in this area has been, and is, the white rat, maze learning has been recorded for a number of other vertebrates. Thorndike (1899), Churchill (1916), Welty (1934), Spooner (1936), French (1942), Greenberg (1947),

---

1. Now *Xiphophorus maculatus*.

and Hale (1956) all discussed maze learning in fishes. Some of the maze designs involved partitioned tanks with holes at various levels, others contained solid partitions that the fish learned to swim around in order to reach the reward. None of the studies with fishes employed devices comparable to the simple "T" maze used in this study.

This study represents an attempt to determine if any correlation exists between learning ability and hierarchy position. Noble and Borne (1938), Braddock (1945, 1949), and Greenberg (1947) all suggested that hierarchies serve as social facilitators. According to these investigators, the initial contacts between fishes are used to establish dominance-subordination relationships. After these are formed, very little time and effort are needed to maintain them. Once the hierarchies are formed the fish are free to feed and mate. The more dominant fish get more food and also the first choice of mates. The possibility exists that the hierarchies serve other functions. This study will attempt to establish whether or not learning occurs through hierarchy formation, and if such learning can then be transferred to other situations.

METHODS AND MATERIALS

Xiphophorus helleri was chosen as the experimental fish because it is known to form hierarchies and its size and hardiness make it convenient to handle. Breeding pairs were purchased from local dealers. The young from each female parent were reared separately as a group in stock aquaria 15 by 17 by 29 inches. This was done so that possible behavioral differences due to differences in age and genetic composition might be identified. The problem of genetic composition was complicated by the fact that female *Xiphophorus helleri* are known to store sperm from several matings. Accordingly, each sibling group had only one known parent, the mother. Analysis of the performance of the four groups demonstrated no statistical difference in their maze running abilities.

The young were fed brine shrimp until they reached sufficient size to be fed Wardley's Supermix Medium dry fish food.[2] The temperature of the stock aquaria was maintained at approximately 80° F. Aged tap water was used when they were initially filled, and evaporation losses were replaced

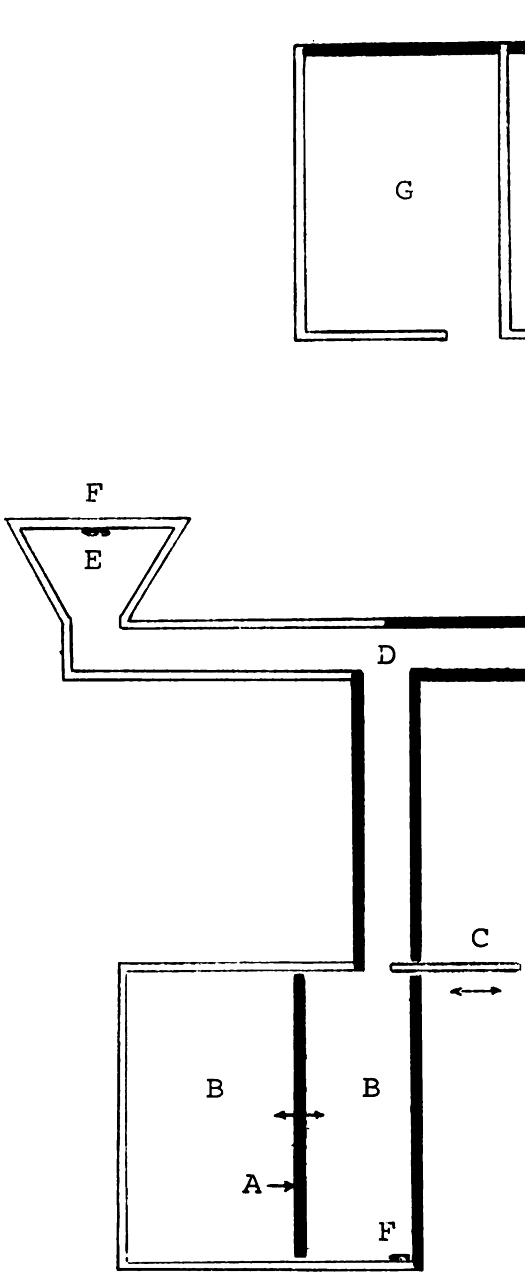
---

2. A standard dry fish food made from ground shrimp, insects and various meals.

by distilled water. One aquarium was used to establish and maintain the hierarchies before testing in the maze. It was divided in half by an opaque sheet of green Plexiglas, making two compartments ten by eight by seven and one-half inches. This aquarium was covered on three sides by cardboard, while the front was left open for observation of the hierarchies. The bottom of each compartment was covered with one-half inch of loose gravel. This hierarchy aquarium was maintained in the same manner as the stock aquaria.

A "T" maze (Fig. 1) was chosen for simplicity of construction and ease of statistical analysis. Thorndike (1899), Churchill (1916), Welty (1934), French (1942), and Greenberg (1947) used as mazes partitioned tanks, in which openings were cut in the partitions at various levels. In order to reach the goal the fish had to pass through the openings. There were no fixed positions through which they approached the openings. Thus, the approaches involved not only making proper turns but also selecting the proper depth. The probability of successfully running this type of maze by chance is difficult to compute mathematically and therefore is usually estimated experimentally.

Figure 1. Maze



A - Moveable Partition
B - Starting Compartment
C - Sliding Door
D - Choice Point
E - Negative Choice Compartment
F - Electrode
G - Goal Compartment

Portion of maze lined with red plastic

Portion of maze lined with green plastic

Scale 1/4" = 1"

The "T" maze involves a fixed approach. The only choice necessary is a left or right turn. The specimen used in this study was originally constructed with two choice points. In order to reach the goal the fish had to turn right at the first and left at the second. Several individuals were tested and none were successful in learning this maze. Since the two-choice maze appeared too complex, it was simplified by replacing the second choice point with a movable goal compartment. The probability of running the modified maze correctly was .5. The probability of any six consecutive trials being positive is substantially less than .05, namely .016, and accordingly, the event six consecutive positive trials was chosen as a criterion that a fish had learned the maze.

The maze was constructed of one-eighth inch opaque green Plexiglas mounted in grooves cut in a waterproof plywood base. There were three compartments; starting, negative choice, and goal, each three and three-fourths inches high. The dimensions of the starting compartment were six by six inches, while the negative choice compartment was triangular, three inches on a side. The goal consisted of a series of three identical compartments mounted on a base of green Plexiglas that was not fastened to the plywood base. Each compartment was six inches long and four inches wide. One end of each contained an opening one inch wide fitted with a sliding green Plexiglas door. The entire group of goal compartments could be moved; so that each door opening could be lined up with the runway leading from the choice point of the maze. Each individual compartment had a masonite cover.[3] The runways of the maze proper were one inch wide and three and three-fourths inches high. They had a basic dimension of six inches, that is, each straight section of runway was six inches long. The bottom of the entire maze, with the exception of the goal compartment, was covered with fine white sand. In order to facilitate learning, the runway leading from the starting compartment to the goal compartment was lined with .0001 inch thin red plastic. The negative choice runway and compartment were green. The wall of each goal compartment opposite the door opening was lined with red plastic. The runway leading to the choice point was separated from the starting compartment by a sliding door. A special removable red plastic divider for the starting compartment was used

---

3. One-fourth inch opaque compressed fiber board.

to form a "starting chute." This was accomplished by inserting the moveable partition at the left side of the starting compartment and sliding it toward the right until it was one inch from the right side. The maze was filled to a depth of three inches throughout all observations. Three electrodes were placed inside the maze, one in the starting compartment, one in the negative choice compartment and a third in the runway near the goal compartment. The second and third electrodes were connected to individual switches.

The shocks consisted of twelve volts of alternating current, and their magnitude varied in different portions of the maze. The full intensity occurred at or near the two electrodes. At the choice point it was approximately seven volts. This arrangement was necessary in order to stimulate the fish in the areas midway between the electrodes. This voltage, however, was too high when the fish were in the negative compartment. Repeated shocks at short intervals injured the fish. The larger individuals were injured more readily than the smaller ones, because they absorbed more of the current. In most cases, however, injury did not occur, as one shock was enough to stimulate the fish to move from the negative goal compartment.

In preliminary testing, during which no shocks were administered, many individuals demonstrated "negative learning" which is described elsewhere in this report. The use of shocks largely eliminated this pattern. Thus electrical shocks were used as stimuli and as negative rewards or punishments.

The choice of a reward involved certain difficulties. Welty (1934), French (1942) and Greenberg (1947) all found a food reward satisfactory. Food was not used in this study because the experimental fish were not voracious feeders. As a result of the number of trials necessary and the short intervals between tests their appetites would have been satisfied before testing was completed. The possibility also existed that food particles in the maze would assist the fish to choose the runway leading to the goal compartment. Accordingly, a covered goal compartment where the fish would be undisturbed and in relative darkness was chosen as the reward.

The determination of position in the hierarchies was accomplished in the following manner. The fish were arranged in nineteen monosexual groups of three. The members of each such group were siblings born at the same time.

Each group was then placed in the hierarchy aquarium where it remained for 24 hours. A thorough description of hierarchy formation will not be discussed here.[4] A dominance-subordination relationship determined on the basis of "nips" and "challenges" exists between the three fish in a hierarchy. The fish were fed and observed at the end of the 24 hour period to determine the position held by each. These positions were designated as: alpha (A) dominant to the other two, beta (B) subordinate of alpha and dominant to the third, and omega (O), which was subordinate to both alpha and beta. The "nips" and "challenges" were recorded for each fish and after a sufficient number had been noted the positions were known.

Determination of hierarchy position was generally difficult and usually quite impossible if the same sized individuals were tested, since the wild strain of Xiphophorus helleri exhibit few individual color variations. Therefore, it was necessary to choose fish of three different sizes. The possibility existed that fish within a certain size range might be more able than others to learn the maze. Statistical

---

4. The reader is referred to Braddock (1945, 1949) for a thorough discussion of hierarchy formation.

analysis by means of a one way analysis of variance disposed of this hypothesis.

There were sufficient individuals in all groups to establish twenty sibling hierarchies. In order to test as many individuals as possible two hierarchies were established by using one individual from each of three of the genetic groups. After the testing of these non-sibling hierarchies, the total trials necessary for the three members were tested against and found to be nearly homogeneous with, the sixteen completed sibling hierarchies ($F = 1.551$).

All hierarchies were composed of individuals of the same sex. Braddock (1942), Noble and Borne (1938), and Greenberg (1947) found that males were usually dominant over females. This was avoided by the use of monosexual hierarchies. Also it was noted that males were quicker than females in all movements made. The former were also more easily excited. During the first maze runs it was not unusual for the males upon stimulation with the shock, to jump clear of the maze. After several such trials this tendency decreased. Very few females demonstrated such behavior.

After hierarchical position had been established, the testing was begun. The fish from one hierarchy were removed, one at a time, from the hierarchy aquarium and placed in the goal compartments of the maze. Each was placed in a separate compartment with the door closed. Covers were then placed over each compartment after which the fish remained undisturbed for ten minutes. At this time the first fish was removed from its goal compartment and placed in the starting compartment. Actually, only the individual occupying the first goal compartment remained undisturbed for this period. The second fish was not disturbed until the first had completed its first test. This extended the second individual's undisturbed time to approximately twelve minutes and that of the third to fourteen minutes. This variation of time in the goal compartment did not extend past the first trial.

Each individual, in turn, was rapidly netted and placed in the starting compartment. The empty goal compartment was then lined up with the maze runway, the door removed and the cover replaced. After 30 seconds in the starting compartment the moveable partition was inserted and moved to form the starting chute in such a way that the fish was occupying it and facing toward the maze. The sliding door between the starting compartment and the maze was then opened and the fish allowed to enter. In most cases it was necessary to stimulate it by a one-tenth second electrical shock. When the head of the fish entered the maze the stop watch was started. If the correct choice was made the fish would continue along the positive choice runway to the goal compartment. The time consumed while running the maze was recorded as soon as the entire fish had passed into the goal compartment. The door was then closed. The fish would then remain in its individual covered goal compartment undisturbed for ten minutes. If the negative choice was made, allowing the body and any portion of the tail to enter the negative choice runway, the fish would receive electrical shocks as punishment. These shocks were given at approximately two second intervals, were of one-half second duration, and were administered until a turn around in the negative choice compartment was accomplished, and the fish had returned to the choice point. Once the positive choice runway was entered, the procedure was the same as that discussed under the positive choice. During the ten minute waiting period in the goal compartment the remaining two fish were run through the maze in the same manner as the first. Individual data cards were maintained for each fish. The water temperature and the length of each fish were recorded once, while the number of stimuli, the choices made and the time[5] spent in the maze were recorded for each individual run. The length of each fish was recorded as the distance in millimeters between the tip of the snout and the caudal peduncle. Choices were recorded as negative (-) when a left turn was made at the choice point and positive (+) when the right turn, or correct choice, was made. On rare occasions individuals would turn around in the narrow runways. These instances were recorded as a return (R) and were designated as to the direction in relation to the choice point by the use of + or -. Each fish was tested in the maze until a series of six consecutive positive runs had been made. The fish was then said to have "learned" the maze.

After all three fish had learned the maze they were removed from the goal compartment, measured, and usually placed together in a one gallon wide mouth bottle which was maintained in an 80°F. constant temperature bath. The members of ten of the hierarchies, however, were separated and the fish isolated in bottles in the water bath. After exactly

---

5. Statistics with regard to time are not treated in this study, since the use of strong shocks in certain cases, and not in others produced variability not easily analyzed.

two weeks had elapsed the latter were again tested individually in the maze in the same manner as before.

RESULTS

Twenty-two hierarchies were tested in the maze, but all three members of only sixteen were successful in learning it. These sixteen hierarchies form the basis for most of the results presented here. In two, only two of the three individuals were successful. The remaining four hierarchies were not completed due to injuries or negative learning. The latter occurred when a fish learned to reach the goal by turning left at the choice point, traveling through the negative runway to the negative choice compartment and then back to the positive runway and goal compartment. After a series of such runs, applying the electrical shock was not necessary, as the fish had apparently learned to reach the goal through this method. In several cases the fish were injured by the electrical shocks and were unable to complete learning the maze. The alpha fish in hierarchy 14 was blind in the left eye, which apparently caused him to favor the right turn over the left turn. These results are cited in table 1 but are not considered further in this report.

Table 1 indicates the number of trials required for each fish to complete six consecutive positive choice runs. The

Table 1. Number of Trials Necessary for Maze Learning

Hierarchy Number	Sex	Hierarchy Position			Totals
		A	B	O	
1	♂	20	16*	20	56
2	♂	23	14*	19	56
3	♂	19	11*	11*	41
4	♂	18	15*	21	54
5	♂	18	11*	17	46
6	♀	22	13*	25	60
7	♀	17	9*	16	42
8	♀	21	14*	23	58
9	♀	inj	18	9*	-
10	♀	21	9*	16	46
11	♀	22	19*	22	63
12	♀	20	12*	19	51
13	♀	17	9*	19	45
14	♀	11*	19	inj	-
15	♀	12*	18	18	48
16	♀	22	15	9*	46
17	♀	17	10*	19	46
18	♀	18	9*	16	43
19	♂	NL	inj	NC	-
20	♂	inj	NC	NL	-
21	♂	NL	NC	inj	-
22	♀	inj	NC	inj	-

* Those fish learning in the least number of trials.
inj Injured. Testing terminated.
NL Negative Learning.
NC Not Completed.

numbers with asterisks denote the individual, within each hierarchy, that achieved success in the least number of trials. Hierarchies number 9, 14, 19, 20, 21, and 22 were only partially completed.

Assuming that maze learning ability is independent of hierarchical position one would expect those fish occupying any one position to be successful in about one-third of the hierarchies tested. However in the seventeen hierarchies in which the beta individual was not tied with either of the other positions, it was most successful in thirteen cases. The probability of obtaining by chance alone a discrepancy as great or greater than that observed is .001024. It is reasonable to conclude, therefore, that maze learning ability depends upon hierarchy position.

The data from table 1 were then tested as matched observations (mean of the differences significantly different from zero). Since in the majority of cases the beta individuals completed their learning with fewer trials than the other two, the alpha and omega runs were averaged. This mean was then subtracted from the number of beta runs and recorded as the difference. The number of trials required by the beta fish to learn the maze was significant at .01 when compared with the average of the alpha and omega fish. The observed value of t with 15 degrees of freedom was 6.645. In order to determine if there were any consistent differences between the alpha and omega fish the data for these two positions were also tested to determine if the mean of the differences was significantly different from zero. The value obtained for t with 15 degrees of freedom was .9076 giving no appreciable indication of heterogeneity.

The data from table 1 were subjected to a two way analysis of variance testing hierarchy position versus sex on the basis of runs necessary to learn the maze. There appears to be no evidence for difference between sexes, since the computed value of F with one degree of freedom in the numerator and 42 in the denominator was .05647. There is a very strong indication of heterogeneity among the three hierarchy positions, since the computed value of F with two degrees of freedom in the numerator and 42 in the denominator was 15.37, which is significant at the .001 level. The F value for the interaction between sex and hierarchy position was .2264, which with two degrees of freedom in the numerator and 42 in the denominator was not significant at the .05 level.

Table 2 indicates the length, hierarchy position, and sex of each fish. In fourteen hierarchies the size of the

Table 2. Total Length of Fish in Relation to Hierarchy Position

Hierarchy Number	Sex	Hierarchy Position A	B	O
1	♂	47	44	43
2	♂	53	48	50
3	♂	55	52	48
4	♂	52	51	51
5	♂	49	47	43
6	♀	52	47	42
7	♀	51	47	42
8	♀	48	45	43
9	♀	53	50	48
10	♀	55	48	41
11	♀	51	52	51
12	♀	53	52	51
13	♀	52	53	50
14	♀	56	48	53
15	♀	54	53	51
16	♀	57	59	51
17	♀	55	54	51
18	♀	57	52	49

fish corresponded to the hierarchy position, that is, the alpha fish was largest, the beta fish intermediate and the omega fish smallest. Only four cases deviated from this pattern. The lengths of the fish versus sex and hierarchy position were subjected to a two way analysis of variance. There appear to be differences between sexes with regard to total length, as the computed value of F with one degree of freedom in the numerator and 42 in the denominator was 2.222. There also appears to be significant evidence for heterogeneity among hierarchy positions with respect to total length. The computed value of F with two degrees of freedom in the numerator and 42 in the denominator was 8.172, which is significant at the .01 level. The F value for interaction between hierarchy positions and total length was .3312 which, with two degrees of freedom in the numerator and 42 in the denominator, affords no evidence for interaction.

Table 3 shows the size deviation within each position. The three positions had an area of overlap wherein lay 69% of all fish tested. This overlap area also contained 71% of all fish that learned the maze first. If superior maze learning ability was characteristic of a certain size group, it should also have been distributed evenly among all three positions. The data from table 1 and table 2 do not support such a hypothesis.

A one way analysis of variance was applied to determine if any relationship between total length and maze running ability within each position was present. The members of each position were assembled into two equal groups on the basis of total length. One group consisted of the larger members and the other of the smaller members. The two groups within each position were then compared by a one way analysis of variance on the basis of trials necessary to learn the maze. The F value for the comparison within the alpha position was .5874 with fifteen degrees of freedom. This affords no evidence for any difference in learning. The groups within the beta position, when compared, gave an F value with sixteen degrees of freedom of .1015 offering no evidence for any difference in learning ability. The omega groups when compared gave an F value of .3088, again affording no evidence for a difference in learning ability.

Each hierarchy except numbers 5 and 18 was composed of individuals which were members of the same sibling group. There were four such groups and they were compared with one another by subjecting them to a one way analysis of variance using total number of runs per hierarchy as the basis of comparison. The computed F value of .2666 with three degrees of freedom in the numerator and ten in the denominator provides no evidence of heterogeneity. Hierarchies 5 and 18 consisted of individuals drawn from each of three parental groups. A comparison between these two and the others by a

Table 3. Range of Total Lengths Among Hierarchy Positions

Hierarchy Positions	Length in Millimeters																				
	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
A								1	1	1	0	2	3	3	1	3	1	2			
B					1	1	0	3	3	0	1	1	4	3	0	0	0	0	0	1	
O		1	2	3	0	0	0	0	2	1	2	6	0	1							

Numbers appearing above the lines represent the number of individuals within that length group.

Indicates area of overlap.

one way analysis of variance, on the basis of total runs, with one degree of freedom in the numerator and fourteen in the denominator gave a computed F value of 1.551. Thus, there was not sufficient evidence for heterogeneity to warrant treating these two hierarchies separately from the others.

The temperature of the maze remained constant at 80° F. throughout the observations except during the testing of hierarchies 10 and 11. In these cases it was 82° F. Comparisons were made by a one way analysis of variance on the basis of total trials. The computed F value was .9491, with one degree of freedom in the numerator and fourteen in the denominator. Thus, there was not sufficient indication of heterogeneity to necessitate considering the hierarchies as two separate populations on the basis of temperature, and this was not done.

When the number of trials required before each fish "learned" the maze were used as a criterion the beta individuals were more successful than either the alpha or the omega fish. There were no significant differences between the learning performances of the alpha and omega individuals ($t = .9076$).

Since this work was designed to demonstrate whether or not learning in the maze is in fact influenced by the formation and/or maintenance of hierarchies, 32 individuals from ten of them were isolated for two weeks and then retested. This was done on the assumption that, if the hierarchy situation were incidental to the results in the maze, the fish would duplicate their previous performance in relation to one another. Significant changes in relative performance would indicate the influence of the two different social situations.

Table 4 compares the number of trials required by certain of the isolated fish in learning the maze with the number necessary while in the hierarchies. Both groups of data were subjected separately to a one way analysis of variance comparing the number of trials with hierarchy position. When the maze learning data concerning the fish maintaining hierarchies were tested for heterogeneity, the computed F value with two degrees of freedom in the numerator and eleven in the denominator was 6.059. This is significant at the .025 level. The data from the same individuals after isolation had a computed F value with two degrees of freedom in the numerator and eleven in the denominator of 1.439. Here there was little or no evidence of heterogeneity. These same data were also tested to determine if the mean of the differences was significantly different from zero. The computed t value with thirteen degrees of freedom was .7237. This test did not afford significant evidence for a difference between these two sets of data.

The random results demonstrated by the fish when isolated contrast strongly with the favored position of the beta individuals of hierarchies. Thus, it is reasonable to assume that experience in a hierarchy did, in fact, influence the performance of its members.

Table 4. Performance in Hierarchy vs. Performance When Isolated

Hierarchy Number	Sex	Hierarchy Position A Trials H	I	B Trials H	I	O Trials H	I
2	♂	23	21	-	-	-	-
5	♂	-	-	9	9	-	-
7	♀	-	-	-	-	16	13
8	♀	21	16	-	-	23	12
9	♀	-	-	18	inj	9	20
12	♀	20	17	-	-	19	10
13	♀	-	-	9	18	-	-
16	♀	22	17	15	13	9	10
17	♀	17	13	10	16	-	-
18	♀	18	inj	-	-	-	-

inj Injured. Testing was terminated.

Table 4 also indicates that two out of the four beta individuals, tested both in their original hierarchies and in isolation, were less successful in learning the maze after isolation. They were members of hierarchies number 13 and 17. The beta fish in hierarchy 5 learned the maze in the same number of trials during both tests. The beta fish in hierarchy 16 showed slight improvement; however, the omega fish in this hierarchy was the most successful in both trials.

The data collected while in the hierarchy and while isolated were compared within each position to determine if the means of the differences were significantly different from zero. The data for the individuals in the alpha position had a t value of 6.517, with four degrees of freedom, indicating a significant improvement in maze learning ability after isolation. The fish in the beta position gave a computed t value, with three degrees of freedom, of 1.269 which indicates a possible but slight tendency for regression in maze learning ability after isolation. The data obtained concerning the omega individuals had a computed t value of .5599 with four degrees of freedom which gave no indication of any change in learning ability after isolation.

DISCUSSION

These observations have indicated a relationship between hierarchy position and maze learning, since in thirteen of the eighteen hierarchies, the beta individuals learned the maze in fewer trials than either of the others. The probability of obtaining such a result by chance is very small.

Learning in a maze is a matter of discrimination. In the one used in these observations the fish had to discriminate between right and left turns and/or the colors red and green, since the correct choice was a right turn and all correct runways were lined with red plastic. Whether learning occurred on the basis of "correct turns" or color discrimination is not known.

In the formation and maintenance of the three-fish hierarchies, discrimination was also necessary. Beta individuals were required to distinguish alpha fish, to which they were subordinate, from omega fish which they dominated. Alpha fish were dominant and omega fish subordinate to both of the others and did not necessarily have to discriminate between them, at least where simple maintenance of the hierarchy was concerned.

Two hypotheses might be advanced to explain why the beta individuals were better able to learn the maze. It might be postulated that the fish that occupied the beta position were genetically more capable of discrimination and therefore arrived at that position within the hierarchies.

When the test scores of all isolated individuals were subtracted from their hierarchy test scores and tested to determine if the means of the differences were significantly different from zero, no evidence for a difference was obtained. This indicates that there was no significant improvement or regression in maze learning among all individuals tested after isolation. Thus, the isolation period did not affect the maze running ability of the group, but there was a very definite rearrangement in ability among the hierarchy positions.

It might also be postulated that certain differences were present in the fish during hierarchy formation and maze running that were lost upon isolation. If this were the case, all hierarchy positions should have exhibited improvement or the opposite when isolated. This was not the case.

If the beta fish were innately better able to discriminate or had other characteristics that provided them with greater ability in running the maze, removal from the hierarchy should not have affected their performance appreciably. Since there was regression of their learning ability upon being isolated, experience as members of hierarchies must have affected their discriminatory ability. Since an apparent improvement in ability occurred when the alpha fish were isolated, possible suppression of maze learning by the hierarchy seems indicated for this position.

The second hypothesis seems to be more valid; namely that the fish occupying the beta position were forced by the hierarchy situation to discriminate between the other two members, and this carried over into the situation presented by the maze. The strong evidence for heterogeneity while in hierarchies was the result of the superior maze learning ability of the beta individuals. The lack of evidence for heterogeneity after isolation resulted from a slight regression in maze learning ability of the beta and a marked improvement in the alpha fish. The omega individuals were relatively unchanged.

Other investigators have studied the adaptive significance of hierarchies, largely on the individual, rather than the population level. Guhl (1953) discussed avian hierarchies, specifically those of chickens. He found that alpha birds had certain advantages not shared by those occupying lower positions. Some of these were: greater freedom of movement, freer access to food and water, a greater choice of nest boxes, and the more favorable roosting locations. Similar situations have been described for fish hierarchies. Noble and Borne (1938) found that the alpha individuals in hierarchies of Xiphophorus helleri had greater access to open spaces, food and mates. Greenberg (1947) discovered that, in the case of the green sunfish Lepomis cyanellus, the alpha individuals had the first choice of territories. Guhl (1953) stated that due to their aggressiveness the alpha hens were not mated as often as the more submissive omega hens. The opposite pertained among roosters in that the alpha cocks mated more often and sired more chicks than did lower ranking individuals. Guhl attributed this to their aggressiveness. While there is no positive evidence that chicken and fish hierarchies serve their members in precisely the same ways, similarities have been noted between them when studied as a unit. Pecking or nipping was found by Guhl to be most pronounced during the formation of the hierarchies in chickens; and Noble and

Borne (1938), Braddock (1945), and Greenberg (1947) all noted the same phenomenon in their studies of fish. After the hierarchies were fully established, a marked decrease in the intensity and number of pecks or nips was noted. Braddock (1945) and Greenberg (1947) suggested that the hierarchies might be considered as social facilitators, since their existence reduces fighting among their members, thus permitting them to spend more time searching for food and mates, as well as watching for predators. It should be understood that in nature most fish hierarchies consist of ten to twenty members. All fish between the alpha and omega positions are essentially beta individuals in that they respond differentially to their various hierarchy mates. Here it has been proposed that the beta fish or any others occupying positions between the alpha and omega fish are better able to discriminate both in hierarchy and maze situations. Greenberg (1947) subjected entire hierarchies to maze situations quite different from the one used here and postulated that the alpha individuals should be best able to learn the maze. However, in spite of the fact that the alpha fish actually led its subordinates to the reward in the earlier trials he was not convinced that this individual had greater innate learning ability. The formation of the hierarchy itself could have established this condition of leadership. The alpha fishes' advantages in terms of better access to food and open spaces may have inhibited their subordinates from attempting to reach the food first.

The three-fish hierarchies involved in this study differed from those that occur in nature in several respects. First, natural hierarchies contain individuals of both sexes. Thus the tendency for the larger fish to occupy the alpha position comes into conflict with the tendency for males to dominate females (Noble and Borne, 1938). This results in marked instability of hierarchy order (Braddock, 1945). Secondly natural hierarchies contain more than three individuals (ten - twenty). Braddock (1945) has stated that Poeciliid hierarchies of four individuals and with all members of the same sex have a mean stability factor of only 1.7 days. Stability should be less where more fish and individuals of both sexes are involved. Thus the alpha position is a transitory one, since status changes usually involve overthrow of the despot by a lower-ranking individual (Braddock, 1945). It seems probable, then, that any individual selected at random could be expected to occupy the alpha position for a limited time only. Thus since the position is a temporary one, and correlated with what must be temporary conditions, factors favoring this position might not necessarily favor the entire population, genetically or otherwise. A statistical study is needed to determine whether or not certain individuals occupy the alpha position with a greater frequency than others in large, heterosexual hierarchies.

If the alpha individuals reaped the majority of the advantages offered by the hierarchy, the population as a whole could suffer. This obviously is not the case. If the beta members of the hierarchies are actually more able to discriminate as suggested by the present study this advantage will not fall to the alpha fish, but instead to all the beta individuals, the majority of the population. Since this ability to discriminate generally is present in the majority of the members of the population, it seems probable that it has adaptive significance, although the nature of this is not presently understood.

All previous interpretations of hierarchies in terms of adaptive significance have been concerned with the advantages accruing to individuals. It is the intention here to suggest that perhaps the importance to the population is the chief significance of the hierarchy; while such individual advantages as have been previously noted are merely incidental.

SUMMARY

1. Beta individuals in hierarchies of <u>Xiphophorus helleri</u> were better able to learn a one choice "T" maze than those in either the alpha or the omega positions.

2. Beta individuals tested in the maze after isolation showed a slight regression in learning ability when compared to their former performances in hierarchies.

3. There were no statistical differences in the maze running ability of the two sexes.

4. No relationships were found between maze running ability and size.

5. Strong, relative size differences were recorded among fish occupying each of the hierarchy positions.

6. It was concluded that experience in a social hierarchy has adaptive significance on the population level, since it results in increased discriminatory ability for most of the members.

BIBLIOGRAPHY

Allee, W. C., and M. B. Douglis, 1945. A dominance order in the hermit crab, Pagurus longicarpus. Ecology, 26: 411-412.

Arbit, J., 1957. Diurnal cycles and learning in earthworms, Lumbricus terrestris. Science, 126: 654.

Braddock, J. C. 1945. Some aspects of the dominance-subordination relationship in the fish Platypoecilus maculatus. Physiol. Zool., 18: 176-94.

______________. 1949. The effect of prior residence upon dominance in the fish Platypoecilus maculatus. Physiol. Zool., 22: 161-68.

Churchill, E. P. 1916. The learning of a maze by goldfish. J. Anim. Behav., 6: 247-55.

French, J. W. 1942. The effect of temperature on the retention of a maze habit in fish. J. Exp. Psychol., 31: 79-87.

Greenberg, B. 1947. Some relations between territory, social hierarchy, and leadership in the green sunfish (Lepomis cyanellus). Physiol. Zool., 20: 267-99.

Guhl, A. M. 1953. Social behavior of the domestic fowl. Tech. Bull. 73. Ag. Exp. Sta., Kansas State College.

Hale, E. B. 1956. Social facilitation and forebrain function in maze performance of green sunfish, Lepomis cyanellus. Physiol. Zool., 29: 93-107.

Howard, R. S. 1955. The occurrence of fighting behavior in the grain beetle Tenebrio molitor with the possible formation of a dominance hierarchy. Ecology, 36: 281-84.

Hullo, A. 1948. Role des tendances motrices et des données sensorielles dans l'apprentissage du labyrinthe par les blattes Blattella germanica. Behavior, 1: 297-310.

Noble, G. K., and R. Borne. 1938. The social hierarchy in Xiphophorus and other fishes. Bull. Ecol.Soc. Amer., 19: 14 (abstr.).

Pardi, L. 1948. Dominance order in Polistes wasps. Physiol. Zool. 21: 1-13.

Schjelderup-Ebbe, T. 1922. Beitrage zur social-psychologie des haushuhns. Zeitschr. F. Psychol. 88: 225-52.

Spooner, G. M. 1936. The learning of detours by Wrasse (Etenolabrus rupestris). J. Mar. Biol. Ass. U. K., 21: 497-570.

Thorndike, E. 1899. A note on the psychology of fishes. Am. Nat., 33: 923-25.

Welty, J. C. 1934. Experiments in group behavior of fishes. Physiol. Zool., 7: 85-128.