AN ANALYSIS OF THE EFFECTS OF THE SOCIAL HIERARCHY AND OTHER FACTORS UPON FOOD CONSUMPTION IN THE FISH <u>PLATYPOECILUS MACULATUS</u>

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AN ANALYSIS OF THE EFFECTS OF THE SOCIAL HIERARCHY AND OTHER FACTORS UPON FOOD CONSUMPTION IN THE FISH *PLATYPOECILUS MACULATUS*

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ABSTRACT

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This paper forms part of a series of studies being conducted by Braddock, Duncan and Daitch, et al on _Platypoecilus maculatus_ Guenther. Certain aspects of food consumption have been considered. The amount of food consumed by different individuals was measured by counting the number of worms eaten by fish in various groupings. These numbers were then treated statistically by the use of analysis of variance.

In one phase of the study comparisons were made among fish of different hierarchial positions. There were significant differences in numbers of worms consumed by individuals in each of the positions. The more dominant individuals consumed more worms.

The number of worms consumed by each fish reached an apparent maximum when three were placed together. Consumption was least among isolated individuals.

The relationship of sex to food consumption was studied apart from the social groups. It was found that females consumed more food and varied more among themselves than males. The smaller females when alone in aquaria produced a degree of variation that was significantly higher than

that of any other weight class of males or females observed. This variation may have been caused by the presence in this group of both mature and immature females. It is probable that most of the females became mature during the later experiments, and some no doubt became pregnant. The effect of sex and pregnancy upon food consumption may have been considerable, but the details of this effect were not distinguishable here.

No evidence was found to indicate that the amount of time spent in aquaria effected the number of worms consumed except when larger samples were taken. The amount of food consumed by fish during the first feeding period tended to be less than in the other three in the case of the larger samples.

In *P. maculatus* social groups made up of distinguishable hierarchial positions contained fewer fish and were less complex than those in chickens, but most of the findings here agree with previous studies made on chickens by Guhl and Allee (1944). Also, individuals observed in this report seemed to follow many of the basic activity patterns observed in other hierarchial studies made on fish (Noble and Borne, 1940; Braddock, 1945, 1949; Greenberg, 1946).

H. R. Hunt

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INTRODUCTION

Recent studies of social behavior among fish (Braddock, 1945; Greenberg, 1946; Allee, Greenberg, Rosenthal, Frank, 1948) have described definite group behavior which may take the form of hierarchies, territoriality, schooling, or combinations of these, in the species studied. It has not been clearly established whether social habits represent an aspect of evolution or develop _de novo_ as required. Territoriality, hierarchies and schooling may be separate social entities each evolving along special paths, or different expressions of a basic social behavior. Possibly, the different types of social organization represent different expressions of a fundamental automatic cooperation found in protoplasm (Allee, 1935) which has been modified by the environment and heredity, and which has developed into many different social expressions paralleling structural changes.

The fish _Platypoecilus maculatus_, Guenther, displays definite hierarchial behavior in groups up to and including four individuals, and possibly in larger groups under special conditions. Simple hierarchies exist, the duration of which may vary depending upon individual groups and methods used to study the groups (Greenberg, 1946; Braddock, 1949). Individuals maintain their social status by the nip behavior characteristic of the fish hierarchy (Braddock, 1945).

This study deals with the effects hierarchy establishment and other factors such as weight and sex have upon food consumption. Experiments included single individuals, and individuals in groups of two, three, and four fish.

DEFINITION OF TERMS*

Nip

The nip is a device by which fish establish and maintain dominance or aggressiveness. Typically, one fish lunges toward another and inflicts a bite that does not cause injury or death.

Nip-Right

After a fish has become dominant it nips its subordinates without receiving nips in return. The dominant males display nip-right behavior to a greater degree than the dominant females.

Nip-Dominance

In certain instances dominance is not clear cut, and in such cases the dominant member of a contact pair is recognized by a comparison of the total number of nips given by each

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*(Braddock 1945, 1949)

contesting individual. The individual giving the greater number of nips is judged to be dominant. This is not characteristic of *P. maculatus* but occurs in some instances.

Challenge

The challenge is represented in this species by a tense curved body, upright dorsal fin, extended anal and caudal fins, quivering side movement, slight forward swimming, and a gradual side approach to the individual which occurs from one to ten minutes after two fish are placed together.

Submissive Behavior

When a fish is challenged by another it may either accept the challenge or submit. The typical signs of submission are a flattened dorsal fin, contracted anal and caudal fins, relaxed body, avoidance of the challenger, and lack of jerky side-swimming.

Hierarchial Behavior

The tendency as displayed by this species, to form a simple society based upon relative display of aggressive action is an example of hierarchial behavior. The position of a dominant individual is determined by challenging and nipping. The society eventually consists of a series of positions, and the fish in the number one position displays a nip-right over all others. The individual in the number two position displays nip-right over all but the number one fish and so forth.

Territoriality

Many animals choose territories and live within these territories either alone or with a mate. The animal is dominant within its chosen territory. The size and location of the territory may depend upon a variety of factors. Among fish the Centrarchids and others display this type of behavior at maturity. No direct evidence of territoriality has been observed for P. maculatus.

SCIENTIFIC NAMES OF PLANTS AND ANIMALS MENTIONED IN THIS STUDY

Scientific nomenclature according to Hubbs and Lagler (1947) and Innes (1949) was used for species of fish mentioned in the text. The nomenclature used for invertebrates was according to Pratt (1948) and Bullough (1950). Scientific nomenclature according to Gray (1908) was used for aquatic plants mentioned in the paper.

Animals

Platy	Platypoecilus maculatus Guenther	
Mosquitofish	Gambusia affinis affinis Baird and Girard	
Guppy	Lebistes reticulature or Girardinus guppyi Peters	
Swordtail	Xiphophorus helleri Heckel	Family-Poeciliidae
Scavenger	Cypris spp.	Family-Cypridae
Annelid worm	Enchytreaus spp.	Family-Enchytraeidae
Snails	Heliosoma campanulata Swainson	Family-Planorbidae
	Campeloma spp.	Family-Enchytraeidae

Plants

Elodea	Elodea canadensis Michx.	
Vallisneria	Vallisneria spiralis Linnaeus	Family-Hydrocharitaceae
Duckweed	Lemna spp. Wolffia spp.	Family-Lemnaceae
Salvinia	Salvinia natans Linnaeus	Family-Salviniaceae

THE EXPERIMENTAL ANIMAL AND ITS TREATMENT

The family Poeciliidae, which is exclusively American, ranges from the upper Mississippi valley to Argentina (Hubbs and Lagler, 1947). In southern Michigan one introduced species of this family occurs. The eastern mosquitofish, Gambusia affinis, a surface feeder, was introduced into Michigan in the early 1940's. The value of this species to man lies in its habit of consuming mosquito larvae. Some other fish in the family are the guppy, Lebistes reticulatus; swordtail, Xiphophorus helleri; and platy, Platypoecilus maculatus. This family is ovoviviparous and the males all have an anal fin modified for use as an intromittant organ.

Platys and swordtails produce fertile hybrids when a female swordtail is mated with a male platy. However, the reverse combination seldom results in the production of hybrids (Gordon, 1947; Innes, 1949; Schlosberg, Duncan, Daitch, 1949). In nature, hybrids have not been found, probably because large numbers of males and females of both species are present, and normal mating behavior may be carried on (Gordon, 1947).

P. maculatus normally occurs in sluggish central American streams, and can stand a temperature range from 65° to 90° F. with an optimum of 74° F. (Innes, 1949). Members of this species have been kept in aquaria at Michigan State College where the temperature range was from 60° to 70° F.

The eggs of P. maculatus are retained within the body of the female until they hatch. No placenta is formed, and no direct requirement to supply food energy is placed upon the female from a pregnancy of this sort. Indirectly, however, the greater size and weight of pregnant fish as compared to non-pregnant fish may affect energy relationships considerably. Young fish at the time of birth have absorbed the yolk sac and emerge as fully developed individuals requiring no special care. Each brood consists of from twenty to forty fish (Schlosberg, Duncan, and Daitch, 1949). In captivity older fish occasionally eat the young. This practice may be controlled by feeding adults adequately and by providing concealment for the young.

The normal diet consists of insects and other small invertebrates. In captivity food may be consumed at the surface, in descent, or from the bottom, even though the fish are classed as surface feeders.

The structure of the anal fin indicates the sex. Females have a fan-shaped anal fin, while in males the fin is modified as a gonopodium or intromittant organ. This is an open tubelike structure normally held close to the body along the ventral median line. During times of actual or attempted mating the male organ is rotated forward and to one side as the male attempts to insert it into the vent of the female. After insertion into the vent a small globule of sperm passes along the trough-like organ and serves to fertilize the eggs of five or six broods. Whether the spermatozoa are stored by the female or fertilize a large number of eggs, a few of which complete development at a time, is not known (Schlosberg, Duncan, Daitch, 1949).

The gestation period of females is variable. Development of the eggs within the female depends upon the temperature of the water. Above 80° F. the period of gestation is about five weeks, while below 70° F. it may increase to a maximum of twelve weeks (Innes, 1949; Schlosberg, Duncan, Daitch, 1949).

At maturity females reach a length of three inches, while males rarely exceed one inch. This size difference results from the slower postpubertal growth of the males (Innes, 1949).

The coloration is variable but may be superficially divided into two basic color patterns, black and white, with many minor variations. Some of these variations are black spots, red bands, and reddish fins. The coloration is dependent upon genetic sex-linked characters, with the gene for black dominant over the gene for white (Shull, 1948).

Previous to the experiments the fish were fed a commercial preparation of ground dehydrated insect bodies plus dried shrimp and salts. Once a month this diet was supplemented with living Drosophila larvae and adults. Shortly before starting the experiments small annelid worms of the genus Enchytraeus (Bullough, W. S., 1950) were introduced as food for the fish. These worms were used as the unit of food during the experimental period. They are without a proboscis, have four setae of equal length per segment, and are one centimeter in length at maturity, with a probable total variation in length of 2 millimeters.

Cultures of these worms were obtained from a dealer* and were maintained in the animal house of Michigan State College. The prescribed environment is moist soil with plenty of organic matter and some aeration; however, the animals were tolerant of excess amounts of moisture. Mature worms regularly remain alive twenty-four hours under water.

The worms consume partially decomposed organic matter which they ingest from soil passed through the digestive system. They are slightly heavier than an equal volume of water and sink slowly to the bottom of the tank wriggling constantly. This serves to attract the attention of the fish immediately.

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*Beldt's Aquarium, St. Louis, Missouri.

Experiments were conducted in a constant temperature room in the Zoology Department of Michigan State College. Forty glass aquaria (26 x 21 x 21 cm.) were used to house the fish during each experiment, and were kept bare of sand and plants. Approximately two snails were placed in each aquarium. The aquaria were located on wooden shelves extending along the west, north, and east walls of the room in four units of four shelves in each unit. Two large aquaria (121 x 77 x 51 cm. and 137 x 76 x 50 cm.) served as stock tanks for the mature fish. They were placed in the center of the room on metal racks 60 centimeters in height. Many young fish were kept in three separate aquaria (71 x 21 x 31 cm.) to insure maximum safety and growth.

The large aquaria contained plants, gravel, invertebrates, and fish. The plants used were Elodea, Lemna, Wolffia, Salvinia and Vallisneria (Gray, 1908; Innes, 1949; Atz, 1950). The invertebrates were snails (Heliosoma and Campeloma) and a scavenger, Cypris (Pratt, 1948). The fish used in the experiments were dipped out of the stock tanks at the start and were not returned until the completion of the experiments.

Light entered the room from three windows located on the north and east sides. Six electric lamps were also used as light sources. Four of the lamps were on the ceiling, and one desk lamp was placed on the glass cover of each of the two largest aquaria. The two desk lamps and two of the upper lamps were lit continuously; the other two lamps only during the day (8 a.m. - 6 p.m.).

Water was taken from the college system which obtains water from wells and from the East Lansing city system. Chlorine is present in the water in varying amounts. All water used in the aquaria was first permitted to stand seven to ten days to insure the escape of excess amounts of chlorine.

The observations were divided into four sets of experiments based upon the number of fish dealt with in each aquarium. An immediate purpose of the experiments was to analyse variation in food consumption among fish when one, two, three and four were placed in aquaria.

All fish were isolated for 48 hours before the start of each set of experiments to eliminate possible effects of prior dominance or subordination (Braddock, 1949). Each fish to be observed was transferred into a different aquarium at the start of each experiment in order that possible effects of environmental change might be consistent. The unit of food, as previously described, was the annelid worm Enchytraeus.

Experiment No. I consisted of a series of 40 trials dealing with one individual in each aquarium. Each fish to be tested was placed in a separate aquarium and offered more worms than it would eat during the feeding period. At the end of 20 minutes the excess worms were removed and the number consumed was recorded. Similar feeding procedure was followed for each fish at 24, 48, and 72 hour intervals from the beginning of the experiment.

Experiment No. II involved 40 trials dealing with two individuals in each aquarium. After an isolation period similar to that preceding experiment one, the two fish were placed in an aquarium strange to each. The feeding procedure again consisted of immediately offering the fish worms to eat and noting the numbers eaten by each individual. Each of the four feeding periods lasted 20 minutes with elapsed time between periods being the same as in Experiment No. I. The number of worms consumed by each individual, the social position of each, and the individual which ate the first worm were recorded for each group.

Experiment No. III consisted of 40 similar trials dealing with three individuals, and Experiment No. IV was made up of 40 trials dealing with four in each aquarium.

At the beginning of the study, the experimental animals were selected at random from the population of the large stock tank. Individual identities were established by a method of recording the location and size of color markings, and these were recorded over all the experiments. Each fish was assigned a number for use in keeping records. Sex, and size in terms of water displacement in cubic centimeters, were also recorded at the start of the work. Sex was noted before each experiment but displacement was not rechecked.

In part A of the section entitled RESULTS data from the same 40 fish were used as a basis for the statistical analysis. These fish lived through the entire experimental period. In Part B of the section entitled RESULTS experiments II, III, and IV were treated as separate units and fish used as a basis for the analyses did not necessarily live through the entire experimental period. Also, data from many of the same fish were used for the different experimental units.

Data concerning 50 fish were the basis for the statistical treatment of experiment II, 39 fish for experiment III and 40 fish for experiment IV.

ANALYSIS OF VARIATION IN FOOD CONSUMPTION AMONG FISHES

Analysis of Variance

The analysis of variance is the particular statistical method used in this paper. It permits the investigator to forecast differential performances among experimental units (Snedecor, 1946). Since this method deals primarily with random samples and parent populations, a discussion of these two terms follows. All items of a type that have limiting characteristics in common are collectively known as a parent population. Usually the large number of items in the parent population prevents consideration of the whole group of items in any study. Hence, random samples are taken from the parent group, and are used to represent it. A random sample is indicated when all items in a parent population have an equal chance of becoming a part of the sample. For example, this work is a report on certain aspects of social behavior observed among 200 individuals of the species P. maculatus. These 200 animals represent a sample taken from the thousands found in captivity. The thousands of fish in this case would represent one type of parent population, and the 200 a random sample drawn from this population.

The significance of differences is judged from the variance ratio resulting when the mean square of the error term is divided into the mean square of the factor whose degree of significance is desired.* The mean square is a measure of variability, and significances of differences are judged from relative values of mean squares. The variance ratio, commonly known as F, has been tabulated for different combinations of degrees of freedom and reference is made to such tables to determine significance (Snedecor, 1946).

This work considers that differences among series of items are significant when there is less than one chance in one hundred that differences as great might have arisen by chance in sampling from the same parent population. It follows that results obtained by these methods are subject to one percent error** whenever the differences are exactly at this level.

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* The mean square is a measurement for the variation of items which relate to the factor tested. Literally, the mean square is the average of the squared deviations from their mean for the items of the class concerned. The error mean square represents the variability not accounted for, and is assumed to reflect experimental error. A high value for a mean square indicates a high degree of variation. If no differences exist between individuals then, on the average, the mean square should be expected to equal the error mean square.

**The source of error lies in the fact that in one percent of the samples from the same population "significant differences" may be expected by chance. Strict adherence to these values means a possible one percent error in judgment.

Comparison of Factors Within each Experiment Using the Analysis of Variance

Meaning of Terms Used

Feeding periods. Under the term "feeding periods" are examined differences in numbers of worms consumed at each of the four feeding periods. If differences are found to be significant there is less than one chance in one hundred that differences as great could have arisen from sampling the same parent population.

Individuals. Under the term "individuals" is tested variation in total numbers of worms consumed by each fish over the four feeding periods. If differences are found to be significant there is less than one chance in one hundred that differences as great could have arisen from sampling the same parent population.

The term "individuals" may be subdivided in many ways. Here individual differences have been studied according to "sex" and "within sex"; and "weight" and "within weight." Definitions of these terms follow.

Sex. The term "sex" is applied to differences in numbers of worms consumed by males in contrast to females. Significance indicates the probability that the totals differ beyond the normal random variation expected within a single parent population.

<u>Within sex</u>. Under the term "within sex" the extent of variation in worms consumed among individuals of the same sex is tested. If differences are found to be significant there is less than one chance in one hundred that differences as great could have arisen from sampling the same parent population.

<u>Weight</u>. Variation among individuals in different weight classes* is tested under the term "weight". Significance indicates the probability that weight affects worm consumption beyond the variation expected within a single parent population.

<u>Within Weight</u>. Under the term "within weight" the amount of variation among individuals of the same weight class is tested. Significance indicates the probability that individuals of the same weight class differ beyond the random limits expected within a single parent population.

Interaction

Interaction is a term used to describe possible effects of two factors upon each other when data from each is regarded in terms of the other. There is no interaction

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* For purposes of analysis three weight classes were recognized. Animals in class A displaced 0 - .19 c.c.; in class B .20 - .71 c.c.; in class C .72 - 2.00 cc.

indicated when a change in magnitude of one factor produces the same effect regardless of the level of the second factor. The degree of consistency for the variance for each such comparison is measured by an F test similar to that used for single terms (Snedecor, 1946).

An hypothetical example of absence and presence of interaction is presented in tables 1 and 2, using imaginary data. In table 1 it may be seen that both sexes consumed more in the second period than in the first. In this example, all variability was explained by classification according to sex and feeding period, with interaction being zero. Actually a zero value is not probable, since experimental error would make such close agreement unlikely. Table 2 shows, in contrast, that males increased food consumption from period one to period two, while females ate less. As a result, interaction is high.

Table 1

Feeding Periods	Males	Females	Totals
1	55	22	77
2	66	33	99
Totals	121	55	176

Table 1 is an example of two factors (feeding periods and sex) with interaction absent. In this example differences in numbers of worms consumed among animals of both sexes are not changed by the amount of time spent in aquaria.

Table 2

Feeding Periods	Males	Females	Totals
1	55	22	77
2	66	11	77
Totals	121	33	154

Table 2 is an example of a high degree of interaction between feeding periods and sex. The food consumption of male and female animals was affected differently by the amount of time spent in aquaria.

Variability

The analyses of variance for Part A include one kind of test not mentioned heretofore, i.e. a test for significant differences in variability as distinguished from tests previously mentioned, which are tests of differences in magnitude. If sets of data differ in variability, then data of such diverse nature are difficult to combine in an analysis of variance, according to Cochran and Cox (1950) who state: "The most serious disturbances arise when the experimental variance is not constant for all observations. The effect of this is to increase the percent level at which the data show significant differences... The assumption made in the analysis of variance is that treatment and environmental effects are additive. The experiments must be independently distributed within a common variance."

Two kinds of tests for heterogeneity of variance have been used, following Snedecor (1946). The first of these may be used in a comparison of only two sets of data, and involves a division of the larger of the mean squares under "error" by the smaller. Significance is judged from a table of F values, except that when making such a test the table of F values should be read at twice the significance level indicated, i.e. two percent instead of one percent (Snedecor, 1946).

The second test used was Bartlett's test of homogeneity of variance, which may be used with more than two sets of data. Significance in this test is judged according to chi-square values, which are referred to proper tables according to the number of degrees of freedom (Snedecor, 1946).

RESULTS (Part A)

A separate analysis of variance was completed for animals of each sex in each of three weight classes for experiments I through IV (Tables 3, 4, 5, and 6), as was Bartlett's Test for variability of data (Table 6A). For Tables 3 to 6 the interaction feeding period X individuals was used as the error term. Two stars (**) indicate significance at the one percent level, and no significance is designated by the letters "ns".

The data for these analyses are records of the numbers of worms consumed by the forty fish, eighteen males and twenty-two females, that lived for the duration of the four experiments. A discussion of the results follows later in this section.

These separate analyses were made in order to test the homogeneity of variability for the data. If the degree of variability is found to differ significantly among the sub-classes, then results from any analysis of variance using combined data must be used with great caution. The homogeneity of variance was examined by using Bartlett's Test. A comparison was also made of the general level of variability among pairs of subclasses by the use of Snedecor's F test which compares mean squares under the term "error".

Table 3

Analysis of Variance for Weight Classes
Divided According to Sex

Experiment I
(one fish)

Females

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	31	64.3		31	6.3		23	18.8	
Individuals	7	221.3	**	7	16.1	**	5	39.2	**
Feeding Periods	3	12.7	ns	3	2.3	ns	3	50.7	**
Error	21	19.3		21	3.5		15	5.5	

Males

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	23	1.4		19	6.9		27	9.7	
Individuals	5	3.6	ns	4	11.2	ns	6	23.3	**
Feeding Periods	3	1.0	ns	3	9.3	ns	3	3.3	ns
Error	15	.73		12	4.8		18	6.2	

Table 3, a condensed analysis of variance, shows degrees of freedom, mean square, and indications of significance for each of the factors tested.

Table 4

Analysis of Variance for Weight Classes
Divided According to Sex

Experiment II
(two fishes)

Females

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	31	11.0		31	7.6		23	20.7	
Individuals	7	30.9	**	7	16.4	**	5	65.0	**
Feeding Periods	3	19.7	**	3	17.7	**	3	25.0	**
Error	21	3.2		21	3.3		15	5.1	

Males

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	23	3.8		19	3.7		27	7.1	
Individuals	5	7.4	**	4	1.5	ns	6	12.7	ns
Feeding Periods	3	8.7	**	3	9.0	ns	3	13.0	ns
Error	15	1.7		12	3.1		18	4.3	

Table 4, a condensed analysis of variance, shows degrees of freedom, mean square, and indications of significance for each of the factors tested.

Table 5

Analysis of Variance for Weight Classes
Divided According to Sex

Experiment III
(three fishes)

Females

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	31	21.2		31	24.9		23	59.7	
Individuals	7	57.9	**	7	51.0	**	5	212.6	**
Feeding Periods	3	16.0	ns	3	.3	ns	3	7.3	ns
Error	21	9.8		21	19.7		15	19.2	

Males

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	23	12.0		19	20.6		27	27.1	
Individuals	5	39.4	**	4	79.0	**	6	82.7	**
Feeding Periods	3	4.3	ns	3	1.3	ns	3	8.7	ns
Error	15	4.4		12	5.9		18	11.6	

Table 5, a condensed analysis of variance, shows degrees of freedom, mean square, and indications of significance for each of the factors tested.

Table 6

Analysis of Variance for Weight Classes
Divided According to Sex

Experiment IV
(four fishes)

Females

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	31	54.0		31	55.5		23	18.7	
Individuals	7	122.1	**	7	187.6	**	5	50.8	**
Feeding Periods	3	22.0	ns	3	44.3	**	3	21.3	ns
Error	21	35.9		21	13.0		15	7.5	

Males

Weight Classes	A			B			C		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	23	7.7		19	31.3		27	11.3	
Individuals	5	26.0	**	4	102.5	**	6	34.3	**
Feeding Periods	3	7.0	**	3	14.7	ns	3	5.3	ns
Error	15	1.7		12	11.7		18	4.6	

Table 6, a condensed analysis of variance, shows degrees of freedom, mean square, and indications of significance for each of the factors tested.

Table 6A

Bartlett's Test for Homogeneity of Variances
Among Weight-Sex Subclasses for
Experiments I, II, III and IV

Experiment	Chi-square	DF	Level of Significance
I	40.58	5	** less than .001
II	4.22	5	ns about .55
III	13.01	5	* about .02
IV	14.14	5	** less than .001

Table 6A gives chi-square values from Bartlett's Test for homogeneity of variances among weight-sex subclasses. The level of significance indicates the probability that as great differences in variability among the subclasses could have arisen by chance sampling. Where the probability is small, there is evidence that the differences in variability among subclasses exceed those expected in consistent data. The statistical significance of these differences may be judged by the usual criteria, at the five percent level in this case.

Discussion Part A

The chief purpose of the analysis of variance in Part A was to distinguish the degree of variability between the sexes and among the weight classes. However, variation in worms consumed was compared for individuals and for fish in the four feeding periods.

According to Bartlett's Test (Table 6A) there were significant differences in variability when values from the subclasses were compared in experiment I and IV. There was no significance found among the subclasses for experiment II. In experiment III the variability approached significance closely enough to warrant extreme caution in the use of analyses of variance based upon data composed of combined values from these subclasses.

The variability for females of weight class A was greater than that for fish in any other groupings in experiments I and IV (see tables 3 and 6) and probably was the cause for the high value for chi-square in Bartlett's Test in the two experiments. Females in general showed greater variability in number of worms consumed than did males, but many of the differences in paired comparisons were not significant when compared by Snedecor's F test.

In all comparisons individual females within weight classes varied significantly in number of worms consumed. In eight cases out of twelve, males within the different weight classes also differed significantly. The four exceptions were found in experiments I and II (see tables 3 and 4).

Feeding periods showed no significant differences in 17 out of 24 comparisons. The 7 exceptions were found in experiments I, II, and IV and only 2 out of the 7 exceptions where feeding periods showed significance were among male animals. In cases where significance was observed for feeding periods, the low value for feeding period one was often responsible.

RESULTS (Part B)

Analysis of Variance for Social Groups

The purpose of these experiments was to determine whether food consumption differed significantly when social groups were compared.

In the experiments as a whole, fish usually formed simple hierarchies when two, three and four were placed together. The investigator was unable to distinguish the social relationships among fish in about 30 percent of the cases. The analyses were accordingly divided into two groups: namely, "Distinguishable," those where social positions could be ascertained, and "indistinguishable," those where hierarchial positions were not clearly discernible.

There follows a discussion of results obtained from a series of analyses of variance completed for experiments II, III, and IV. The data for these analyses were based upon the number of worms consumed by the fish. Each experiment was regarded as an entity, and separate analyses were conducted for each. Data from two or more experiments were not combined.

In addition to analyses of variance, graphs showing least significant differences were used to determine the effect of time spent in aquaria upon the amount of food consumed by fish of the different hierarchial positions, and upon food consumption by fish regardless of social status.

Discussion of Tables

Tables 7, 8 and 9 are analyses of variance testing differences in the number of worms eaten by fish of different social status when two, three, or four were placed in each aquarium.

In experiments II and III combined analyses of variance were completed testing variation in the amount of food consumed by fish within distinguishable and indistinguishable groups, see tables 7A and 8A. In experiment IV it was necessary to treat indistinguishable and distinguishable groups separately in the analyses because some of the same animals were included in both sets of data. Separate analyses to test variation in food consumption were next completed for distinguishable and indistinguishable groups within experiments II, III and IV (Tables 7B, 7C, 8B, 8C, 9A and 9B). Within the distinguishable groups for experiments II and III analyses were completed to determine variation in food consumption for members within each hierarchial group (Tables 7D and 8D). Also, within the distinguishable group the amount of food consumed by fish of different social status was compared. (Tables 7D, 8E and 9C).

The term "error" is used in place of the interaction feeding period X individuals. Two stars (**) indicate significance at the one percent level and a lack of significance at this level is designated by the letters "ns."

Least Significant Difference (Simpson and Roe, 1939)

In addition to analyses of variance least significant differences were used to show the effect of the amount of time spent in aquaria upon the amount of food consumed by fish of the different social positions (graphs A to G). The analysis of variance indicated there were significantly different values present. Least significant differences provided a graphical method showing where such differences occurred in the subclasses.

Tables 7A-7D

Experiment II

Analyses of Variance for Social Groupings

Table 7A

Distinguishable and Indistinguishable Groups Combined

Source	DF	MS	SIG
Total	199	9.6	
Feeding Periods	3	71.0	**
Individuals	49	24.1	**
Between Distinguishable and Indistinguishable	1	24.0	**
Error	147	3.5	

Table 7B

Indistinguishable Groups Only

Source	DF	MS	SIG
Total	87	8.2	
Feeding Periods	3	36.0	**
Individuals	21	18.7	**
Between Pairs	10	27.0	**
Within Pairs	11	11.1	**
Error	63	3.4	

Table 7C

Distinguishable Groups Only

Source	DF	MS	SIG
Total	111	10.7	
Feeding Periods	3	39.3	**
Individuals	27	28.3	**
Pairs	13	38.7	**
Within Pairs	14	18.7	**
Dominant vs Subordinate fishes	1	41.0	**
Pair X Dom. vs Sub.	13	17.0	**
Between Kinds of Pairs	2	76.0	**
Within Kinds of Pairs	11	31.9	**
Error	81	3.6	

Tables 7A-7C are a series of analyses of variance completed for different social groups of fish in experiment II.

Table 7D

Within Distinguishable Groups

	Dominant Fishes Only			Subordinate Fishes Only		
Source	DF	MS	SIG	DF	MS	SIG
Total	55	14.9		55	5.6	
Feeding Periods	3	20.3	**	3	20.0	**
Individuals	13	42.6	**	13	13.0	**
Sex	1	258.0	**	1	37.0	**
Within Sex	12	44.5	**	12	11.0	**
Feeding Periods X Sex	3	2.0	ns	3	1.3	ns
Error	39	5.1		39	2.1	

Table 7D separates data within distinguishable groups into dominant and subordinate groupings. An analysis of variance is completed for each group.

Tables 8A-8E

Experiment III

Analyses of Variance for Different Social Groups

Table 8A

Distinguishable and Indistinguishable Groups Combined

Source	DF	MS	SIG
Total	155	28.7	
Feeding Periods	3	53.3	**
Individuals	38	90.0	**
Between Distinguishable and Indistinguishable	1	146.0	**
Error	114	7.7	

Table 8B

Indistinguishable Groups Only

Source	DF	MS	SIG
Total	71	25.5	
Feeding Periods	3	12.0	ns
Individuals	17	72.3	**
Between Trios	5	145.0	**
Within Trios	12	42.4	**
Error	51	10.1	

Table 8C

Distinguishable Groups Only

Source	DF	MS	SIG
Total	83	34.8	
Feeding Periods	3	5.4	ns
Individuals	20	102.9	**
Between Trios	6	51.0	**
Within Trios	14	125.5	**
Error	60	11.2	

Tables 8A-8C are a series of analyses of variance completed for different social groups of fishes in experiment III. Table 8A is an analysis of distinguishable and indistinguishable groups combined. Tables 8B and 8C treat distinguishable and indistinguishable groups separately.

Table 8D

Within the Distinguishable Group

	#1 fishes			#2 fishes			#3 fishes		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	27	30.6		27	28.6		27	20.7	
Feeding Periods	3	43.0	**	3	29.7	**	3	8.3	ns
Individuals	6	68.0	**	6	83.3	**	6	69.7	**
Error	18	16.1		18	10.2		18	6.4	

Table 8D consists of analyses of variance for fishes within each of the three social positions under distinguishable groups.

Table 8E

A Comparison of Fishes in the Different Hierarchial Positions within the Distinguishable Group by the Analysis of Variance

	1 vs 2			1 vs 3			2 vs 3		
Source	DF	MS	SIG	DF	MS	SIG	DF	MS	SIG
Total	55	28.9		55	38.4		55	28.9	
Feeding Periods	3	72.0	**	3	35.6	*	3	24.3	**
Individuals	13	90.8	**	13	119.1	**	13	90.1	**
Between Positions	1	95.0	**	1	722.0	**	1	262.0	**
Error	39	4.9		39	11.6		39	8.7	

Table 8E consists of analyses of variance of comparisons between social groups.

Tables 9A-9C

Experiment IV

Analysis of Variance for Two Social Groups Distinguishable and Indistinguishable

Table 9A

Indistinguishable

Source	DF	MS	SIG
Total	79	53.4	
Feeding Periods	3	18.3	ns
Individuals	19	149.4	**
Sex	1	975.0	**
Within Sex	18	103.6	**
Between Groups	4	123.2	**
Within Groups	15	156.4	**
Feeding Periods X Sex	3	11.3	ns
Error	57	23.2	

Table 9B

Distinguishable

Source	DF	MS	SIG
Total	79	22.1	
Feeding Periods	3	5.3	ns
Individuals	19	63.6	**
Sex	1	166.0	**
Within Sex	18	37.9	**
Between Groups	4	19.3	ns
Within Groups	15	29.1	**
Feeding Periods X Sex	3	3.0	ns
Error	57	9.1	

Table 9C

A Comparison of Fishes in Different Hierarchial Positions by the Analysis of Variance Within Distinguishable Groups

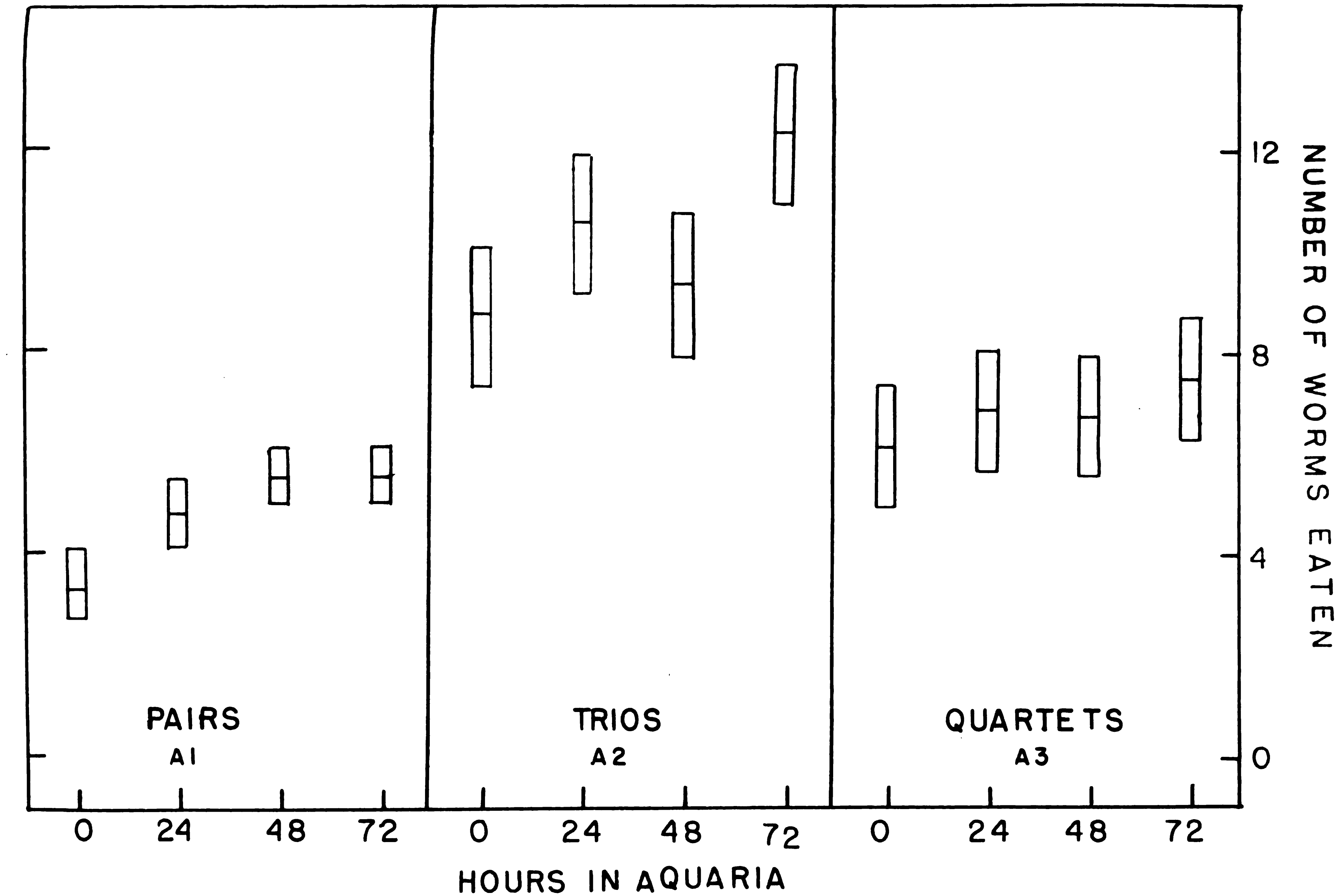
		1 vs 2		1 vs 3		1 vs 4	
Source	DF	MS	SIG	MS	SIG	MS	SIG
Total	39	26.9		26.0		29.2	
Feeding Periods	3	1.3	ns	6.0	ns	4.0	ns
Individuals	9	71.2	**	73.5	**	88.8	**
Between Fishes	1	97.0	*	250.0	**	404.0	**
Error	27	15.0		13.2		12.1	

		2 vs 3		2 vs 4		3 vs 4	
Source	DF	MS	SIG	MS	SIG	MS	SIG
Total	39	15.0		14.3		8.3	
Feeding Periods	3	14.3	ns	10.7	ns	4.3	ns
Individuals	9	43.3	**	49.0	**	26.6	**
Between Fishes	1	30.0	*	96.0	**	18.0	*
Error	27	5.7		3.2		2.7	

Tables 9A-9C are a series of analyses of variance for experiment IV. Tables 9A and 9B are analyses for distinguishable and indistinguishable groups treated as separate units. Table 9C is a group of analyses comparing fishes of different social position, all within the distinguishable group.

GRAPH $A_{1,2,3}$

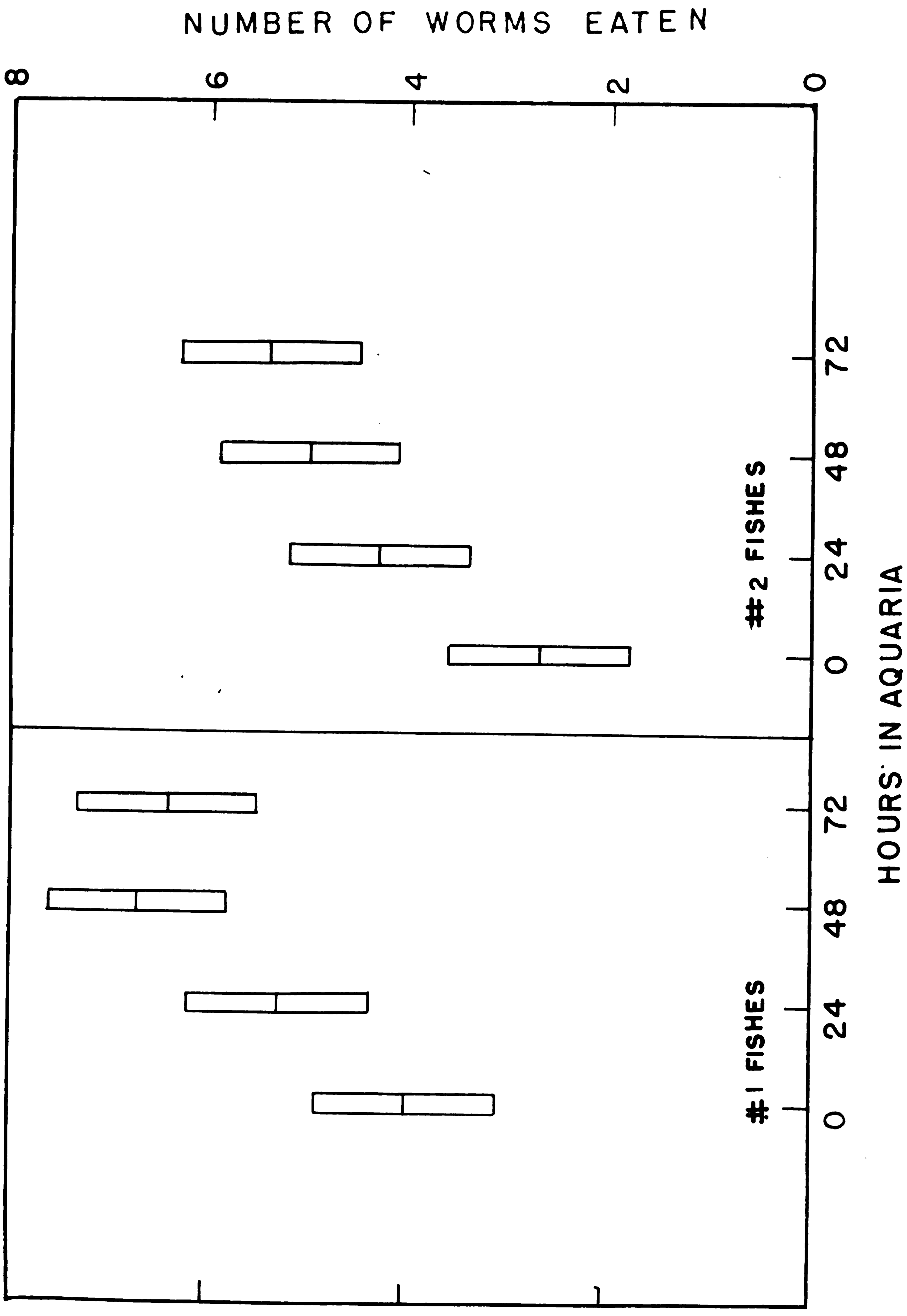
A Comparison of Least Significant Differences in Worms Consumed by Fish
During Each of the Feeding Periods
Within Pairs (A1), Trios (A2), and Quartets (A3)



PAIRS
A1
TRIOS
A2
QUARTETS
A3
0
24
48
72
HOURS IN AQUARIA
12
8
4
0
NUMBER OF WORMS EATEN

GRAPH B

A Comparison of Least Significant Differences in Worms Consumed by Fish Of the Same Dominance Potential for each of the Four Feeding Periods (Two Fish in Each Aquarium)


NUMBER OF WORMS EATEN
8
6
4
2
0
#1 FISHES
#2 FISHES
0
24
48
72
HOURS IN AQUARIA

DISCUSSION (Part B)

No significant difference in variability of data was noted when comparisons of error terms of smaller groups such as distinguishable, indistinguishable, number one fish, number two fish, etc. were completed. The consistency of the data among the groups discussed above permitted the use of combined analyses of variance for the groups. However, inconsistencies of data noted between sexes and among weight classes in part A (page 27) were operating here, and for experiment III may have been important enough to affect results. It is assumed that the findings of experiment III are basically reliable, but should be interpreted with some reservations, especially in border-line cases (Cochran and Cox, 1950).

The amount of time spent in aquaria was found to have had a significant effect upon food consumption by fish when the distinguishable and indistinguishable groups were combined in the analyses of variance (Tables 7A and 8A). The trend for fish in distinguishable groups regardless of social status, as shown in graphs $A_{1, 2, 3}$, appears to have been a gradual irregular increase in food consumed as the amount of time spent in aquaria increased. As data were divided into smaller groups with fewer fish considered in

GRAPH C

A Comparison of Least Significant Differences in Worms Consumed by Fish of the Two Hierarchial Positions for Each of the Four Feeding Periods (Two Fish in Each Aquarium) each subclass, the effect of feeding periods was significant in fewer cases in experiments III and IV, but remained significant in experiment II.

When individual fish were compared it was found that they varied significantly in food consumption in all groupings. These significant differences persisted for individuals of the same sex, social group and hierarchial position indicating that these classifications did not explain all differences between individuals. Variation among such social groups as pairs in experiment II, trios in experiment III and quartets in experiment IV was also significant. In experiments II and III fish of social groups where hierarchial positions could be distinguished ate significantly more than those in groups where it was impossible to observe social status (see Tables 7A and 8A). This fact was not tested in experiment IV because in that experiment distinguishable and indistinguishable groups could not be compared in the analyses.

When food consumption by fish within each of the hierarchial positions was compared in experiments II and III differences were found to be significant. On the whole fish in the more dominant positions consumed a significantly greater amount of food than their subordinates. Experiment IV was unlike experiments II and III in that the degree of dominance had to be greater in order that significant differences in the amount of food consumed might be recognized (see Table 9C).

Information based upon least significant differences, as indicated in graphs C, E, G, shows that the more dominant fish did not consume the greatest amount of food at all times. The number of worms consumed by the number one fish as compared to those consumed by the number two fish was seldom significantly more when two, three or four fish were present in each social group, but a trend to that effect was evident. The number of worms consumed by the number three and four fish in the social hierarchy was usually significantly less than the number consumed by fish in the more dominant social positions. A trend, however, showing a positive correlation between dominance, amount of time spent in aquaria, and number of worms consumed is evident and consistent in all experiments, as shown by graphs A through G.

GRAPH D

A Comparison of Least Significant Differences in Worms Consumed by Fish of the Same Dominance Potential for the Four Feeding Periods
(Three Fish in Each Aquarium)

RESULTS (Part C)

Table 10

The Number of Times Fish in Different Hierarchy Positions Ate First

Experiment	Number One	Number Two	Number Three	Number Four
II	31	20	--	--
III	53	37	20	--
IV	24	20	22	6

When groups containing two or three fish were placed in each aquarium the dominant member in each group ate first more frequently, but only by a narrow margin in experiment II, than fish in other positions.

When groups containing four fish were observed it was found that those of the first three positions ate first with approximately the same frequency while the number four fish ate first only about eight percent of the time.

DISCUSSION

The object of these experiments was to determine whether differences in food consumption occurred among and within social groups, and, if such differences were found, to study their distribution and possible causes.

In experiment I, isolated females of the lowest weight class exhibited greater variation in worm consumption than those of any other weight class. It has been assumed that in the presence of males, females of this species are pregnant from puberty to death (Schlosberg, Duncan, Daitch, 1949). The high variability in food consumption among smaller female fish may possibly be explained by the presence of pregnant and non-pregnant individuals in the same group, or it may be the result of the mixture of sexually immature with sexually mature fish. Since these same fish, when used in later experiments, did not show such high variability, it appears possible that most of them had then become sexually mature, with the result that the group was more homogeneous in physiological status.

Females as a group tended to show more variability in worm consumption than males. This may seem paradoxical, since males display more obvious social differences which might possibly affect food consumption. However, females

GRAPH E

A Comparison of Least Significant Differences in Worms Consumed by Fish of the Three Hierarchial Positions for Each of the Feeding Periods (Three Fish in Each Aquarium) attain twice the size of males, and the resulting greater range of size or the physiological differences arising from stages of pregnancy or both together, could account for the greater variability.

Groups of females consumed more food than groups of males. It might be expected that the opposite should be the case, since males appear to use more energy than females in fighting for social position. However, certain characteristics of females may account for these results. Females are larger than males, are usually pregnant and are much less aggressive. Perhaps even more important, hierarchies composed of females are more stable than male hierarchies, and it was found fish in stable hierarchies consume more food than those in unstable ones.

Females in groups were much less aggressive toward one another than were males, and seldom interfered with each other's feeding. This may partially explain the higher food consumption among females. Male groups were scenes of battle until definite social hierarchies were formed. Dominant males prevented their subordinates from consuming food during the period of hierarchy formation. In groups containing fish of both sexes males were dominant in approximately 65 percent of the cases, but females ate more. The dominant males seldom interfered with the females' feeding.

In mixed groups males often attempted to impregnate females, and showed little interest in food at such times. The smaller males were the most active in their attempts to mate. The larger males seldom attempted to mate, and in fact, were often the targets of the smaller males' thrusts. This suggests that successful mating usually involves the smaller males.

Innes (1949) cites evidence in which swordtails (Xiphophorus helleri) have changed from females to males during a normal life span. No cases have been noted wherein male fish have become females. Observations in this study, while incomplete, seem to indicate the possibility of the latter trend in P. maculatus.

When food consumption was compared for the four feeding periods in experiments I through IV mixed results were obtained. If social groupings were ignored, the amount of time spent in aquaria showed no significant affect upon number of worms consumed. However, when the analysis took cognisance of dominance-subordination relationships, differences in worms consumed during certain of the feeding periods became evident. When two or three fish were placed together the number of worms consumed during feeding period one was often significantly less than in each of the other three feeding periods.

GRAPH F

A Comparison of Least Significant Differences in Worms Consumed by Fish of the Same Dominance Potential for Each of the Feeding Periods (Four Fish in Each Aquarium)

A combination of social and physical environmental effects may have been responsible for differences in worm consumption between feeding period one and the others. When one fish is placed in an aquarium the individual must become acquainted with the physical environment only, and this single problem does not seem to affect food consumption. However, when two or three fish are placed together and fed, each has to adjust both to the new physical environment and the presence of other individuals. These combined environmental situations, social and physical, evidently affect fish sufficiently to decrease food consumption until the period of adjustment is over. From this standpoint it takes less than 24 hours to complete adjustment to the new situation when two and three fish are placed together. The later feeding periods are characterized by a similar level of food consumption which is greater than that during the first period.

To summarize: The relationship between feeding periods and food consumption was not always consistent. However, when significance occurred, usually the small totals for the first feeding period as compared to the other three were responsible.

Sexual activity and mating behavior possibly initiated the formation of hierarchies and this may account for the differences in stability between the hierarchies of the two sexes. The groups of males that followed individual females at certain times in order to mate must have been aggressive. It follows that the most aggressive males in each group usually mated first and with the greatest frequency (Braddock, 1945). Thus the social character, "aggressiveness" again may be considered a product of selection but in the opposite direction to that mentioned previously, since, in this case the gene frequency of the more aggressive fish would increase. This probably accounts for the greater aggressiveness displayed by males as compared to females.

In the large stock tank three or four small males followed one large female continuously until one, or possibly more, had succeeded in mating with her. The smaller size of the males enabled them to outmaneuver the larger female and succeed in carrying out the mating process with greater ease. Assuming the sexes were originally of equal size, selection could have worked effectively in decreasing the size of the male, since the frequency of successful matings was higher among the small males. The tendency would have been to increase the frequency of the genes for small size in the male population.

One male fish may impregnate many females over a long period of time (Schlosberg, Duncan, and Daitch, 1949). This

GRAPH G

A Comparison of Least Significant Differences in Worms Consumed by Fish of the Four Hierarchial Positions for Each of the Feeding Periods
(Four Fish in Each Aquarium)

causes the lives of females to be more valuable to the population than those of males. Females are also larger than males. In nature this could be an advantage both from the standpoint of protection from dangers of the environment and from the more aggressive males.

In the present experiments there were some social groups in which the positions of fish within the hierarchy could not be distinguished, while there were others, probably more stable, in which the positions were quite evident. The fish within the distinguishable groups ate significantly more than the fish within the indistinguishable groups.

These results resembled those in the study made by Guhl and Allee (1944) on chickens, where settled groups, i.e. groups having members whose social positions were definite, ate more and were in better health than groups in which the social positions were unsettled.

The percentage of indistinguishable groups in this series of experiments was considerably greater than that found by Braddock in his work on P. maculatus (1945, 1949). Presence of food may have been an additional factor that affected fish in their attempts to establish comparative social status. This may have been sufficient to prevent some fish, perhaps those close to one another in dominance potential, from establishing hierarchies that could be distinguished with ease.

DISCUSSION (Part B)

No significant difference in variability of data was noted when comparisons of error terms of smaller groups such as distinguishable, indistinguishable, number one fish, number two fish, etc. were completed. The consistency of the data among the groups discussed above permitted the use of combined analyses of variance for the groups. However, inconsistencies of data noted between sexes and among weight classes in part A (page 27) were operating here, and for experiment III may have been important enough to affect results. It is assumed that the findings of experiment III are basically reliable, but should be interpreted with some reservations, especially in border-line cases (Cochran and Cox, 1950).

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order that more may become known about this particular species and about the social hierarchy which it displays. One of the objectives of studies of the social life of lower organisms is to supply man with the means for eventual understanding of his social systems. It is becoming increasingly evident that social systems did not "just appear"; they have evolved from something less complex.

Caryl P. Haskins in, <u>Of Societies and Men</u>, (1951), states "There are suggestive resemblances between the evolution of human society and that of other social organizations of the world. Some of these resemblances are superficial. Others are deceptive. But many are more than fortuitous. Their significance is the result of parallel evolution, and of the pressure of a basically similar environment upon man, who does not differ fundamentally in his constitution from the rest of the life of the earth."

John Dewey states much the same idea in a different way in <u>Human Nature and Conduct</u>, "A morale based upon study of human nature instead of upon disregard for it would find the facts of man continuous with those of the rest of nature, and would thereby ally ethics with physics and biology. It would find the nature and activity of one person coterminous with those of other human beings,..."

SUMMARY

1. Among fishes tested individually (Experiment I) the smallest females, those in weight class A, exhibited greater variability than those of the other two weight classes; also, more than any class of the males.

2. Females in general were more variable than males.

3. When dominance-subordination relationships were not considered, there was no consistent relationship between feeding periods and worm consumption. However, when social status was considered such a relationship was demonstrated.

4. In analyses involving social status, fish in the first feeding period consumed less than during the other three periods.

5. Fish in groups whose dominance-subordination relationships could be ascertained ate more than those in which this was not the case.

6. Groups of females consumed more food than did groups of males.

7. Hierarchial relationships were most easily distinguished in groups of three individuals and these groups of three fish also ate most.

8. The extent of variation among dominant fishes resembled that of the subordinate ones. The same relationship prevailed when "distinguishable" and "indistinguishable" groupings were compared.

attain twice the size of males, and the resulting greater range of size or the physiological differences arising from stages of pregnancy or both together, could account for the greater variability.

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Sexual activity and mating behavior possibly initiated the formation of hierarchies and this may account for the differences in stability between the hierarchies of the two

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