# SOME ASPECTS OF THE POPULATION DYNAMICS OF ASPIDOGASTRID TREMATODE PARASITES IN OKLAHOMA PELECYPODS 

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Submitted to the Faculty of the Graduate College of the Oklahoma State University in partial fulfillment of the requirements<br>for the Degree of<br>DOCTOR OF EDUCATION<br>December, 1976

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Thesis Approved:


## PREFACE

This study concerns itself with the distribution of the trematodes Aspidogaster conchicola and Cotylapsis insignis, symbionts in the host population of unionid pelecypods in certain freshwater habitats in the eastern half of Oklahoma. A large body of data was accumulated to test a number of hypotheses pertaining to sympatric relationships of the two symbionts and environmental factors that may affect the population dynamics of the aspidogastrid-unionid system. One of the major problems encountered in the course of this study was the widespread collecting sites. Often only one collection was made while water levels were such that made the naiads accessible, without resorting to self-contained underwater breathing apparatus. Often the unpredictability of the presence of certain species made some collections dificient in one species or another. This problem presented difficulty in the interpretation of the statistics of some analyses of variance due to absence of numbers of host naiads in some cells.

The author wishes to express his appreciation to his graduate advisory committe, Dr. Kenneth St. Clair, Dr. James Yelvington, Dr. Kenneth Wiggins, and Dr. L. Herbert Bruneau for their indispensable assistance in the preparation of this manuscript.

I wish to acknowledge the initial inspiration, encouragement, and participation of Dr . Horace H. Bailey in the collection of data and the rudiments of experimental design for this project.

Acknowledgment is due also to Dr . Loren Hill, Director, University
of Oklahoma Biological Station, and Dr. Paul Risser, Director, Oklahoma Biological Survey for financial support and facilities for research.

My junior colleagues during the past five years, Janet Fitzpatrick, Holly Scoville, Carol Conners, Karen Meyers, Judith Starks, James Workman, Dwight 01sen and Pamela Conard are deserving of special appreciation for their long hours on arduous collecting trips and in laboratory work. Their interest and companionship made the study more pleasant than it ordinarily would have been.

I am particularly indebted to Dr . Ronald McNew of the Department of Statistics for his helpful assistance in applying appropriate computer programs to the data and in the interpretation of difficult or obscure relationships.

A note of thanks is due also to Mrs. Edna Paul and Mrs. Kayte Nelson for typing preliminary drafts of the manuscript, and Mrs. Norma Buttress for the preparation of the final draft.

Finally, special gratitude is expressed to my wife, Elsie, my sons, Steven and Joel, and my daughters, Heidi and Marianne, for their encouragement, understanding, and untold sacrifices that made this accomplishment possible.

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## CHAPTER I

## THE RESEARCH PROBLEM

Introduction

The aspidogastrid trematodes parasitize freshwater mollusks and have been so reported in China, North Africa, Central Europe and North America (Dollfus, 1958; Faust, 1922). The primary host species come from the family Unionidae. One aspidogastrid has been reported from several gastropod species (Faust, 1922, Michelson, 1970), although this appears to be a rare occurrence. Even rarer occurrences have been reported from fish (Simer, 1929), a soft-shell turtle (Fulhage, 1954), and a snapping turtle (Rumbold, 1927). Generally it is conceded that infections in animals other than the Unionidae are accidental and transient (VanCleave and Williams, 1943).

Two of the best known aspidogastrids in North America are Aspidogaster conchicola (Von Baer, 1826), and Cotylaspis insignis (Leidy, 1857). The former is clearly an obligate endoparasite inhabiting the pericardial and renal cavities of freshwater naiads. The latter appears to be a facultative ectoparasite that inhabits the mantle cavity in a specific position at the juncture of the ctenidia and visceral mass of the mollusk.

The hypothetical evolutionary position of the Aspidogastrea is quite distinct from that of other trematodes (Williams, 1942). The
ancestral trematode will in all probability be associated with a gastropod mollusk. Since aspidogastrids are usually associated with pelecypods, they are considered to be rather more highly evolved than trematodes. Their relatively simple life cycle involves, as far as it is known, but a single host, the freshwater clam. Stunkard (1917) suggests that since freshwater environments tend to obliterate larval life, Aspidogaster and Cotylaspis both may have secondarily lost the more complex multiple host life cycle found in marine members of the family Aspidogastridae.

Statement of the Problem

A number of authors have reported on the distribution of these symbionts of freshwater mollusks and on selected aspects of the hostparasite relationship. With the exception of Kelly (1899), Flook and Ubelaker (1972), and Nelson, et al (1975), studies relating to the intensity and extensity of infection of these two species in naiads, few data are available regarding the biological and physical parameters which affect their population dynamics either individually or in sympatry. The dearth of existing data makes it impossible to test a number of hypotheses relating to sympatric and environmental relationships. A large body of data is needed to test these hypotheses with any degree of reliability or validity.

Purpose of the Study

The objectives of this investigation are (1) to determine the influences of selected physical and biological factors upon the intensity and extensity of occurrence of Aspidogaster and Cotylaspis within
unionid naiads in certain natural habitats in Oklahoma, (2) to determine the sympatric relationships, if any, of the two parasites with each other, (3) to determine the symbiotic relationships between the parasites and host species, and (4) to determine whether the distribution of these two forms in natural populations of naiads fits the Negative Binomial model. Specifically, the following hypotheses will be tested.

Null Hypotheses

1. The habitat has no effect on the mean intensity of the occurrence of $\underline{A}$. conchicola.
2. The species has no effect on the mean intensity of the occurrence of $\underline{A}$. conchicola.
3. There is no interaction of effects of species and habitat on the mean intensity of occurrence of $\underline{A}$. conchicola.
4. The habitat has no effect on the mean extensity of the occurrence of $\underline{A}$. conchicola.
5. The species has no effect on the mean extensity of the occurrence of $\underline{A}$. conchicola.
6. There is no interaction between the effects of habitat and species on the extensity of the occurrence of $\underline{A}$. conchicola.
7. The habitat has no effect on the mean intensity of the occurrence of $\underline{C}$. insignis.
8. The species of naiad host has no effect on the mean intensity of the occurrence of $\underline{G}$. insignis.
9. There is no interaction between the effects of habitat and host species on the intensity of the occurrence of $\underline{C}$. insignis.
10. The habitat has no effect on the extensity of the accurrence of $\underline{C}$. insignis.
11. The species of naiad host has no effect on the extensity of the occurrence of $\underline{C}$. insignis.
12. There is no interaction between the effects of habitat and host species on the extensity of the occurrence of $\underline{C}$. insignis.
13. There is no correlation between the volume of any individual naiad of the various host species and the intensity of the occurrence of $\underline{A}$. conchicola in the pericardial or renal cavities or both cavities combined.
14. There is no correlation between the volume of any individual naiad of the various host species and the intensity of the occurrence of $C$. insignis in the viscero-ctenidial junction.
15. There is no correlation in any of the various host species between the intensity of the occurrence of $\underline{A}$. conchicola in the pericardial cavity with that in the renal cavity.
16. There is no correlation in any species of host naiad between the intensity of the occurrence of $\underline{A}$. conchicola in the pericardial and renal cavities combined and the intensity of the occurrence of $\underline{C}$. insignis in the viscero-ctenidial junction.
17. In any population of naiads considered, the distribution of A. conchicola among the individual hosts does not fit the Negative Binomial distribution.
18. In any population of naiads considered, the distribution of $\underline{C}$. insignis among the individual hosts does not fit the Negative Binomial distribution.

## Rationale

Parasitism has been defined in many ways. The definitions fall into three main categories: those that state that a parasite injures the host and ultimately causes its death; those that state that a parasite derives benefit from the host but does not kill it; and those that state that there is an equilibrium between individual hosts and their parasites based on evolutionary adaptation which, under ideal conditions, ensures continuity of the relationship by the survival of the unharmed host.

The first two definitions are contradictory. The first is held to be crude and unrefined. The second statement is based on the assumption that if the host is killed, the parasite will not persist. The third definition introduces the specious idea of 'poorly adapted' and 'well adapted' if the existence of parasitic disease and subsequent death of the host are not to be denied.

The qualitative and to some extent the quantitative nature of the definitions cause incongruities. Their most obvious fault is that they are based on relationships between individual hosts and their parasites. The commonly studied physiological adaptations that are most often emphasized are only mechanisms through which individual relationships can be regulated. These facts tend to obscure the fact that parasitism is an ecological relationship that should be expressed quantitatively in terms of populations.

The most important problem with a population approach is to find relevant parameters which will give a quantitative definition. Koztitzin (1934, 1939) and Lotka (1934) emphasized the relationship between host and parasite populations. It appeared to be the lack of refined tech-
niques of fitting distributions at the time that these papers were written that prevented a full development of the quantitative relationships inherent in the ecosystem under consideration. More recently, Milne (1943) considered the frequency distributions of ticks on sheep and found that they were greatly overdispersed. Fisher (1941) had access to Milne's data and showed that the Negative Binomial distribution fully described the data.

Crofton (1970) suggests that the Negative Binomial distribution is a 'fundamental model' of parasitism in so far as it describes the distribution of parasites among hosts. He described six ways that Negative Binomial distributions could originate.

1. As a result of a series of exposures to infection in which each exposure is random but the chance of infection differs at each exposure or wave of infection.
2. As a result of infective stages not being randomly distributed.
3. As a result of infection increasing the chances of further infections occuring.
4. As a result of infection decreasing the chances of further infection (i.e., an immune reaction).
5. As a result of the variation in host individuals which makes the chances of infection unequal. There are morphological differences in host individuals that result from age, habits, rate of development and genetic constitution which can alter the probability of individuals becoming infected.
6. As a result of the chances of infection of individual hosts changing with time, the habits and susceptibility of hosts may change with the passage of time.

With these rudimentary ideas of frequency distributions in mind, it is difficult not to hypothesize that similar host-parasite population dynamics are functioning in the particularly intriguing system that involves the aspidogastrid parasites of unionid pelecypods.

## METHOD AND PROCEDURE

## The Environment

Living naiads were collected in three lentic environments-Oologah Reservoir, Tenkiller Ferry Reservoir and Lake Texoma--and in four lotic environments--Verdigris River, Clear Boggy River, and Blue River. All of these environments are located in the northeast and southeast quadrants of the State of Oklahoma.

For purposes of tabulation, the collecting sites will be abbreviated as follows:

00LO. Oologah Reservoir, Salt Creek Arm, 5 km north of Oologah Dam, Nowata County.

TENK. Tenkiller Ferry Reservoir, 6 km north of Gore, on State Highway 100 at Pine Creek Cove, Sequoyah County.

UOBS. Lake Texoma, University of Oklahoma Biological Station Boat Basin, 2 km east of Willis, Marshall County.

VERD. Verdigris River, 2 km east of Lenapah, Nowata County.
CLBY. Clear Boggy River, 2.5 km east of Boggy Depot Recreation Area, . 1 km upstream from the confluence with Sandy Creek, Atoka County.

PENN. Lake Texoma, Pennington Creek Arm, 2 km south of Murray State College, Tishomingo, Johnson County.

BLD1, BLD2, BLD3. Blue River, 0.4 km north of Armstrong, downstream from Durant Dam 100-600 meters, Bryan County. The multiple designation
was used here to distinguish the data from three different teams of junior colleagues that assisted in the examination of this exceptionally large sample. A $\underline{t}$ test of the differences between the means showed that the samples all came from the same population. This precaution was taken to prevent a sampling bias attributable to an observer from being incorporated into the study.

BLUP. Blue River, 5 km north of Tishomingo at the Blue River Public Recreation Area, Johnson County. This site was distinguished from the other Blue River site because of its contrasting substrate characteristics, being granite rather than limestone and clay, as was the case with all the other collecting sites. In addition, its unionid fauna is distinctly different from that of the previous downstream site.

## Laboratory Procedures

Naiad identification was made during necropsy utilizing a University of Oklahoma Biological Station reference collection prepared by B. D. Valentine, a shell key by Valentine and Stansberry (1971), and a taxonomic key by Eddy and Hodson (1958) requiring the use of internal as well as external characteristics.

Aspidogaster conchicola is found primarily in the pericardial cavity, although it is commonly encountered in the renal cavity, particularly when the intensity of occurrence is high (Kelly, 1899). However, occasionally it may be found also in the branchial tubes, on either the external or internal lamellae (Hendrix and Short, 1965), in the pericardium (Kelly, 1899), and on the foot (Fulhage, 1954).

With this variability in location of the parasites in mind, and because intensity data is desired, the necropsy was designed to consist
of twelve distinct steps, with each carried out in the same sequence for every naiad examined.

Initially, the adductor muscles were severed and the left valve opened; after opening the pericardial cavity, the visible parasites were removed and then the cavity was rinsed with a jet of water under slight pressure. The rinsings were examined later for parasites. The renal cavity was opened, scraped, and rinsed. Following this, the left mantle was lifted and its junction with the external lamella examined and rinsed. A similar research of the internal lamella, visceral mass, foot, right lamellae, labial palps, and mantle was made.

Numbers of each type of parasite recovered from each individual were tabulated. Numbers of Aspidogaster found in the pericardial cavity were distinguished from numbers found in the renal cavity. Additional data from the naiad hosts such as length, width, height (dorsoventral) and volume were recorded and used to determine an index of host age.

Analysis of Data

The data obtained for each individual naiad were entered on coding forms and key punched on tab cards. The accumulated data were analyzed by means of computer software packages called Statistical Analysis System (SAS) (Barr and Goodnight, 1972) and Statistical Package for the Social Sciences (SPSS) (Nie, Bent and Hull, 1970). These two packages were selected because of their availability in the University Computer Center at Oklahoma State University.

The data from 854 naiads was subjected to the following subprograms from each software package.

1. SPSS subprogram FREQUENCIES was used to compute the various
sample mean parasite intensities and their variances. This program was capable of producing a sample mean, standard deviation, variance, standard error, mode, median, kurtosis, skewness, and range of each of eight variables, for each host species from the various collection sites.

The variables selected were four host parameters and four parasite parameters. The host parameters were length, height, width, and volume (VOLU). The parasite parameters were (ASPP) number of Aspidogaster in the pericardial cavity, (ASPR) number of Aspidogaster in the renal cavity, (ASPT) the total number of Aspidogaster in each naiad, and (COTY) the number of Cotylaspis in each host naiad.

In addition, this subprogram produced a histogram and frequency summary table of each of the eight variables.
2. SAS procedure REGRESSION was used to compute an analysis of variance attributable to the two environmental variables habitat (HAB) and location (LOC), the variable of host species (SPE), the variables of parasite intensity (ASPP, ASPR, ASPT, and COTY) and the variables of parasite extensity (EXAP, EXAR, EXAT, and EXCO). Variable EXAP is the percent of host naiads that harbor at least one Aspidogaster in the pericardial cavity. EXAR is the percent of host naiads that harbor at least one Aspidogaster in the renal cavity. EXAT is the percent of host naiads that harbor at least one Aspidogaster in either the pericardial or renal cavity. Variable EXCO is the percent of host naiads that harbor at least one Cotylaspis in the viscero-ctenidial junction.
3. SPSS subprogram PEARSON CORRELATION was used to compute the Pearson product-moment coefficient of correlation ( $\underline{r}$ ) between each of the eight variables, in each host species from the various collection sites.
4. From the several sample means, variances, and numbers of naiads from each species and habitat, a short computer program was written that would calculate $k$ of the Negative Binomial Distribution from the formula;

$$
k=\frac{\bar{x}^{2}}{s^{2}-\bar{x}}
$$

Once the $k$ value of each species was determined, the probability of the occurrence of $n$ parasites in a given host was calculated using the following formulae:

$$
\begin{aligned}
& n=0 \quad P(0)=\frac{k^{k}}{\bar{x}+k} \\
& n=1 \quad P(1)=-\stackrel{\bar{X}}{-} \cdot P(0) \\
& 1 \bar{X}+k \\
& n=2 \quad P(2)=\frac{k+1}{2} \cdot \frac{\bar{X}}{\bar{X}+k} \cdot P(1) \\
& n=3 \quad P(3)=\frac{k+2}{3} \cdot \frac{\bar{x}}{\bar{X}+k} \cdot P(2) \\
& n=4 \quad P(4)=\frac{k+3}{4} \cdot \frac{\bar{x}}{\bar{x}+k} \cdot P(3) \\
& n=5 \quad P(5)=\frac{k+4}{5} \cdot \frac{\bar{X}}{\bar{X}+k} \cdot P(4) \\
& \text { etc. . . }
\end{aligned}
$$

The calculated probabilities were then multiplied by the number of naiads of each species that were collected.

The expected frequency tables generated in this manner were compared with the frequency tables generated by the SPSS subprogram FREQUENCIES. With this data a chi-square statistic was calculated. The chi-square value demonstrates the goodness of fit between the observed parasite frequencies and their expected frequencies if they were indeed distributed according to the Negative Binomial Distribution.

## CHAPTER III

## RESULTS

Eight hundred fifty-four naiads of 22 species were examined for
this study. The species and number collected are the following:
Subfamily: Anodontinae
Anodonta grandis Say, 1829 ..... 95
Anodonta imbicilis Say, 1829 ..... 24
Lasmigona complanata (Barnes, 1823) ..... 9
Subfamily: Ambleminae
Crenodonta costata (Rafinesque, 1820) ..... 19
Amblema plicata (Rafinesque, 1820) ..... 99
Tritogonia verrucosa (Rafinesque, 1820) ..... 66
Fusconaia flava (Rafinesque, 1820) ..... 15
Quadrula quadrula (Rafinesque, 1820) ..... 90
Quadrula pustulosa (Lea, 1828) ..... 35
Pleurobema cordatum (Conrad, 1886) ..... 8
Subfamily: Lampsilinae
Obliquaria reflexa Rafinesque, 1820 ..... 38
Truncilla truncata Rafinesque, 1820 ..... 43
Truncilla donaciformis (Lea, 1828) ..... 6
Leptodea fragilis (Rafinesque 1820) ..... 77
Leptodea laevissima (Lea, 1829) ..... 3
Potamilus purpuratus (Lamark, 1819) ..... 112
Subfamily: Lampsilinae (Continued)
Potamilus alatus (Say, 1817) 11
Lampsilis anodontoides (Lea, 1831) 32
Lampsilis radiata (Barnes, 1823) 33
Lampsilis ovata (Barnes, 1823) 23
Ptychobranchus occidentalis (Conrad, 1886) 7
Obovaria olivaria (Rafinesque, 1820) 3
Descriptive Statistics

The mean parasite intensities and their standard deviations, the parasite extensities and the number of specimens upon which these statistics are based are summarized in Tables I, II, III, IV, and V. Table I summarizes the statistics on $\underline{A}$. conchicola from naiads taken in lotic environments. Table II summarizes the statistics on $\underline{A}$. conchicola from naiads taken in lentic environments. Table III summarizes the statistics on $\underline{C}$. insignis from naiads taken in lotic environments. Table IV summarizes the statistics on $\underline{C}$. insignis from naiads taken in lentic environments. Table $V$ consists of statistics on the two parasites from pooled data from each of the two types of habitats.

The descriptive statistics listed in the first four tables (I-IV) reveal only the barest outline of the relationship hypothesized to be present within them. Several species of naiads $\underline{Q}$. quadrula $\underline{P}$. purpuratus and $\underline{L}$. fragilis are clearly present in both lotic and lentic habitat locations (Table V). Q. quadrula is extensively inhabited by A. conchicola ( $90 \%$ lotic, $82 \%$ lentic) but they are present in low intensities (8.2, 6.5). Cotylaspis insignis inhabits this same species much less

TABLE I
THE EXTENSITY AND INTENSITY OF THE OCCURRENCE OF ASPIDOGASTER CONCHICOLA IN NAIAD SPECIES COLLECTED IN LOTIC HABITATS

| SPECIES | VERD |  | BLUP |  | BLDI |  | BLD2 |  | BLD3 |  | CLBY |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| T. verrucosa | 80\% | 4/5b | 75\% | 3/4 | 86\% | 12/14 | 95\% | 39/41 | 100\% | $2 / 2$ | 100\% | 1/1 |
|  | 5.6c | 5.7d | 1.3 | 1.3 | 7.6 | 5.7 | 8.7 | 7.0 | 13.0 | 5.7 | 2.0 | 0.0 |
| Q. quadrula | 100\% | 2/2 | 33\% | 1/3 | 92\% | 12/13 | 100\% | 13/13 | (0) |  | 90\% | $\begin{aligned} & 9 / 10 \\ & 7.4 \end{aligned}$ |
|  | 4.5 | 2.1 | 0.7 | 1.2 | 5.0 | 6.4 | 10.4 | 6.3 |  |  | 12.3 |  |
|  | (0) |  | 100\% | 2/2 | (0) |  | 87\% | 14/15 | (0) |  | 94\% | 17/18 |
| Q. pustulosa |  |  | 3.0 | 2.8 |  |  | 3.5 | 2.6 |  |  | 2.4 | 1.2 |
|  | (0) |  |  |  | 94\% | 15/16 | 90\% | 18/20 | 50\% | 1/2 | 83\% | 50/60 |
| A. plicata |  |  | (0) |  | 4.4 | 3.1 | 4.0 | 4.3 | 1.5 | 2.1 | 2.8 | 2.6 |
|  |  | 0/1 |  | 0/1 | 25\% | 4/16 | 63\% | 10/16 | (0) |  | (0) |  |
| O. reflexa | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.7 | 0.9 | 0.9 |  |  |  |  |  |
|  | 33\% | 1/3 | 100\% | 1/1 | 100\% | 15/15 | 100\% | 20/20 | (0) |  |  |  |
| P. purpuratus | 6.7 | 4.2 | 16.0 | 0.0 | 28.6 | 32.4 | 28.3 | 23.4 |  |  | (0) |  |
|  | 100\% | 5/5 |  |  | 96\% | 24/25 | 100\% | 10/10 | 100\% | 7/7 | 100\% | 1/1 |
| L. fragilis | 8.0 | 2.0 | (0) |  | 14.6 | 16.1 | 21.9 | 18.6 | 15.7 | 16.5 | 5.0 | 0.0 |
|  | (0) |  |  |  | 27\% | 3/11 | 25\% | 1/4 | 50\% | 1/2 | 31\% | 8/26 |
| T. truncata |  |  | (0) |  | 0.6 | 1.2 | 0.3 | 0.5 | 2.0 | 2.8 | 0.3 | 0.5 |
|  | 100\% | 5/5 | (0) |  | 71\% | 10/14 | 20\% | 2/10 |  |  | 100\% | 2/2 |
| L. anodontoides | 24.0 | 27.6 |  |  | 1.9 | 1.9 | 0.3 | 0.7 |  | (0) | 4.5 | 3.5 |
|  | (0) |  | $\begin{array}{ll}0.0 & 0 / 22 \\ 0.0\end{array}$ |  | (0) |  | 33\% | 4/12 | (0) |  | (0) |  |
| L. radiata |  |  | 1.9 | 4.5 |  |  |  |  |  |  |  |

a. Extensity b. Parasitized naiads/Total naiads c. Sample Mean d. Standard Deviation

TABLE II
THE EXTENSITY AND INTENSITY OF THE OCCURRENCE OF ASPIDOGASTER CONCHICOLA IN NAIAD SPECIES COLLECTED IN LENTIC HABITATS

| SPECIES | TENK |  | 00 LO |  | UOBS |  | PENN |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 41\%a | 7/17b | 74\% | 14/19 | 97\% | 57/59 |  |  |
| Anodonta grandis | 4.1 c | 8.9d | 8.8 | 10.9 | 7.7 | 7.2 |  | (0) |
|  | 20\% | 1/5 | (0) |  | 63\% | 12/19 | (0) |  |
| Anodonta imbicilis | 0.4 | 0.9 |  |  | 3.2 | 5.4 |  |  |
|  |  | 0/6 | 100\% | 3/3 | 91\% | 19/21 | 95\% | 18/19 |
| Quadrula quadrula | 0.0 | 0.0 | 2.0 | 1.0 | 7.7 | 5.9 | 7.9 | 9.3 |
|  | 35\% | 23/65 | 86\% | 6/7 | (0) |  | 100\% | 1/1 |
| Potamilus purpuratus | 3.6 | 10.0 | 21.3 | 21.7 |  |  | 6.0 | 0.0 |
|  | 25\% | 1/4 | 20\% | 1/5 | (0) |  | (0) |  |
| Potamilus alatus | 1.5 |  | 2.8 |  |  |  |  |  |
|  | (0) |  | (0) |  | 90\% | 26/29 | (0) |  |
| Leptodea fragilis |  |  | 6.8 | 10.0 |  |  |  |  |

a. Extensity b. Parasitized naiads/Total naiads c. Sample Mean d. Std. Dev.

TABLE III
THE EXTENSITY AND INTENSITY OF THE OCCURRENCE OF
COTYLASPIS INSIGNIS IN NAIAD SPECIES
COLLECTED IN LOTIC HABITATS

| SPECIES | VERD |  | BLUP |  | BLD1 |  | BLD2 |  | BLD3 |  |  | CLBY |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 40\%a | 2/5b | (0) |  | 50\% | 7/14 | 61\% | 25/41 | (0) |  |  | (0) |  |
| T. verrucosa | 0.6c | 0.9d |  |  | 0.6 | 0.8 | 1.4 | 1.4 |  |  |  |  |  |
|  |  | 0/2 |  | 0/3 |  | $0 / 13$ | 10\% | 4/41 |  |  |  |  | 0/10 |
| Q. quadrula | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.7 |  | (0) |  | 0.0 | 0.0 |
|  | (0) |  |  | $0 / 2$ | (0) |  | 7\% | 1/15 |  |  |  |  | 0/18 |
| Q. pustulosa |  |  | 0.0 | 0.0 |  |  | 0.07 | 0.3 |  | (0) |  | 0.0 | 0.0 |
|  | (0) |  | (0) |  |  | 0/16 |  | 0/20 |  |  | 0/2 | 2\% | 1/60 |
| A. plicata |  |  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |  | 0.0 | 0.02 | 0.1 |  |  |
|  | (0) |  |  |  | (0) |  |  | 0/16 | 6\% | 1/16 | (0) |  |  | (0) |  |
| O. reflexa |  |  | 0.0 | 0.0 |  |  | 0.06 | 0.3 |  |  |  |  |  |  |  |  |  |  |
|  |  | 0/3 | 0.0 | 0/1 | 7\% | 1/15 | 10\% | 2/20 | (0) |  |  | (0) |  |  |  |
| P. purpuratus | 0.0 | 0.0 |  | 0.0 | 0.07 | 0.26 | 0.1 | 0.3 |  |  |  |  |  |  |  |  |  |  |
|  | 80\% | 4/5 | (0) |  | 64\% | 16/25 | 10\% | 1/10 | 29\% |  | 2/7 |  | 0/1 |  |  |
| L. fragilis | 5.0 | 5.2 |  |  | 1.8 | 2.0 | 0.1 | 0.3 | 0.4 |  | 0.8 | 0.0 | 0.0 |  |  |
|  | (0) |  | (0) |  |  | $0 / 17$ |  | 0/4 |  |  | 0/2 |  | 0/26 |  |  |
| I. truncata |  |  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |  | 0.0 | 0.0 | 0.0 |  |  |  |  |
|  | 60\% | 3/5 |  |  | (0) |  | 7\% | 1/14 |  | 0/10 | (0) |  |  |  | 0/2 |
| L. anodontoides | 2.6 | 3.4 | 0.1 | 0.5 |  |  | 0.0 | 0.0 | 0.0 | 0.0 |  |  |  |  |  |  |  |
|  |  | 0/5 | (0) |  |  | 0/4 |  | $0 / 5$ | 100\% |  | 1/7 |  | $0 / 8$ |  |  |
| L. ovata | 0.0 | 0.0 |  |  | 0.0 | 0.0 | 0.0 | 0.0 | 1. |  | 0.0 | 0.0 | 0.0 |  |  |

TABLE IV
THE EXTENSITY AND INTENSITY OF THE OCCURRENCE OF COTYLASPIS INSIGNIS IN NAIAD SPECIES COLLECTED IN LENTIC HABITATS

a. Extensity
b. Parasitized Naiads/Total Naiads
c. Sample Mean
d. Std. Dev.

TABLE V
THE EXTENSITY AND INTENSITY OF THE OCCURRENCE OF EITHER PARASITE IN NAIAD SPECIES THAT INHABIT BOTH LOTIC AND LENTIC HABITATS

|  | A. conchicola |  | C. insignis |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| SPECIES | LOTIC |  | LENTIC |  | LOTIC |  | LENTIC |  |
| Quadrula quadrula | $\begin{aligned} & 90 \% \mathrm{a} \\ & 8.15 \mathrm{c} \end{aligned}$ | $\begin{array}{r} 37 / 41 \mathrm{~b} \\ 7.11 \mathrm{~d} \end{array}$ | $\begin{aligned} & 82 \% \\ & 6.49 \end{aligned}$ | $\begin{array}{r} 40 / 49 \\ 7.39 \end{array}$ | $\begin{aligned} & 10 \% \\ & 0.12 \end{aligned}$ | $\begin{aligned} & 4 / 41 \\ & 0.4 \end{aligned}$ | $\begin{aligned} & 4 \% \\ & 0.041 \end{aligned}$ | $\begin{aligned} & 2 / 49 \\ & 0.042 \end{aligned}$ |
| Potamilus purpuratus | $100 \%$ 26.41 | $\begin{aligned} & 39 / 39 \\ & 26.42 \end{aligned}$ | $44 \%$ 5.28 | $32 / 73$ 12.45 | $8 \%$ 0.08 | $3 / 39$ 0.27 | $\begin{gathered} 16 \% \\ 0.36 \end{gathered}$ | $12 / 73$ 1.06 |
| Leptodea fragilis | $98 \%$ 15.41 | $47 / 48$ 15.85 | $90 \%$ 6.79 | $26 / 29$ 9.97 | $52 \%$ 1.56 | $25 / 48$ 2.53 | 93\% 12.66 | $27 / 29$ 9.03 |

a. Extensity b. Parasitized Naiads/Total Naiads c. Sample Means d. Std. Dev.
extensively ( $10 \%$ lotic, $4 \%$ lentic) and in very low numbers, on the order of 0.12 and .04 parasites per host from each of the two habitats.

Potamilus purpuratus is inhabited by $\underline{A}$. conchicola in every lotic specimen examined and in large numbers per host (26.4). Less than half (44\%) of the lentic specimens were inhabited by $\underline{A}$. conchicola and this was at one-fifth the intensity found in lotic specimens. Cotylaspis insignis is found in $8 \%$ of the lotic specimens and in $16 \%$ of the lentic specimens of $\underline{P}$. purpuratus. Lotic specimens contained on the average only one-fourth the number of parasites found in lentic specimens. This condition is the reverse of that found in Q. quadrula for $\underline{C}$. insignis.

The naiad host L. fragilis contained $\underline{A}$. conchicola $98 \%$ of the time from lotic habitats and $90 \%$ of the time from the single lentic habitat in which they were collected. The difference in intensity between these habitats is on the order of two times the lentic host intensity in lotic hosts. Cotylaspis insignis occurred in $93 \%$ of the naiad hosts of this species that were taken from the UOBS site, the only lentic site from which they were taken. The intensity of the occurrence of $\underline{C}$. insignis in this population was over 10 times that of all the lotic sites combined.

The three host species mentioned above must of necessity form the basis of any analysis of variance that attempts to test the null hypotheses relating to the effects of habitat. The host species Obliquaria reflexa was used in one analysis of variance. Subsequent review of the data from this species reveals that only four specimens were identified in collections from lentic habitats and that among these four specimens there was found but a single specimen of $\underline{A}$. conchicola, a total extensity of $25 \%$ and an intensity of 0.25 worms per host. The lotic specimens of ㅇ. reflexa of which there were 34 , were parasitized by A. conchicola $26 \%$
of the cases and contained on the average 0.6 worms per host. Cotylaspis insignis inhabited this species only once out of the 34 cases ( $3 \%$ ) and then there was only one worm for a mean burden of .03 worms per host naiad. These statistics show that if this species is used in an analysis of variance it will contribute very little to the variance due to species in either habitat for either parasite extensity or intensity.

## Analysis of Variance

The statistics in Table VI were derived from an SAS regression procedure which processed the data by species according to a model statement that designated the number of $\underline{A}$. conchicola in each naiad (ASPT), the number of naiads inhabited by this form (EXAT), the number of C. insignis in each naiad (COTY) and the number of naiads inhabited by this form (EXCO) as dependent variables that are to be with independent variables volume (VOLU), habitat (lotic or lentic) and location within habitat [Location (Hab)].

Most species collected were found in either lotic or lentic habitats. Variance due to habitat in these cases cannot be determined. The species that were collected were found in both habitats and in large enough numbers to satisfy confidence limits. Tests of hypotheses related to the effects and interaction of habitat variance will be limited to these species, Q. quadrula, P. purpuratus and L. fragilis. (Table VII).

Certain other species that were collected in only one location are not included in the tabulation that makes up table VI. The host species omitted were C. costata, L. complanata, E. flava, ․ cordatum, I. donaciformis, L. laevissima, ㄹ. alata, P. occidentalis and $\underline{0}$. olivaria. When effects were noted that showed a 0.015 to 0.05 probability
that they would show a greater F value they were marked with a single asterisk (*). If the effects showed a 0.014 or less probability of a greater $\underline{F}$ value they were marked with a double asterisk (**).

TABLE VI
ANOVA SUMMARY OF MEAN SQUARES OF PARASITE VARIABLES FROM NAIADS COLLECTED IN SEVERAL LOCATIONS

| SPECIES | INDEPENDENT VARIABLES |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \text { DEP } \\ & \text { VAR } \end{aligned}$ | LOCATION <br> (HAB) | D.F. | VOLUME | D.F. | ERROR | D.F. |
| A. grandis | ASPT | 98.00 | 2 | 9.44 | , | 70.00 | 93 |
|  | COTY | 305.00** | 2 | 501.00 | 1 | 53.00 | 93 |
|  | EXAT | 2.62** | 2 | 0.00 | 1 | 0.11 | 93 |
|  | EXCO | 0.42 | 2 | 0.34 | 1 | 0.20 |  |
| A. imbicilis | ASPT | 25.82 | 1 | 212.00** | 1 | 14.83 | 23 |
|  | COTY | 0.97 | 1 | 18.71** | 1 | 4.64 | 23 |
|  | EXAT | 0.02 | 1 | 1.63** | 1 | 0.17 | 23 |
|  | EXCO | 0.14 | 1 | 0.04 | 1 | 0.26 | 23 |
| I. verrucosa | ASPT | 51.00 | 5 | 65.66 | 1 | 41.28 | 66 |
|  | COTY | 1.38 | 5 | 2.28 | 1 | 1.36 | 66 |
|  | EXAT | 0.03 | 5 | 0.03 | 1 | 0.09 | 66 |
|  | EXCO | 0.26 | 5 | 1.26** | 1 | 0.22 | 66 |
| Q. pustulosa | ASPT | 0.25 | 2 | 7.67 | 1 | 4.01 | 34 |
|  | COTY | 0.00 | 2 | 0.01 | 1 | 0.03 | 34 |
|  | EXAT | 0.05 | 2 | 0.04 | 1 | 0.09 | 34 |
|  | EXCO | 0.00 | 2 | 0.01 | 1 | 0.03 | 34 |
| A. plicata | ASPT | 14.34 | 3 | 4.60 | 1 | 9.57 | 98 |
|  | COTY | 0.00 | 3 | 0.00 | 1 | 0.01 | 98 |
|  | EXAT | 0.12 | 3 | 0.00 | 1 | 0.12 | 98 |
|  | EXCO | 0.00 | 3 | 0.00 | 1 | 0.01 | 98 |
| I. truncata | ASPT | 1.45 | 4 | 0.20 | 1 | 0.70 | 47 |
|  | EXAT | 0.06 | 4 | 0.28 | 1 | 0.21 | 47 |
| L. radiata | ASPT | 47.65** | 1 | 21.51 | 1 | 6.58 | 38 |
|  | EXAT | 0.75** | 1 | 0.02 | 1 | 0.09 | 38 |
| L. anodontoides | ASPT | 699.39** | 3 | 68.85 | 1 | 116.97 | 26 |
|  | COTY | 9.14** | 3 | 2.01 | 1 | 1.88 | 26 |
|  | EXAT | 0.96 | 3 | 0.00 | 1 | 0.17 | 26 |
|  | EXCO | 0.48** | 3 | 0.14 | 1 | 0.08 | 26 |

TABLE VI (CONTINUED)

| SPECIES | INDEPENDENT VARIABLES |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \text { DEP } \\ & \text { VAR } \end{aligned}$ | LOCATION <br> (HAB) | D.F. | VOLUME | D.F. | ERROR | D.F. |
| L. ovata | ASPT | 6.85 | 4 | 3.18 | 1 | 13.74 | 16 |
|  | COTY | 0.21** | 4 | 0.00 | 1 | 0.00 | 16 |
|  | EXAT | 0.14 | 4 | 0.00 | 1 | 0.19 | 16 |
|  | EXCO | 0.21** | 4 | 0.00 | 1 | 0.00 | 16 |
| * signific <br> ** signific | t effe | ct at 0.05 ct at 0.01 | prob prob | bility <br> bility |  |  |  |

A review of Table VI reveals that in the cases of L. radiata and L. anodontoides the location within habitat is a significant source of variance that effects the intensity of $\underline{A}$. conchicola (ASPT). The extensity of this form is effected by location within habitat as it relates to A. grandes, ㄴ. radiata and L. anodontoides. The intensity of infection of $\underline{C}$. insignis appears to be related to differences in location within habitat in $\underline{A}$. grandis, ㄴ. anodontoides and L. ovata. The extensity of C. insignis (EXCO) appears to be effected by location within habitat only in L. ovata.

The independent variable volume appears to strongly effect the intensity of C. insignis (COTY) only in A. grandis, A. imbicilis and L. anodontoides. The extensity of this form (EXCO) appears to be effected by volume only in I. verrucosa. The intensity of $\underline{A}$. conchicola (ASPT) and its extensity (EXAT) are seemingly related to volume in $\underline{A}$. imbicilis.

No clear cut trend of effects on the various parasite variables
are evident at this stage of the analysis. The host species themselves are a great source of variance within habitats. It is clearly evident that this is a multivariate system and that results must be interpreted with considerable caution.

Table VII contains a summary of mean squares from an analysis of variance of data from four species of host naiads that were obtained from both lotic and lentic habitats. From this summary it appears that habitat is an important source of variance in two $\underline{C}$. insignis variables (COTY, EXCO) from the species $\underline{P}$. purpuratus and L. fragilis.

Location within habitat appears to have an effect on the extensity and intensity of $\underline{A}$. conchicola (ASPT, EXAT) only in Q. quadrula. This same independent variable is a source of significant variance in the $\underline{C}$. insignis variables of intensity and extensity (COTY, EXCO) in the host species $\underline{Q}$. quadrula, P. purpuratus and L. fragilis.

The independent variable volume effects the $\underline{A}$. conchicola variable of intensity (ASPT) in the host species $\underline{O}$. reflexa and $\underline{P}$. purpuratus.

TABLE VII
ANOVA SUMMARY OF MEAN SQUARES OF PARASITE
VARIABLES FROM NAIAD HOSTS COLLECTED
IN BOTH LOTIC AND LENTIC HABITATS

| SPECIES | DEP |  |  | INDEPENDENT VARIABLES |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | VAR | $\begin{aligned} & \text { HABI- } \\ & \text { TAT } \\ & \hline \end{aligned}$ | DF | $\begin{aligned} & \text { LOCAT } \\ & (\mathrm{HAB}) \end{aligned}$ | DF | VOLUME | DF | ERROR | DF |
| Q. quadrula | ASPT | 28.22 | 1 | 123.69** | 7 | 39.39 | , | 45.79 | 80 |
|  | COTY | 0.03 | 1 | 0.33** | 7 | 0.18 | 1 | 0.07 | 80 |
|  | EXAT | 0.05 | 1 | 0.60** | 7 | 0.30* | 1 | 0.06 | 80 |
|  | EXCO | 0.05 | 1 | 0.27** | 7 | 0.16* | I | 0.04 | 80 |

TABLE VII (CONTINUED)

|  | DEP |  |  | INDEPEND | DENT | VARIABLES |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| SPECIES | VAR | $\begin{aligned} & \text { HABI- } \\ & \text { TAT } \\ & \hline \end{aligned}$ | DF | $\begin{aligned} & \text { LOCAT } \\ & \text { (HAB) } \end{aligned}$ | DF | VOLUME | DF | ERROR | DF |
| O. reflexa | ASPT | 0.49 | 1 | 0.16 | 4 | 2.93* | 1 | 0.56 | 31 |
|  | COTY | 0.00 | 1 | 0.00 | 4 | 0.02 | 1 | 0.03 | 31 |
|  | EXAT | 0.01 | 1 | 0.23 | 4 | 0.12 | 1 | 0.24 | 31 |
|  | EXCO | 0.00 | 1 | 0.00 | 4 | 0.02 | 1 | 0.03 | 31 |
| P. purpuratus | ASPT | 77.10 | 1 | 559.20 | 5 | 3732.00** | 1 | 293.75 | 104 |
|  | COTY | 8.77** | 1 | 6.32** | 5 | 0.03 | 1 | 0.49 | 104 |
|  | EXAT | 0.15 | 1 | 0.29 | 5 | 0.80** | 1 | 0.14 | 104 |
|  | EXCO | 1.67** | 1 | 0.83** | 5 | 0.01 | 1 | 0.09 | 104 |
| L. fragilis | ASPT | 467.12 | 1 | 215.84 | 4 | 51.65 | 1 | 196.07 | 76 |
|  | COTY | 807.77** | 1 | 66.12* | 4 | 626.50** | 1 | 26.65 | 76 |
|  | EXAT | 0.17 | 1 | 0.03 | 4 | 0.18 | 1 | 0.05 | 76 |
|  | EXCO | 2.54** | 1 | 0.56** | 4 | 0.47 | 1 | 0.15 | 76 |

*Significant effect at 0.05 probability.
**Significant effect at 0.01 probability.

This variable effects the extensity of $\underline{A}$. conchicola (EXAT) in both $\underline{Q}$. quadrula and $\underline{P}$. purpuratus. The variable volume exerts a significant effect on the intensity of $\underline{C}$. insignis (COTY) only in L. fragilis. The extensity of this form (EXCO) is effected by volume only in Q. quadrula.

The preceding analyses of variance were based on a number of cells without data as can be seen by reexamining Tables I, II, III and IV. In order to avoid the problem of the null cell the data from $\underline{L}$. fragilis, O. reflexa, ․ purpurata and Q. quadrula from selected locations that would circumvent the empty cell where pooled and subjected to an SAS regression procedure designed to effect an analysis of variance. A model was set up that had the usual four parasite variables as the dependent variables with the variables of host species, location, the
interaction between location and species and volume as the independent variables. Table VIII is a summary of the mean squares of the parasite variables resulting from this analysis of variance.

## TABLE VIII

> ANOVA SUMMARY OF MEAN SQUARES OF PARASITE VARIABLES FROM FOUR HOST SPECIES FROM THREE LOTIC LOCATIONS

|  | DF | ASPT | COTY | EXAT | EXCO |
| :--- | :---: | :---: | :---: | :--- | :--- |
| SOURCE |  |  |  |  |  |
| LOCATION | 2 | 551.54 | 4.71 | $0.27^{*}$ | 0.03 |
| SPECIES | 3 | 328.49 | $28.34 * *$ | $0.99 * *$ | $1.02 * *$ |
| LOC*SPE | 6 | 216.25 | $8.54 * *$ | 0.13 | $0.52 * *$ |
| VOLUME | 126 | $1661.89 *$ | 3.75 | 0.04 | 0.03 |
| ERROR |  |  |  |  |  |
|  |  |  |  |  | 0.11 |

[^0]** Significant effect at 0.01 probability.

## Coefficients of Correlation

The computer output from SPSS subprogram Pearson Correlation was used to develop Tables IX through XXI. The variable (VOLU) was selected over the variables length, width, and height as an indication of the age of the naiad, because the computer output revealed a more consistent degree of correlation than the other three variables.

Ten species which were collected in the largest numbers and in the most varied locations were selected to illustrate the correlation between four parasite intensity variables and volume. The intensity
of A. conchicola in the pericardial cavity (ASPP), in the renal cavity (ASPR), and in the pericardial cavity combined (ASPT) are the first three variables in each table. The last variable (COTY) is the intensity of C. insignis on the visceroctenidial junction. Each of the coefficients of correlation recorded was checked against partial correlations generated in the SAS subprogram Regression to ascertain that the apparent correlation was not due to marked differences in volume means of naiads among collection sites.

PEARSON r BETWEEN VOLUME AND PARASITE VARIĀBLES IN ANODANTA GRANDIS

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :---: | :---: | :---: | :---: | :---: |
| Tenkiller Res. | 0.153 a | ------ | 0.153 | 0.623** |
| $\mathrm{N}=17$ | 0.558 b | -- | 0.558 | 0.008 |
| Oologah Res. | 0.150 | 0.113 | 0.153 | 0.253 |
| $\mathrm{N}=19$ | 0.540 | 0.645 | 0.531 | 0.296 |
| UOBS Dock | -0.155 | 0.0278 | -0.133 | 0.290* |
| $N=59$ | 0.241 | 0.834 | 0.315 | 0.026 |
| All locations | -0.001 | 0.183 | 0.047 | 0.148 |
| $N=95$ | 0.990 | 0.075 | 0.692 | 0.152 |

a. Pearson $\underline{r}$ b. Probability of greater $\underline{r}$

* Significan $\bar{t}$ at 0.05 ** Significant at 0.01

A significant correlation appears between volume and the intensity of infection by $\mathbb{C}$. insignis (COTY) in two of the three locations where $\underline{A}$. grandis was collected. This correlation does not persist when the data were pooled.

TABLE X
PEARSON $r$ BETWEEN VOLUME AND PARASITE
VARIABLES IN TRITOGONIA VERRUCOSA

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :--- | :--- | :--- | :--- | :--- |
|  |  | a | -0.025 |  |
| $N=5$ | 0.962 | b | 0.968 | 0.357 |
| Blue River 1 | 0.076 | 0.117 | 0.980 | 0.555 |
| $N=14$ | 0.795 | 0.689 | 0.724 | 0.442 |

TABLE X (CONTINUED)

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :--- | :--- | :--- | :--- | :--- |
|  |  |  |  |  |
| Blue River 2 | 0.235 | -0.027 | 0.189 | 0.115 |
| $N=41$ | 0.138 | 0.863 | 0.235 | 0.470 |
| A11 Locations | 0.234 | 0.035 | 0.209 | $0.324 * *$ |
| $N=67$ | 0.056 | 0.779 | 0.089 | $0.007^{* *}$ |
| a. Pearson $r$ |  |  |  |  |
| $* *$ Significant at 0.01 | b. Probability of a greater $\underline{r}$ |  |  |  |

In the data from I. verrucosa there is no correlation of any significance between volume and any parasite variable until all data are pooled, then a significant correlation for COTY occurs.

TABLE XI
PEARSON r BETWEEN VOLUME AND PARASITE VART $\bar{I} A B L E S$ IN AMBLEMA PLICATA

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :---: | :---: | :---: | :---: | :---: |
| Blue River 7 | -0.129 a | 0.248 | 0.019 | ----- |
| $N=16$ | 0.633 b | 0.353 | 0.944 | ----- |
| Blue River 2 | -0.183 | 0.342 | -0.092 | ----- |
| $N=20$ | 0.438 | 0.139 | 0.699 | ----- |
| Clear Boggy | -0.097 | -0.008 | -0.070 | 0.113 |
| $\mathrm{N}=60$. | 0.460 | 0.948 | 0.591 | 0.386 |
| A11 Lotic |  |  |  |  |
| Locations | -0.201* | 0.112 | -0.1109 | 0.073 |
| $N=98$ | 0.047 | 0.272 | 0.277 | 0.470 |
| $\begin{aligned} & \text { Pearson } \frac{r}{} \\ & \text { Significant } \end{aligned}$ | b. Probability of a greater $\underline{r}^{\text {. }}$ |  |  |  |

Only one significant correlation appears in these data and this one is a negative correlation. This means that as volume increases the intensity of infection by $\underline{A}$. conchicola in the pericardium decreases. This trend develops significance only after the data from three locations were pooled. It is interesting to note that this trend of negative correlation is evident in each location where $\underline{A}$. plicata was collected.

TABLE XII
PEARSON r BETWEEN VOLUME AND PARASITE VARI $\bar{A} B L E S$ IN QUADRULA QUADRULA

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :---: | :---: | :---: | :---: | :---: |
| Tenkiller | -- | - | ---- | ---- |
| $N=6$ | -- | ---- | ---- | ---- |
| Verdigris | --- | ---- | ---- | ---- |
| $\mathrm{N}=2$ | ---- | ---- | ---- | ---- |
| Oologah | -0.189 a | -0.500 | -0.866 | -1.000** |
| $\mathrm{N}=3$ | 0.879 b | 0.667 | 0.333 | 0.001 |
| Blue River p | -0.970 | -0.970 | -0.970 | ---- |
| $\mathrm{N}=3$ | 0.154 | 0.154 | 0.154 | ---- |
| B7ue River 1 | -0.478 | 0.132 | -0.367 | ---- |
| $\mathrm{N}=13$ | 0.098 | 0.666 | 0.216 | ---- |
| Blue River 2 | -0.056 | -0.026 | -0.059 | -0.253 |
| $N=13$ | 0.854 | 0.932 | 0.847 | 0.403 |
| UOBS Dock | 0.196 | 0.659** | 0.360 | -- |
| $N=21$ | 0.394 | 0.001 | 0.108 | ---- |
| Pennington | 0.272 | 0.406 | 0.356 | ---- |
| $N=19$ | 0.259 | 0.085 | 0.134 | ---- |
| Clear Boggy | -0.459 | 0.261 | -0.229 | ---- |
| $N=10$ | 0.182 | 0.465 | 0.524 | ---- |
| A | -0.412** | 0.039 | -0.317* | -0.256 |
| $N=41$ | 0.007 | 0.806 | 0.043 | 0.105 |
| A | 0.331* | 0.466** | 0.420** | -0.291* |
| $\mathrm{N}=49$ | 0.020 | 0.001 | 0.003 | 0.042 |
| Al1 Locations | 0.088 | 0.272** | 0.167 | -0.222* |
| $\mathrm{N}=90$ | 0.408 | 0.010 | 0.115 | 0.036 |
| Pearson $r$ Significant | b. Probability of a greater $\underline{r}$ ** Significant at 0.01 |  |  |  |

The apparently missing data in this table is due to the fact that the specimens from Tenkiller Reservoir were not found to be inhabited by either parasite (Tables II, IV). In the Verdigris River collection the parasite $\underline{A}$. conchicola was found only in the pericardium of the two specimens examined (Tables I, III). The remaining missing correlations in the column COTY are due to the fact that no $\underline{C}$. insignis were found in specimens of $\underline{Q}$. quadrula from these locations (Tables III, IV).

A contrasting correlation is evident between pooled lotic and lentic data. The correlation is negative in lotic collections and positive in lentic collections for $A$. conchicola. The correlation appears to be negative each instance for $\underline{C}$. insignis. The number of Q. quadrula inhabited by the latter form is quite small (16/90) and this fact may render this statistic of doubtful value.

The correlations between the various parasite variables and the host variable volume of $\underline{P}$. purpuratus are summarized in Table XIII. The only correlations of interest are those for $\underline{A}$. conchicola in host naiads from Oologah Reservoir. By the time all the data are pooled into lotic and lentic locations the pattern of correlation between volume and $\underline{A}$. conchicola variables are clearly positive. The variable COTY shows a weak trend toward negative correlation.

TABLE XIII
PEARSON r BETWEEN VOLUME AND PARASITE VARIABLES IN POTAMILUS PURPURATUS

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :---: | :---: | :---: | :---: | :---: |
| Tenkiller | 0.228 a | -- | 0.228 | 0.121 |
| $\mathrm{N}=65$ | 0.068 b | ---- | 0.068 | 0.335 |
| Verdigris | 0.348 | 0.0826 | 0.993 | ---- |
| $\mathrm{N}=3$ | 0.774 | 0.381 | 0.072 | ---- |
| 0ologah | 0.805* | 0.809* | 0.834* | -0.127 |
| $N=7$ | 0.029 | 0.027 | 0.020* | 0.785 |
| B7ue River 7 | 0.278 | 0.232 | 0.284 | -0.535* |
| $\mathrm{N}=15$ | 0.315 | 0.404 | 0.304 | 0.040 |
| Blue River 2 | 0.225 | 0.722** | 0.363 | 0.011 |
| $\mathrm{N}=20$ | 0.340 | 0.001 | 0.115 | 0.963 |
| Al1 Lotic | 0.259 | 0.476** | 0.333* | -0.130 |
| $\mathrm{N}=39$ | 0.111 | 0.002 | 0.038* | 0.427 |
| All Lentic | $0.326^{* *}$ | $0.327^{* *}$ | 0.354** | 0.206 |
| $\mathrm{N}=77$ | 0.005 | 0.005 | 0.002 | 0.080 |
| Pearson $r$ Significan $\bar{t}$ at 0.050 | $\begin{aligned} & \text { b. Prob } \\ & * * \text { Signi } \end{aligned}$ | $\begin{aligned} & \text { lity of a } \\ & \text { ant at } 0 \text {. } \end{aligned}$ | $\begin{aligned} & \text { reater } \underline{r} \\ & 0 \text {. } \end{aligned}$ |  |

TABLE XIV
PEARSON r BETWEEN VOLUME AND PARASITE
VARIAB̄̄ES IN OBLIQUARIA REFLEXA

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :---: | :---: | :---: | :---: | :---: |
| Tenkiller | -0.500 a | ---- | -0.500 | ---- |
| $\mathrm{N}=3$ | 0.667 b | ---- | 0.667 | ---- |
| Blue River 1 | 0.632** | 0.000 | 0.508* | ---- |
| $\mathrm{N}=16$ | 0.009 | 1.000 | 0.045 | -- |
| Al1 Lotic Locations | 0.501** | 0.0773 | 0.489** | 0.210 |
| $\mathrm{N}=34$ | 0.003 | 0.664 | 0.003 | 0.233 |
| Al1 Lentic Locations | -0.382 | ---- | -0.384 | ---- |
| $N=38$ | 0.618 | ---- | 0.618 | --- |
| All Locations | 0.403** | 0.163 | 0.443** | 0.195 |
| $\mathrm{N}=38$ | 0.012 | 0.328 | 0.005 | 0.239 |

a. Pearson $r$ b. Probability of a greater $\underline{r}$

* Significan $\bar{t}$ at 0.05 ** Significant at 0.01 .

In locations where number of naiads was the largest a distinct positive correlation between volume and the $\underline{A}$. conchicola variables can be noted. By the time the data from all locations are pooled this correlation is distinctly significant. No such correlation with volume of host naiad is evident in the $\underline{C}$. insignis variable.

TABLE XV
PEARSON r BETWEEN VOLUME AND PARASITE
IN LAMPSILIS ANODONTOIDES

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :--- | ---: | ---: | ---: | ---: |
|  |  |  |  |  |
| Verdigris R. | 0.607 a | 0.107 | 0.597 | 0.553 |
| $N=5$ | 0.277 | b | 0.864 | 0.287 |
| B7ue River 1 | -0.371 | 0.447 | -0.195 | 0.333 |
| $N=14$ | 0.197 | 0.109 | 0.503 | 0.834 |
| B7ue River 2 | 0.065 | -0.173 | -0.040 | --- |
| $N=10$ | 0.858 | 0.632 | 0.911 | ---- |
| A11 Lotic Locations | -0.180 | 0.043 | -0.160 | -0.135 |
| $\mathrm{~N}=31$ | 0.333 | 0.816 | 0.390 | 0.466 |

a. Pearson $\underline{r}$. b. Probability of a greater $\underline{r}$.

TABLE XVI
PEARSON r BETWEEN VOLUME AND PARASITE VARIĀBLES IN LAMPSILIS RADIATA


TABLE XVII
PEARSON $r$ BETWEEN VOLUME AND PARASITE VAR $\bar{I} A B L E S$ IN LAMPSILIS OVATA

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :---: | :---: | :---: | :---: | :---: |
| Verdigris R. | - | 0.557 | 0.557 | ---- |
| $N=5$ | ---- | 0.329 | 0.329 | ---- |
| B7ue River 1 | ---- | -- | ---- | ---- |
| $\mathrm{N}=4$ | ---- | --- | ---- | ---- |
| Blue River 2 | 0.460 | -0.497 | 0.192 | ---- |
| $N=5$ | 0.435 | 0.394 | 0.757 | ---- |
| Clear Boggy R. | 0.137 | 0.063 | 0.133 | ---- |
| $\mathrm{N}=8$ | 0.746 | 0.881 | 0.752 | ---- |
| All Locations | 0.186 | 0.038 | 0.157 | -0.314 |
| $\mathrm{N}=23$ | 0.393 | 0.863 | 0.474 | 0.145 |

a. Pearson r. b. Probability of a greater $\underline{r}$.

TABLE XVIII
PEARSON $r$ BETWEEN VOLUME AND PARASITE IN LEPTODEA FRAGILIS

| LOCATION | ASPP | ASPR | ASPT | COTY |
| :---: | :---: | :---: | :---: | :---: |
| Verdigris R. | 0.204 | -0.343 | -0.391 | 0.839 |
| $N=5$ | 0.742 | 0.572 | 0.515 | 0.076 |
| B7ue River 1 | -0.132 | 0.104 | -0.067 | 0.366 |
| $N=25$ | 0.528 | 0.618 | 0.747 | 0.072 |
| B7ue River 2 | 0.299 | 0.672* | 0.386 | -0.128 |
| $\mathrm{N}=10$ | 0.401 | 0.033 | 0.270 | 0.724 |
| UOBS Dock |  |  |  |  |
| (A11 Lentic) | 0.233 | 0.201 | 0.271 | 0.587** |
| $\mathrm{N}=29$ | 0.223 | 0.295 | 0.155 | 0.001 |
| B7ue River 3 | -0.231 | -0.376 | -0.274 | 0.427 |
| $\mathrm{N}=7$ | 0.617 | 0.405 | 0.552 | 0.339 |
| A11 Lotic | -0.097 | 0.032 | -0.074 | 0.266 |
| $\mathrm{N}=48$ | 0.508 | 0.829 | 0.615 | 0.067 |
| AT1 | -0.013 | 0.075 | 0.007 | $0.343 * *$ |
| $N=77$ | 0.911 | 0.513 | 0.952 | 0.002 |
| $\begin{aligned} & \text { Pearson } \frac{r}{} \text { Significant at } \end{aligned}$ | b. Probability of a greater <br> ** Significant at 0.01 |  |  |  |

In the host species $\underline{L}$. fragilis only the $\underline{C}$. insignis variable shows a significant correlation with host volume. This species harbored the largest mean number of $\underline{C}$. insignis per host of all species, 12.6 worms per naiad in the only lentic environment in which this host species was taken. None of the lotic environments produced a sample mean of more than 5.0 worms per naiad.

TABLE XIX
PEARSON r BETWEEN PERICARDIAL AND RENAL INTENSITTIES OF ASPIDOCASTER CONCHICOLA

| SPECIES | LOCATION | $r$ | $N$ | $p>r$ |
| :---: | :---: | :---: | :---: | :---: |
| A. grandis | Tenkiller Res. | ---- | 17 | ----- |
|  | Oologah Res. | 0.585** | 19 | 0.008 |
|  | Lake Texoma | 0.193 | 59 | 0.142 |
|  | A11 Lentic | 0.299** | 95 | 0.003 |
| I. verrucosa | Verdigris R. | 0.508 | 5 | 0.381 |
|  | Blue R. 1 | 0.379 | 14 | 0.181 |
|  | Blue R. 2 | 0.202 | 41 | 0.204 |
|  | Al1 Lotic | 0.269* | 67 | 0.027 |
| Q. quadrula | Tenkiller Res. | -- | 6 | ----- |
|  | Oologah Res. | -0.755 | 3 | 0.454 |
|  | Blue R. Up | 1.000** | 3 | 0.001 |
|  | Blue R. 1 | 0.127 | 13 | 0.679 |
|  | Blue R. 2 | 0.143 | 13 | 0.640 |
|  | Clear Boggy R. | 0.275 | 10 | 0.441 |
|  | Lake Texoma (UOBS) | 0.313 | 21 | 0.166 |
|  | Lake Texoma (PENN) | 0.199 | 19 | 0.414 |
|  | Al1 Lotic | 0.280 | 41 | 0.076 |
|  | All Lentic | 0.320* | 49 | 0.025 |
|  | All Locations | 0.300 | 90 | 0.004 |
| A. plicata | Blue R. 1 | 0.237 | 16 | 0.376 |
|  | Blue R. 2 | 0.391 | 20 | 0.088 |
|  | Clear Boggy R. | 0.194 | 60 | 0.137 |
|  | Al1 Lotic | 0.164 | 98 | 0.106 |

TABLE XIX (CONTINUED)

| SPECIES | LOCATION | $\underline{r}$ | N | $\mathrm{P}>\mathrm{r}$ |
| :---: | :---: | :---: | :---: | :---: |
| A. plicata | Blue R. 1 | 0.237 | 16 | 0.376 |
|  | Blue R. 2 | 0.391 | 20 | 0.088 |
|  | Clear Boggy R. | 0.194 | 60 | 0.137 |
|  | All Lotic | 0.164 | 98 | 0.106 |
| 0. reflexa | Blue R. 1 | 0.169 | 16 | 0.531 |
|  | Blue R. 2 | -0.282 | 16 | 0.288 |
|  | All Lotic | -0.067 | 34 | 0.704 |
|  | All Locations | -0.055 | 38 | 0.739 |
| P. purpuratus | Verdigris R. | -0.240 | 3 | 0.846 |
|  | Blue R. 1 | 0.676** | 15 | 0.006 |
|  | Blue R. 2 | 0.417 | 20 | 0.067 |
|  | Tenkiller Res. | ---- | 65 | ---- |
|  | Oologah Res. | 0.842** | 7 | 0.017 |
|  | All Lotic | 0.536** | 39 | 0.001 |
|  | All Lentic | 0.482** | 73 | 0.001 |
|  | All Locations | 0.622** | 112 | 0.001 |
| L. fragilis | Verdigris R. | -0.093 | 5 | 0.881 |
|  | Blue R. 1 | 0.749** | 25 | 0.001 |
|  | Blue R. 2 | 0.258 | 10 | 0.471 |
|  | Blue R. 3 | 0.615 | 7 | 0.141 |
|  | Lake Texoma (UOBS) | 0.118 | 29 | 0.541 |
|  | All Lotic | 0.561** | 48 | 0.001 |
|  | All Lentic | 0.118 | 29 | 0.541 |
|  | All Locations | 0.469** | 77 | 0.001 |
| L. anodontoides | Verdigris R. | 0.269 | 5 | 0.661 |
|  | Blue R. 1 | 0.028 | 14 | 0.923 |
|  | Blue R. 2 | 0.666* | 10 | 0.035 |
|  | All Lotic | 0.496** | 31 | 0.004 |
| L. radiata |  |  | 21 |  |
|  | Blue R. 2 | $0.799 \star *$ | 12 | 0.001 |
|  | All Lotic | 0.820** | 33 | 0.001 |
| L. ovata | Verdigris R. Blue R. 1 | ----- | 5 | ----- |
|  | Blue R. 2 | 0.372 | 5 | 0.537 |
|  | Clear Boggy R. | 0.305 | 8 | 0.461 |
|  | All Lotic | 0.351 | 23 | 0.100 |

TABLE XIX (CONTINUED)


TABLE XX (CONTINUED)

| SPECIES | LOCATION | $\underline{r}$ | N | $p>r$ |
| :---: | :---: | :---: | :---: | :---: |
| A. plicata | Blue R. 1 | ---- | 16 | ---- |
|  | Blue R. 2 | ---- | 20 |  |
|  | Clear Boggy R. | 0.262* | 60 | 0.043 |
|  | All Lotic | 0.153 | 98 | 0.131 |
| 0. reflexa | Blue R. 1 | ---- | 16 | ---- |
|  | Blue R. 2 | 0.037 | 16 | 0.890 |
|  | All Lotic | 0.088 | 34 | 0.618 |
|  | All Locations | 0.093 | 38 | 0.576 |
| P. purpuratus | Verdigris R. | ---- | 3 | ---- |
|  | Blue R. 1 | 0.063 | 15 | 0.823 |
|  | Blue R. 2 | -0.223 | 20 | 0.344 |
|  | Tenkiller Res. | 0.047 | 65 | 0.709 |
|  | Oologah Res. | -0.147 | 7 | 0.753 |
|  | All Lotic | -0.063 | 39 | 0.701 |
|  | All Lentic | 0.221 | 73 | 0.059 |
|  | All Locations | 0.021 | 112 | 0.825 |
| L. fragilis | Verdigris R. | -0.649 | 5 | 0.236 |
|  | Blue R. 1 | 0.007 | 25 | 0.973 |
|  | Blue R. 2 | -0.092 | 10 | 0.799 |
|  | Blue R. 3 | -0.245 | 7 | 0.596 |
|  | Lake Texoma (UOBS) | 0.325 | 29 | 0.085 |
|  | All Lotic | -0.137 | 48 | 0.352 |
|  | A11 Lentic | 0.325 | 29 | 0.085 |
|  | All Locations | -0.133 | 77 | 0.247 |
| L. anodontoides | Verdigris R. | 0.540 | 5 | 0.347 |
|  | Blue R. 1 | -0.279 | 14 | 0.334 |
|  | Blue R. 2 | ---- | 10 | ---- |
|  | All Lotic | 0.688** | 31 | 0.001 |
| L. radiata | Blue R. UP | - | 21 | ---- |
|  | Blue R. 2 | - | 12 | ---- |
|  | A11 Lotic | ---- | 33 | ---- |
| L. ovata | Verdigris R. | -- | 5 | ---- |
|  | Blue R. 1 | ---- | 4 | ---- |
|  | Blue R. 2 | ---- | 5 | ---- |
|  | Clear Boggy R. | ---- | 8 | ---- |
|  | Al1 Lotic | -0.089 | 23 | 0.686 |

TABLE XX (CONTINUED)

| SPECIES | LOCATION | $\underline{r}$ | $N$ | $P>r$ |
| :---: | :---: | :---: | :---: | :---: |
| Combined species | All Lotic | 0.146** | 556 | 0.001 |
|  | Al1 Lentic | 0.237** | 298 | 0.001 |
|  | All Locations | 0.131** | 854 | 0.001 |

Fitting the Negative Binomial Distribution

In order to illustrate the chi-square goodness of fit test of the observed parasite frequencies of parasite number and their expected frequency on the basis of the formulae presented on p. 12, 21 tables were constructed (Tables XXII to XLIII, Appendix A). The chi-square, degrees of freedom and critical value of chi-square at the 0.05 probability level from each of these tables are summarized in Tables IX and $X$.

Only eight of the twenty-two species of naiads collected were used to demonstrate the existence of the negative binomial distribution of Aspidogaster conchicola among various sample populations. The eight species chosen were those collected in largest numbers, and in some instances, species that were collected in both lotic and lentic habitats (Table IX).

Six species of host naiad were used to demonstrate that $\underline{C}$. insignis is distributed also after the negative binomial. Species were selected that were collected in fairly large numbers and that were collected in fairly large numbers and that were collected in both lotic and lentic habitats (Table X).

TABLE XXI

## FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN EIGHT NAIADS FROM VARIOUS LOCATIONS

| SPECIES | N | d.f. | Chi-square | critical value |
| :--- | ---: | :---: | :---: | :---: |
| A. grandis (all) | 95 | 12 | 10.07 | 21.03 |
| I. verrucosa (all) | 67 | 11 | 7.47 | 19.68 |
| A. plicata (all) | 98 | 9 | 6.06 | 16.92 |
| P. purpuratus (lotic) | 39 | 7 | 4.01 | 14.07 |
| P. purpuratus (lentic) | 73 | 6 | 3.16 | 12.59 |
| P. purpuratus (all) | 112 | 13 | 19.57 | 22.36 |
| A. imbicilis (all) | 24 | 4 | 2.47 | 9.49 |
| Q. quadrula (lotic) | 41 | 11 | 5.39 | 19.68 |
| Q. quadrula (lentic) | 49 | 12 | 15.85 | 21.03 |
| Q. quadrula (all) | 90 | 13 | 11.14 | 22.36 |
| L. fragilis (lotic) | 48 | 9 | 5.94 | 16.92 |
| L. fragilis (lentic) | 29 | 5 | 10.05 | 11.07 |
| L. fragilis (all) | 77 | 13 | 13.25 | 22.36 |
| O. reflexa (lotic) | 34 | 4 | 5.34 | 9.49 |

Table XXI is derived from Tables XXII-XXIV in Appendix A. Of particular interest is the fact that none of the chi-square values exceeds the critical value given from a table of chi-square at the 0.05 probability level. This observation is clearly indicative of the fact that there appears to be a good fit between the observed and expected frequencies of hosts harboring a given number of parasites.

TABLE XXII
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INSIGNIS IN SIX NAIAD SPECIES FROM VARIOUS LOCATIONS

| SPECIES | $N$ | d.f. | chi-square | critical value |
| :--- | :---: | :---: | :---: | :---: |
| A. grandis (all) | 95 | 9 | $31.74^{*}$ | 16.92 |
| I. verrucosa (al1) | 67 | 4 | 5.20 | 6.49 |
| Q. quadrula (lotic) | 41 | 2 | 0.39 | 5.99 |
| Q. quadrula (lentic) | 49 | 1 | 0.00 | 3.84 |
| Q. quadrula (a11) | 90 | 2 | 0.23 | 5.99 |
| P. purpuratus (lotic) | 39 | 7 | 6.88 | 14.07 |
| P. purpuratus (lentic) | 73 | 7 | 6.28 | 14.07 |
| P. purpuratus (all) | 112 | 7 | 7.34 | 14.07 |
| L. fragilis (lotic) | 48 | 5 | 0.89 | 11.07 |
| L. fragilis (lentic) | 29 | 10 | $21.17 *$ | 18.31 |
| L. fragilis (all) | 77 | 10 | 12.26 | 18.31 |
| A. imbicilis (all) | 24 | 3 | 0.26 | 7.82 |
| * chi-square exceeds critical value. |  |  |  |  |

This table is derived from Tables XXXV-XLV in Appendix A. The fit between observed and expected frequencies of host harboring $\mathbb{C}$. insignis breaks down in the case of $\underline{A}$. grandis a lentic species and in the lentic location from which L. fragilis was collected. Otherwise the fit is remarkably good.

## CHAPTER IV

## CONCLUSIONS AND SUMMARY

The assumption underlying the null hypotheses stated at the beginning of the paper was that all the naiads in Oklahoma were essentially one large population. Since all the streams flow eventually into the Mississippi River, they are all interconnected, and a sample of naiads from the Verdigris River in northeastern Oklahoma will give the same estimate of the mean of the parasite subpopulation as a sample taken from the Blue River in southeastern Oklahoma. Even the lentic waters of Oklahoma are all artificial impoundments of the various streams. A sample of naiads from Lake Texoma should give as good a sample of the parasite intensity as a sample from Tenkiller Reservoir.

## Lotic and Lentic Comparisons

A casual perusal of the data in Tables, I, II, III, IV and V shows the validity of this assumption. Streams in the same locality, like the Blue River and Clear Boggy River, shòw marked similarity in mean parasite intensity of 4 worms per naiad and in the Clear Boggy River, less than 20 miles away, this same species has a similar worm burden of $\underline{A}$. conchicola of 3 worms per naiad. Sample populations of Quadrula quadrula in Lake Texoma (UOBS) have a mean burden of $A$. conchicola of 7.7 worms per naiad in contrast with 7.9 worms per naiad in the same lake at Pennington Creek (PENN). When these means are compared with the cross state
population of this same species in Tenkiller Reservoir, the worm burden is zero, and in Oologah Reservoir it is 2.

Contrasting the A. conchicola burden of the Blue River sample population of Q. quadrula with that of the nearby Lake Texoma sample populations shows an identical 7.7 to 7.7 parasite burden for both sample populations.

Another species of Quadrula Q. pustulosa reveals another similar parasite load when the population from the Blue River is compared with that from the Clear Boggy River, 3.5 and 2.4 worms per naiad respectively.

These similarities are not as distinct for a species like $\underline{P}$. purpuratus, but contrasting relationships can be demonstrated. The sample population from Tenkiller Reservoir has a mean of 3.6 worms per naiad and that of nearby ( 60 mi ) Oologah Reservoir is 21.3 . The sample population from the Verdigris River, which when impounded is Oologah Reservoir, has only a 6.7 worm burden per host naiad, a three-fold difference. Contrasting the Pennington Creek and Blue River population shows 6 worms per naiad in the lentic population and 28.5 worms in the lotic population, just the reverse of the northern contrast. The only flaw in this comparison was that the Pennington Creek sample population consisted of just one naiad.

The Blue River sample populations of Leptodea fragilis showed a mean worm burden of 16.5 worms per naiad, while the nearby lentic population from Lake Texoma (UOBS) had 6.8, a 2.5-fold difference between lotic and lentic sample populations.

The pattern that emerges from these contrasts between species that are found both in streams (lotic) and lakes (lentic) is the sample populations that come from lotic habitats tend to have greater $\underline{\text { A. }}$
conchicola intensities.
The intensity of $\underline{C}$. insignis in the host naiad $\underline{Q}$. quadrula seldom exceeded zero. In only one lotic population (BLD2) there was 0.4 worm per naiad and in only one lentic population (00LO) there was 0.7 worm per naiad.

In $\underline{P}$. purpuratus also, the worm burden of $\underline{C}$. insignis seldom exceeded zero in lotic habitants. In the Blue River population there was .09 worms per host. In the lentic habitats combined there were 1.13 worms per naiad, a 12-fold difference.

The sample lotic populations of $\underline{L}$. fragilis possessed a 1.6 worm per host intensity, while the lentic population had 12.7 worms per naiad, an 8-fold difference.

Generally, in the case of $\underline{C}$. insignis, a substantially higher parasite intensity is encountered in lentic populations in the case of Q . quadrula, $\underline{P}$. potamilus, and L. fragilis. Q. reflexa may be added to this list when the lentic population parasite mean intensity was 0.03 and the lotic mean intensity was also 0.03 worms per naiad. The very small sample from the lentic habitats of $\underline{Q}$. reflexa makes it difficult to support that the parasite load in lentic population is greater.

In the case of these four species again as they relate to extensities of infection by $\underline{A}$. conchicola, lotic extensities are higher except the anomaly of Q. reflexa which shows an opposite trend, but this trend will not contribute a great deal of variance to the system.

The situation with the extensity of C. insignis in L. fragilis is not as clear, but the trend is decidedly greater extensity in lentic populations. Once again Q. reflexa shows the opposite trend. Once again the small lentic sample places a low confidence limit on this
conclusion.
The analysis of variance reveals essentially the same trend (Table 7) that the descriptive statistics show. In the case of these four host species, Q. reflexa, Q. quadrula, P. purpuratus, and L. fragilis, the null hypotheses that the habitat has no effect on the intensity or extensity of the occurrence of either $\underline{A}$. conchicola or $\underline{C}$. insignis ( 1 , $4,7,10$, pp. 3-4) must be rejected.

## Aspidogaster-Cotylaspis Correlations

Since both parasites are using the same host as a habitat, but because each has a particular niche, it was hypothesized that there would be no correlation between the intensities of $\underline{A}$. conchicola and $\underline{C}$. insignis in the same host.

Only in A. grandis, A. plicata, and L. anodontoides need this hypothesis be rejected. In all the other species for which correlations between the two species of parasite was calculated, the hypothesis must be accepted.

Cotylaspis insignis was reported by Osborn (1904) to be a commensal of unionid pelecypods rather than even an ecto-parasite. He suggested that this was a form of cleaning symbiosis (p. 207). It is not surprising then, in view of the very different modes of existence in the living host, that these two forms do no interact with each other. Why they appear to in $\underline{A}$, grandis, $\underline{A}$. plicata, and $\underline{\text { L. }}$ anodontoides is not clear.

## Parasite-Volume Correlations

The lentic species $\underline{A}$. grandis (Table IX) shows little or no correlation between $\underline{A}$. conchicola intensity and the volume of the
host. The intensity of $\underline{C}$. insignis showed a significant $\underline{r}$ in the data from Tenkiller Reservoir and from Lake Texoma (UOBS). This $\underline{r}$ does not persist when the lentic data are pooled in this species.
A. grandis is a thin-shelled form that has a tendency to gape under functional and undisturbed conditions. This fact may account for the fairly high extensity ( $83 \%$ ) in the combined data from all collections of this species.

A closely related thin-shelled species with a gaping habit, Anodonta imbicilis, shows an $\underline{r}$ of 0.57 between volume and the total A. conchicola, and only 0.17 with C. insignis and volume.

A third species, Leptodea fragilis (Table $X$ ), has the thin shell and gaping habit of the two previous forms. The sample population of this form from the Verdigris River shows a high $\underline{r}$ ( 0.84 between $\underline{C}$. insignis intensity and volume, but it is not significant because of the small sample. A large sample was taken from the lentic location in Lake Texoma (UOBS). A high $\underline{r}$ (0.59) that is highly significant ( $P>r=0.00$ ) was found in this sample population between host volume and $\underline{C}$. insignis intensity. This trend continues when all locations, both lentic and lotic, are combined $\underline{r}=0.34(P>\underline{r}=0.00)$. In lotic locations, combined data reveals that $r=0.26(P>\underline{r}=.067)$, a level just shy of the alpha level selected for the rejection of the null hypothesis. In this species the A. conchicola variables show a correlation with volume only in the Blue River 2 sample. Here there is a coefficient of correlation only between A. conchicola intensity in the renal cavity of $0.67(P>\underline{r}=0.03)$. Beyond this there is no evidence that the $\underline{A}$. conchicola variables are correlated with volume.

With data from Potamilus purpuratus (Table XII), a good pattern
of correlation between the $\underline{A}$. conchicola variables and host volume develops as more and more specimens are added to the data pool. There is very little difference in correlation between lotic and lentic populations. A similar trend is evident for $\underline{\text { C. }}$ insignis, but it is not significant at the 0.05 level of probability for rejecting the null hypothesis that there is no correlation. This naiad form has a thick shell but has the gaping habit of L. fragilis. Obliquaria reflexa (Table XXII) is another thick-shelled naiad, but it lacks the gaping habit of $\underline{P}$. purpuratus. A distinct correlation coefficient of $0.44(P>\underline{r}=0.00)$ between $\underline{A}$. conchicola and naiad volume is seen in this data from primarily a lotic sample population. No corresponding significant correlation is seen for the C. insignis variable.

Another thick-shelled, tightly closing host species Tritogonia verrucosa (Table XII) is characterized by moderately high extensity $(91 \%)$ of A. conchicola and a considerably lower extensity (51\%) of $\underline{C}$. insignis. The table of correlations between the parasite variables and volume does not show a significant one for any variable except $\underline{C}$. insignis when the data is pooled.

The data from Quadrula quadrula (Table XIII) shows an $\underline{r}$ between A. Conchicola and host volume of 0.42 ( $P>\underline{r}=0.00$ ) in the lentic sample and $\underline{r}=-0.32(P>\underline{r}=0.04)$ in the lotic population. For $\underline{C}$. insignis, the $\underline{r}=-0.27(P>\underline{r}=0.11)$ in the lotic sample and -0.29 $(P>\underline{r}=0.04)$ in the lentic sample. When all the lotic and lentic data from this species are combined, the negative correlation of the lotic sample reduces the overall correlation to 0.17 ( $P>\underline{r}=0.11$ ), which is not enough to reject the hypothesis that there is no correla-
tion. The $\underline{C}$. insignis $\underline{r}$ in the total sample persists at 0.22 $(P>\underline{r}=0.04)$, enough to reject the hypothesis of no correlation.

A group of host species that show varied extensities and intensities of both parasites all belong to the genus Lampsilis. Morphologicall, L. anodontoides and L. ovata resemble each other. Both species have relatively thick shells and tend to gape at rest. L. anodontoides has an $\underline{r}$ of -0.16 between $\underline{A}$. conchicola and volume ( $\mathrm{P} \quad \underline{r}=0.39$ ). L. ovata has an $\underline{r}$ of $.16(P>\underline{r}=.47)$. Intensities of $\underline{C}$. insignis have an $\underline{r}$ of -0.14 in $\underline{L}$. anodontoides ( $P>r=.47$ ) and $-0.31(P>\underline{r}=0.15)$ in $\underline{L}$. ovata. None of these correlations are large enough to reject the hypothesis that there is no correlation.

Of this genus there remains only L. radiata. No clear relationship between volume and parasite intensity can be demonstrated in this species.

The picture presented by the statistics is very difficult to interpret. In the case of $\underline{A}$. conchicola in $\underline{P}$. purpuratus and $\underline{O}$. reflexa, the hypothesis that there is no correlation must be rejected. The correlation in these cases is independent of parasite intensity or extensity. In all the other species for which coefficients were calculated, A. grandis, I. verrucosa, A. plicata, Q. quadrula, L. fragilis, $\underline{\text { L. anodontoides, }}$ L. radiata, and L. ovata, the hypothesis that there is no correlation between parasite intensity and host volume must be accepted, unless the alpha is increased to 0.1 , and then only $Q$. quadrula will be excluded from this list.

With respect to $\underline{C}$. insignis, the hypothesis of no correlation must be rejected for the data on $\underline{T}$. verrucosa, $\underline{Q}$. quadrula, and $\underline{L}$. fragilis. In all the other species for which coefficients were calculated, $\underline{A}$. grandis, A. plicata, ㄹ. purpuratus, ㅇ. reflexa, ․
anodontoides, L. radiata, and L. ovata, the hypothesis of no correlation must be accepted.

Morphological characteristics and habitat do not appear to have any effect on the parasite-volume relationship.

## Pericardial and Renal Correlations

It appears that the presence of $\underline{A}$. Conchicola in the renal cavity is a function of the intensity of this parasite in the pericardial cavity. Kelly (1899) observed that the parasite appeared in the renal cavity when the pericardium, which lies dorsal to it, was overcrowded. It may be that the renal cavity is the first step toward the outside environment to infect new hosts. Eggs pass into the renal cavity on the way to the excurrent siphon. The eggs when released from mature adult worms are fully embryonated and the slightest mechanical or chemical stimulus will cause hatching and the release of an active larva. Perhaps the changes in tonicity between the pericardium and kidney is sufficient to effect hatching. The larvae so hatched being no longer passive like the egg that remains in the pericardium.

Whatever the cause for this phenomenon the data clearly shows a significant $\underline{r}$ between pericardial and renal intensities for every species for which coefficients were caluculated except A. plicata, Q. reflexa and L. ovata (Table XX). Even A. plicata and L. ovata had correlations that were consistent with rejecting the hypothesis that there is no correlation. This leaves $\underline{Q}$. reflexa the only real anomaly.

## Negative Binomial Distributions

In fitting the theoretical negative binomial distribution to the observed distribution of $A$. conchicola in sampe populations of eight species of host naiads the observed distribution fitted the expected distribution in every case. This evidence is sufficient to reject the hypothesis of no fit.

In fitting the observed distribution of $\underline{C}$. insignis to the theoretical distribution to six species only two anomalons distributions were observed. A grandis was one clearly disjunct distribution. The other was observed for the lentic population of L. fragilis. The other population (lotic) of L. fragilis was a very good fit. The combined lotic and lentic populations of $\underline{L}$. fragilis was a fairly good fit. There is ample evidence that the hypothesis of no fit should be rejected in the case of the distribution of $\mathbb{C}$. insignis also.

If these two symbionts are distributed in the host population according to the negative binomial then this situation may have been caused by one or more of the six ways the negative binomial distribution could originate (Crofton, 1970).

In view of the statistics set forth in this paper it appears that accepting the alternative hypothesis of both parasites being distributed according to the negative binomial distribution in the host population implies that one of the conditions set forth by Crofton (1971) probably exists. Of the six alternatives presented the most likely is that variations exist in host individuals that makes the chance of infection unequal. There are morphological differences in host individuals that result from age, habits, rate of development and genetic constitution which can alter the probability of individuals becoming infected.

The second most likely condition that may cause the parasites to be distributed in this unique manner is the result of the infective stages not being randomly distributed. Williams (1942) proposed a transmission mechanism whereby a first-stage larva of A. conchicola is carried from one host to another by water currents. Huehner and Etges (1972) demonstrated a transmission mechanism whereby eggs of the parasite are ingested by the host. In either case, the infective stages would be distributed among the host population in the same manner as the adult parasite were distributed. The motility of the larva would improve the probability that it would reach a new host. Transmission by means of an infective egg would result in a more random distribution.

The fact remains that when either parasite is found it tends to be aggregated in certain few individual hosts. The reason for this perhaps is that as soon as two worms become established in the same host, a reproductive cycle is initiated and the worm population in the host increases in a geometrical progression. As long as there is only one worm in the host the number does not increase. When host naiads possess large numbers of parasites they probably tend to release larger numbers of infective stages into the environment.

The data supports a hypothesis that lotic environments increase the probability that passive stages will be transmitted to uninfected hosts by the action of water currents. This may account for the higher incidence of $\underline{A}$. conchicola in hosts from lotic environments than from lentic environments. The reverse trend is in evidence for C. insignis. In this case, the infective larva is the agency by which new hosts are colonized. An active larval form could conceivably have an advantage
in the less turbulent lentic environment. The more turbulent conditions in a flowing stream would sweep the released larvae to their destruction.

The aggregated distribution of $\underline{C}$. insignis in host individuals could be accounted for by the same mechanism proposed for $\underline{A}$. conchicola. Once two worms became established in a host naiad the population would increase in a geometric progression.

## Summary

Host naiad species that inhabit both lotic and lentic habitats have greater intensity of $\underline{A}$. conchicola infestation in lotic habitats. C. insignis occurrs in greater intensities in these same species in lentic habitats (Table V, p. 20).

Host naiad species that occur exclusively in lotic habitats have greater intensities and extensities of the parasite $\underline{A}$. conchicola than host naiad species that occur exclusively in lentic habitats (Table I, II).

Host naiad species that occur exclusively in lotic habitats have lower intensities of $\underline{C}$. insignis than host naiad species that occur only in lentic habitats. (Table III, IV).

Within any location in a habitat the species of host naiad is a significant source of variance of parasite intensities (Table VIII). Some host species such a P. purpuratus and L. fragilis are inhabited $98 \%$ of the time by $\underline{A}$. conchicola in lotic habitats with a mean worm intensity of 26.4 and 15.4 worms per host respectively. Q. quadrule, I. verrucosa, Q. pustulosa, and A. plicata are inhabited by A. conchicola over $85 \%$ of the time in lotic habitats with a mean worm
burden of $8.15,7.8,2.9$ and 3.3 per host respectively. ㄴ. reflexa, I. truncata, L. anodontoides, L. radiata, and L. ovata from lotic habitats are inhabited less than $50 \%$ of the time with mean worm burdens of $0.5,0.4,4.9,0.7$ and 1.46 worms per host.

Lentic species with the highest extensities of $\underline{A}$. conchicola are $\underline{A}$. grandis, $\underline{Q}$ quadrula and L. fragilies $83 \%, 82 \%$ and $90 \%$ respectfully. These three host species have mean worm burdens of $7.4,6.5$, and 6.8 worms per host. Lentic host species with lesser extensities are A. imbicilis, P. purpuratus and $\underline{P}$. alatus with $54 \%, 44 \%$ and $36 \%$ extensities. These three species have mean worm burdens of $2.6,5.3$ and 2.9 A. conchicola per host.

Lotic host species most extensively inhabited by $\underline{C}$. insignis are I. verrucosa ( $51 \%$ ) and L. fragilis ( $52 \%$ ). These two species have mean intensities of 1.01 and 1.56 worm per host. Lotic host species with lesser extensities are Q. quadrula (10\%) Q. pustulosa (3\%) A. plicata ( $1 \%$ ) Q. reflexa (3\%) P. purpuratus (8\%) L. anodontoides (13\%) and P. cordatum (13\%). These seven species exhibited mean worm burdens of $0.12,0.03,0.01,0.03,0.08,0.47$, and 0.25 worm per host repectively.

Potamilus purpuratus and Leptodea fragilis are two host species with contrasting morphological characteristcs and they also illustrate parasite population trends clearly that are less obvious in other species pairs. The sample means of these two species will be used to illustrate these trends.

In $\underline{P}$. purpuratus the total intensity of $\underline{A}$. conchicola from the sample population in lotic habitats is five times that from lentic habitats. In lentic populations $\underline{C}$. insignis is 4.5 times the mean from lotic populations.

The Leptodea fragilis population taken from lentic habitats was inhabited by A. conchicola $90 \%$ of the cases having a 6.9 worm burden per host. In lotic habitats this species was inhabited $98 \%$ of the cases with a 15.9 mean worm burden per host. Between these two habitats there is only a difference in extensity of $8 \%$ while the intensity shows an increase of 2.3 times or $233 \%$ more in the lotic populations.

Again the reverse trend is the case for C. insignis. In the lotic sample population this form occurred in $52 \%$ of the host specimens
 examined. The mean worm burden in hosts from lotic habitats was 1.6 worms per naiad. From the lentic sample the mean worm burden in this species is 12.7 per naiad, a $793 \%$ increase in lentic specimens.

Quadrula quadrula is a host species taken in both habitats. The differences in extensity and intensity of $\underline{A}$. conchicola is not as marked as that in the previous two species. None-the-less there are more naiads inhabited in lotic environments ( $90 \%$ ) than in lentic environments ( $82 \%$ ). The mean worm burden is just a trifle more (8.2) in the lotic population than in the lentic one (6.5) The $\underline{C}$. insignis is less extensively found in the lentic population (4\%) than in the lotic one (10\%). This is a reversal of the condition found in the two previous species.

Taking all host naiads as a total population $96 \%$ of the lotic population was inhabited by A. conchicola. Sixty-nine percent were inhabited in lentic populations. The mean worm burden in the lotic population was 6.2 worms per naiad. In lentic population it was 5.8.

Cotylaspis insignis inhabited $52 \%$ of the total naiad population sampled from lotic habitats. Ninety-three percent of the lentic population harbored this worm. In the lotic population the mean worm burden
was 0.3 worm per naiad. In the lentic population the worm burden was on the average 8.7 times as great (2.8 per host).

The reversed extensity of infection by the two symbionts in naiads from these contrasting habitats may be due to differences in the mode of transmission from one host to another. Aspidogaster conchicola may be transmitted passively as an egg or small larva assisted by water currents. Cotylaspis insignis, on the other hand, may be transmitted more actively from host to host by the locomotion of the adult worms. The quiet conditions of the lentic environment may prevent the worm that ventures out of the host from being swept away to destruction, as may be the case in a lotic environment.

Morphological differences among host species may also account for observed differences in extensities and intensities that deviate from the general trend. Thick-shelled tightly closing species like P. purpuratus, $Q$ quadrula, $Q$ pustulosa and Q. reflexa appear to be less likely to acquire $\underline{C}$. insignis. Thin-shelled species like $\underline{A}$. grandis and L. fragilis that tend to gape open when at rest appear to be more likely to acquire $\underline{C}$. insignis. Since $\mathbb{C}$. insignis is an ecto-parasite it may be more likely to appear in species that inhabit a more eutrophic environment with more detritus. C. insignis is obviously a detritus feeding, cleaning symbiont and is more likely to occur where there is an abundance of organic detritus in suspension. A. conchicola is a true endoparasite that feeds upon its host's tissue. Therefore, it will occurr more extensively in host populations that live in environments that assist in the transmission of infective stages from host to host.

There is little evidence to show that there is any correlation between the presence of $\underline{A}$. conchicola and $\underline{C}$. insignis in the same host.

These two forms clearly occupy different niches in the host organism and do not effect each other.

In only two species of host naiad was there any indication that the volume of the host is correlated to the number of $\underline{A}$. conchicola that inhabit it. The two species that showed correlation were: $\underline{P}$. purpuratus and Q. reflexa. Only three species showed a correlation between volume of the host and the numbers of $\underline{C}$. insignis that utilize the host as a habitat. These three species were: I. verrucosa, $\underline{\text {. }}$ quadrula and L. fragilis.

Both symbionts appear to be distributed in the host population according to the negative binomial distribution. This fact is probably the reason why in most cases the standard deviation is equal to or larger than the mean (Crofton, 1971). This distribution of the symbionts in the host population has its roots in the differences in host species morphology and the mode of transmission of the infective stages of the symbiont.

## Continuing Research

Once the mean extensities and intensities of symbionts characteristics of certain habitats and locations have been determined as they have in this study, each location needs to be visited at yearly intervals to see if the pattern of relative abundance remains constant from year to year. If it can be demonstrated that they do, these new samples can be added to the former ones and perhaps some of the gaps in the data can be filled in this manner.

Experiments in the mode of transmission can be set up in a series of artificial ponds or large aquaria. By exposing a population of hosts
with a low incidence of infection to one with a high incidence for a year it can be determined if the relative abundance of the symbionts increases when compared to a control population not so exposed. Populations of hosts that are symbiont-free could be raised and exposed to a known number of eggs and/or larvae of the symbionts. It is possible to culture the symbionts in vitro (VanCleave and Williams, 1943).

The existence of the negative binomial distribution of the symbionts in the host population has a number of consequences that should be investigated. One of the first steps is to transform all data that has already been collected to the negative binomial series. Such a transformation will have the effect of normalizing the distributions of symbionts so they will be more symmetical. The data in its present form produced extremely asymmetrical distribution curves with extreme positive skewness and non-zero kurtosis. The non-zero kurtosis has a profound effect on the $\underline{F}$ test and if this can be rectified by transformation of the data a more robust $\underline{F}$ test will be possible and may give further insights into the effects of location, habitat and species on symbiont sample means.
C. B. Willaims (1964) has suggested:

If we can find a mathematical model that closely fits the data, we will be nearer to an understanding of our problem, for at that stage we could see what follows mathematically from the theory and so devise further tests and experiments. Also it might be possible later to find what combinations of previous conditions would bring about such a frequency distribution, and to see if these can be justified on biological grounds. Thus we could throw light on the mechanism of population balance (p.4).

It is just this point around which this study of population dynamics of aspidogastrid parasites revolves. Only further research and refinement of techniques will reveal the mechanism that underlies the phenomena that have been demonstrated to exist in this study. There is enough data gathering, analysis, and experimentation to last this author's remaining professional life.

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## APPENDIX

## TABLES FITTING THE NEGATIVE

 BINOMIAL DISTRIBUTIONTABLE XXIII
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN

ANODONTA GRANDIS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :---: | :---: |
| 0 | 17.000 | 14.017 |
| 1 | 9.000 | 10.604 |
| 2 | 13.000 | 8.767 |
| 3 | 4.000 | 7.443 |
| 4 | 6.000 | 6.416 |
| 5 | 4.000 | 5.569 |
| 6 | 6.000 | 4.864 |
| $7-9$ | 7.000 | 8.019 |
| $9-10$ | 3.000 | 6.223 |
| $11-13$ | 5.000 | 6.869 |
| $14-17$ | 10.000 | 5.033 |
| $18-24$ | 8.000 | 4.674 |
| $25-45$ | 3.000 | chi-square $=10.06$ |
|  | $N=95$ | d.f. $=12$ |
|  | $\bar{X}=7.30$ | .05 level $=21.03$ |

TABLE XXIV
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPRIDOGASTER CONCHICOLA IN TRITOGONIA VERRUCOSA

NUMBER
PARASITES

OBSERVED
FREQUENCY

EXPECTED FREQUENCY

| 0 | 6.000 | 3.571 |
| :--- | ---: | ---: |
| 1 | 6.000 | 5.005 |
| 2 | 2.000 | 5.613 |
| 3 | 4.000 | 5.641 |
| 4 | 5.000 | 5.472 |
| 5 | 5.000 | 5.992 |
| 6 | 5.000 | 4.677 |
| $7-8$ | 10.000 | 7.993 |
| $9-10$ | 5.000 | 6.265 |
| $11-13$ | 8.000 | 6.700 |
| $14-18$ | 8.000 | 6.216 |
| $19-38$ | 3.000 | 4.718 |
|  | $N=67$ | chi-square $=7.46$ |
|  |  |  |
|  |  |  |
|  |  | d. f. $=11$ |

TABLE XXV
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN

AMBLEMA PLICATA

| NUMBER PARASITES | OBSERVED FREQUENCY | EXPECTED <br> FREQUENCY |
| :---: | :---: | :---: |
| 0 | 14.000 | 15.631 |
| 1 | 19.000 | 17.542 |
| 2 | 14.000 | 15.641 |
| 3 | 15.000 | 12.740 |
| 4 | 9.000 | 9.878 |
| 5 | 11.000 | 7.438 |
| 6 | 2.000 | 5.488 |
| 7 | 6.000 | 3.989 |
| 8-9 | 4.000 | 4.900 |
| 10-18 | 4.000 | 4.578 |
|  | $N=98$ | $r e=6.06$ |
|  | $\bar{X}=3.306$ | f. $=9$ |
|  | $s^{2}=9.740$ | $1=16.92$ |

TABLE XXVI
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION
TO ASPIDOGASTER CONCHICOLA IN
LOTIC POPULATIONS OF
POTAMILUS PURPURATUS

| NUMBER PARASITES | OBSERVED FREQUENCY | EXPECTED <br> FREQUENCY |
| :---: | :---: | :---: |
| 0 | 0.000 | 1.303 |
| 1-4 | 4.000 | 5.023 |
| 5-9 | 5.000 | 5.483 |
| 10-15 | 9.000 | 5.441 |
| 16-23 | 5.000 | 5.939 |
| 24-34 | 6.000 | 5.480 |
| 35-51 | 5.000 | 5.058 |
| 52-108 | 5.000 | 5.195 |
|  | $N=39$ | chi-square $=4.01$ |
|  | $\bar{X}=26.41$ | d. f. $=7$ |
|  | $s^{2}=698.038$ | .05 level $=14.07$ |

TABLE XXVII
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN LENTIC POPULATIONS OF POTAMILUS PURPURATUS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :---: | ---: |
| 0 | 43.000 | 38.851 |
| 1 | 7.000 | 7.008 |
| 2 | 1.000 | 4.015 |
| $3-4$ | 5.000 | 5.001 |
| $5-9$ | 5.000 | 6.526 |
| $10-19$ | 6.000 | 5.665 |
| $20-65$ | 6.000 | chi-square $=3.15$ |
|  | $N=73$ |  |
|  |  | d. f. $=6$ |
|  | $\bar{X}=5.288$ |  |
|  | $s^{2}=155.041$ | .05 leve1 $=12.59$ |

TABLE XXVIII
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN THE TOTAL SAMPLE POPULATION OF POTAMILUS PURPURATUS

| NUMBER PARASITES | OBSERVED FREQUENCY | EXPECTED FREQUENCY |
| :---: | :---: | :---: |
| 0 | 43.000 | 29.803 |
| 1 | 7.000 | 10.786 |
| 2 | 3.000 | 7.190 |
| 3 | 5.000 | 5.522 |
| 4 | 2.000 | 4.525 |
| 5-6 | 8.000 | 7.179 |
| 7-8 | 2.000 | 5.600 |
| 9-11 | 4.000 | 5.752 |
| 12-15 | 11.000 | 6.585 |
| 16-20 | 4.000 | 6.217 |
| 21-27 | 5.000 | 5.959 |
| 28-36 | 7.000 | 5.074 |
| 37-52 | 4.000 | 5.153 |
| 53-108 | 7.000 | 5.174 |
|  | $N=112$ | chi-square $=19.56$ |
|  | $\bar{X}=12.643$ | d. f . $=13$ |
|  | $s^{2}=441.709$ | . 05 level $=22.36$ |

## TABLE XXIX

## FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN THE SAMPLE POPLLLATION OF ANODONTA IMBICILIS

| NUMBER PARASITES | OBSERVED FREQUENCY | EXPECTED FREQUENCY |
| :---: | :---: | :---: |
| 0 | 11.000 | 11.7964 |
| 1-3 | 8.000 | 6.7085 |
| 4-7 | 2.000 | 1.7868 |
| 8-11 | 1.000 | 2.2521 |
| 12-18 | 2.000 | 0.8741 |
|  | $N=24$ | chi-square $=2.47$ |
|  | $\bar{X}=2.625$ | d.f. $=4$ |
|  | $S^{2}=24.158$ | . 05 level $=9.49$ |

TABLE XXX
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN THE LOTIC SAMPLE POPULATION OF QUADRULA QUADRULA

| NUMBER PARASITES | OBSERVED FREQUENCY | EXPECTED FREQUENCY |
| :---: | :---: | :---: |
| 0 | 4.000 | 2.358 |
| 1 | 5.000 | 3.094 |
| 2 | 3.000 | 3.328 |
| 3 | 2.000 | 3.317 |
| 4 | 1.000 | 3.175 |
| 5 | 3.000 | 2.964 |
| 6 | 2.000 | 2.720 |
| 7 | 2.000 | 2.466 |
| 8-10 | 6.000 | 5.867 |
| 11-14 | 5.000 | 5.120 |
| 15-18 | 4.000 | 2.949 |
| 19-25 | 4.000 | 2.956 |
|  | $N=41$ | chi square $=5.38$ |
|  | $\bar{X}=8.146$ | d.f. $=11$ |
|  | $s^{2}=50.578$ | . 05 leve1 = 19.68 |

## TABLE XXXI

FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN THE LENTIC SAMPLE POPULATION OF QUADRULA QUADRULA

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :--- | :--- |
| 0 | 9.000 |  |
| 1 | 3.000 | 7.598 |
| 2 | 4.000 | 5.858 |
| 3 | 1.000 | 4.839 |
| 4 | 5.000 | 4.087 |
| 5 | 5.000 | 2.489 |
| 6 | 6.000 | 2.997 |
| 7 | 5.000 | 2.238 |
| 8 | 1.000 | 1.942 |
| $9-12$ | 3.000 | 5.550 |
| $13-15$ | 2.000 | 2.566 |
| $14-25$ | 4.000 | 3.835 |
| $26-38$ | 1.000 | 1.156 |

$$
\begin{array}{lrl}
N=49 & \text { chi-square }=15.85 \\
\bar{X}=6.49 & \text { d. f. } & =12 \\
s^{2}=54.63 & .05 \text { level }=21.03
\end{array}
$$

TABLE XXXII
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN THE TOTAL SAMPLE POPULATION OF QUADRULA QUADRULA

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | ---: | :--- |
| 0 | 13.000 |  |
| 1 | 8.000 | 9.153 |
| 2 | 7.000 | 9.081 |
| 3 | 3.000 | 7.634 |
| 4 | 6.000 | 6.840 |
| 5 | 8.000 | 6.075 |
| 6 | 8.000 | 5.373 |
| 7 | 7.000 | 4.734 |
| 8 | 5.000 | 4.167 |
| $9-10$ | 4.000 | 6.858 |
| $11-12$ | 3.000 | 5.227 |
| $13-15$ | 6.000 | 5.616 |
| $16-20$ | 5.000 | 5.463 |
| $21-38$ | 7.000 | 4.916 |

$$
\begin{array}{lr}
N=90 & \text { chi-square }=11.13 \\
\bar{X}=7.244 & \text { d. f. }=13 \\
s^{2}=52.883 & .05 \text { leve } 1=22.36
\end{array}
$$

## TABLE XXXIII

FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO ASPIDOGASTER CONCHICOLA IN THE LOTIC SAMPLE POPULATION OF LEPTODEA FRAGILIS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :--- | :--- |
| 0 | 1.000 | 2.883 |
| 1 | 3.000 | 2.727 |
| $2-3$ | 4.000 | 4.987 |
| $4-5$ | 7.000 | 4.411 |
| $6-8$ | 4.000 | 5.670 |
| $9-12$ | 9.000 | 6.082 |
| $13-17$ | 6.000 | 5.741 |
| $18-23$ | 3.000 | 4.884 |
| $24-33$ | 4.000 | 4.969 |
| $34-71$ | 6.000 | 5.136 |

$$
\begin{aligned}
N=48 & \text { chi-square }=5.94 \\
\bar{X}=15.417 & \text { d. f. }
\end{aligned}=9 .
$$

## TABLE XXXIV

FITTING THE NEGATIVE BINOMIAL DISTRIBUTION
TO ASPIDOGASTER CONCHICOLA IN THE
LENTIC SAMPLE POPULATION OF LEPTODEA FRAGILIS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :--- | :--- |
| 0 | 3.000 |  |
| 1 | 5.000 | 7.620 |
| 2 | 6.000 | 3.536 |
| $3-5$ | 7.000 | 4.467 |
| $6-12$ | 4.000 | 5.481 |
| $13-49$ | 4.000 | 4.941 |

$$
\begin{array}{rlrl}
N=29 & \text { chi-square } & =10.05 \\
\bar{X}=6.793 & \text { d. f. } & =5 \\
s^{2}=99.456 & .05 \text { leve } 1 & =11.07
\end{array}
$$

TABLE XXXV
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION
TO ASPIDOGASTER CONCHICOLA IN THE TOTAL SAMPLE POPULATION OF LEPTODEA FRAGILIS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :---: | :--- |
| 0 | 4.000 |  |
| 1 | 8.000 | 9.116 |
| 2 | 8.000 | 6.436 |
| 3 | 2.000 | 5.303 |
| 4 | 5.000 | 4.578 |
| $5-7$ | 10.000 | 4.043 |
| 8 | 3.000 | 9.848 |
| $9-10$ | 9.000 | 4.706 |
| $11-12$ | 5.000 | 4.027 |
| $13-14$ | 3.000 | 3.4365 |
| $15-19$ | 6.000 | 6.624 |
| $20-24$ | 3.000 | 4.607 |
| $25-32$ | 2.000 | 5.467 |
| $33-71$ | 6.000 | 6.0105 |

$$
N=77 \quad \text { chi-square }=13.24
$$

$$
\begin{array}{rlrl}
\bar{x}=5.74 & \text { d. f. } & =13 \\
s^{2}=63.3 & .05 \text { leve } 1 & =22.36
\end{array}
$$

TABLE XXXVI
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INISIGNIS IN THE SAME POPULATION OF

ANODONTA GRANDIS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :--- | :--- |
| 0 | 31.000 | 43.675 |
| 1 | 19.000 | 11.745 |
| 2 | 18.000 | 7.055 |
| 3 | 4.000 | 5.018 |
| 4 | 5.000 | 3.847 |
| 5 | 3.000 | 3.076 |
| $6-7$ | 2.000 | 4.646 |
| $8-10$ | 2.000 | 4.681 |
| $11-17$ | 3.000 | 4.628 |
| $18-41$ | 8.000 | 4.817 |

$$
\begin{aligned}
N=95 & \text { chi-square }=31.73 \\
\bar{X}=3.979 & \text { d. f. }
\end{aligned}=9
$$

TABLE XXXVII
Fitting the negative binomial distribution to
COTYLASPIS INSIGNIS IN THE SAMPLE POPULATION OF ANODONTA IMBICILIS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :--- | :--- |
| 0 |  |  |
| 1 | 13.000 | 12.9102 |
| 2 | 4.000 | 3.4388 |
| $3-10$ | 2.000 | 2.3574 |

$$
\begin{array}{lr}
N=24 & \text { chi-square }=0.26 \\
\bar{X}=1.33 & \text { d. f. }=3 \\
s^{2}=5.28 & .05 \text { level }=7.82
\end{array}
$$

## TABLE XXXVIII

## FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INSIGNIS IN THE SAMPLE POPULATION OF TRITOGONIA VERRUCOSA

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :---: | :---: |
| 0 | 33.000 | 29.225 |
| 1 | 13.000 | 20.073 |
| 2 | 11.000 | 10.138 |
| 3 | 7.000 | 4.451 |
| 4 | 3.000 | 1.867 |

$$
\begin{array}{lrl}
N=67 & \text { chi-square }=5.20 \\
\bar{X}=1.015 & \text { d. f. } & =4 \\
s^{2}=1.5 & .05 \text { level }=9.49
\end{array}
$$

TABLE XXXIX
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INSIGNIS IN THE LŌTIC SAMPLE POPULATION OF QUADRULA QUADRULA

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :---: | :--- |
|  |  |  |
| 0 | 37.000 | 36.8688 |
| 1 | 3.000 | 3.4297 |
| 2 | 1.000 | 0.5668 |

$$
\begin{array}{lr}
N=41 & \text { chi-square }=0.385 \\
\bar{X}=0.122 & \text { d.f. }=2 \\
s^{2}=.16 & .05 \text { leve }=5.99
\end{array}
$$

## TABLE XLII

FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INSIGNIS IN THE LENTIC SAMPLE POPULATION OF QUADRULA QUADRULA

| NUMBER | OBSERVED | EXPECTED |
| :--- | :--- | :--- |
| PARASITES | FREQUENCY | FREQUENCY |
| 0 | 47.000 | 47.0195 |
| 1 | 2.000 | 1.9617 |

$$
\begin{array}{lc}
N=49 & \text { chi-square }=.00 \\
\bar{X}=0.0408 & \text { d. f. }=1 \\
s^{2}=.0399 & .05 \text { level }=3.84
\end{array}
$$

TABLE XL
FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INSIGNIS IN THE LENTIC SAMPLE POPULATION OF POTAMILUS PURPURATUS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :--- | :--- |
| 0 |  |  |
| 1 | 60.000 | 60.3663 |
| 2 | 8.000 | 6.8248 |
| 3 | 2.000 | 2.7145 |
| 4 | 1.000 | 1.3373 |
| 5 | 1.000 | 0.7222 |
| 6 | 0.000 | 0.4106 |
| 7 | 0.000 | 0.2413 |

$$
\begin{aligned}
\text { chi-square } & =6.27 \\
\text { d. f. } & =7 \\
.05 \text { level } & =14.07
\end{aligned}
$$

## TABLE XLI

FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INSIGNIS IN THE TOTAL SAMPLE POPULATION OF POTAMILUS PLRPURATUS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | :---: | :---: |
| 0 |  |  |
| 1 | 96 | 97.0734 |
| 2 | 11 | 8.4569 |
| 3 | 2 | 3.1745 |
| 4 | 1 | 1.4967 |
| 5 | 0 | 0.7775 |
| 6 | 0 | 0.4263 |
| 7 | 1 | 0.2420 |

$$
\begin{array}{lc}
N=112 & \text { chi-square }=7.34 \\
\bar{X}=0.259 & \text { d. f. }=7 \\
s^{2}=0.77 & .05 \text { level }=14.07
\end{array}
$$

## TABLE XLII

## FITTING THE NEGATIVE BINOMIAL DISTRIBUTION <br> TO COTYLASPIS INSIGNIS IN THE LOTIC SAMPLE POPULATION OF LEPTODEA FRAGILIS

| NUMBER PARASITES | OBSERVED <br> FREQUENCY | EXPECTED FREQUENCY |
| :---: | :---: | :---: |
| 0 | 25.000 | 23.5876 |
| 1 | 8.000 | 8.9729 |
| 2 | 4.000 | 5.1012 |
| 3 | 3.000 | 3.2199 |
| 4 | 5.000 | 5.3533 |
| 5-12 | 6.000 | 4.6200 |
|  | $N=48$ | chi-square $=0.87$ |
|  | $\bar{X}=1.563$ | d. f. $=5$ |
|  | $s^{2}=6.422$ | . 05 level $=11.07$ |

## TABLE XLIII

## FITTING THE NEGATIVE BINOMIAL DISTRIBUTION

 TO COTYLASPIS INSIGNIS IN THE LENTIC SAMPLE POPULATION OF LEPTODEA FRAGILIS| NUMBER PARASITES | $\begin{aligned} & \text { OBSERVED } \\ & \text { FREQUENCY } \end{aligned}$ | EXPECTED <br> FREQUENCY |
| :---: | :---: | :---: |
| 0 | 2 | 0.3820 |
| 1 | 3 | 0.7498 |
| 2 | 2 | 1.0527 |
| 3 | 0 | 1.2817 |
| 4 | 0 | 1.4411 |
| 5 | 0 | 1.5398 |
| 6-7 | 1 | 3.1829 |
| 8-10 | 4 | 4.5489 |
| 11-14 | 6 | 4.9878 |
| 15-20 | 6 | 4.9133 |
| 21-31 | 5 | 3.7239 |
|  | $N=29$ | chi-square $=21.16$ |
|  | $\bar{X}=12.655$ | d. f. $=10$ |
|  | $s^{2}=81.591$ | .05 leve1 $=18.31$ |

## TABLE XLIV <br> FITTING THE NEGATIVE BINOMIAL DISTRIBUTION TO COTYLASPIS INSIGNIS IN THE TOTAL SAMPLE POPULATION OF LEPTODEA FRAGILIS

| NUMBER <br> PARASITES | OBSERVED <br> FREQUENCY | EXPECTED <br> FREQUENCY |
| :--- | ---: | :--- |
| 0 | 27.000 | 19.4853 |
| 1 | 11.000 | 10.1432 |
| 2 | 6.000 | 7.2518 |
| 3 | 3.000 | 5.6544 |
| 4 | 2.000 | 4.5921 |
| 5. | 3.000 | 3.8186 |
| $6-7$ | 2.000 | 5.9783 |
| $8-9$ | 4.000 | 4.4225 |
| $10-12$ | 5.000 | 4.7175 |
| $13-17$ | 5.000 | 4.7695 |
| $18-31$ | 8.000 | 4.1878 |

$$
\begin{array}{rrl}
N=77 & \text { chi-square }=12.25 \\
\bar{X}=5.7403 & \text { d. } f .=10 \\
\mathrm{~s}^{2}=63.2995 & .05 \text { leve }=18.31
\end{array}
$$

## VITA 2

Edward Norman Nelson
Candidate for the Degree of
Doctor of Education
Thesis: SOME ASPECTS OF THE POPULATION DYNAMICS OF ASPIDOGASTRID TREMATODE PARASITES IN OKLAHOMA PELECYPODS

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Education: Graduated from Ferndale High School, Ferndale, Washington, in May, 1945; received Bachelor of Liberal Arts and Bachelor of Education degrees from Western Washington College of Education in 1950; received Master of Education and Master of Science degree from Oregon State College in 1959; completed requirements for the Doctor of Education degree at Oklahoma State University in December, 1976.

Professional Experience: Sixth grade teacher at Toledo, Oregon, 1950-1954; junior high school science teacher, Oak Harbor, Washington, 1954-1958; instructor of biology, Clark College, Vancouver, Washington; 1959-1968; assistant professor of science education, Western Washington State College, Bellingham, Washington, summer sessions 1959, 1960, 1961, 1962 and 1963; assistant professor of biological sciences, Oral Roberts University, Tulsa, Oklahoma, 1968- to date.

Professional Memberships: Southwestern Association of Parasitologists, 1971- to date; National Science Teachers Association, 1959-1968; National Association of Biology Teachers, 1964-1974; American Association for the Advancement of Science, 1959-1968; American Institute of Biological Sciences, 1965- to date; American Scientific Affiliation, 1963- to date; Creation Research Society, 1967- to date; American Society of Ichthyologists and Herpetologists, 1968to date; American Society of Mammologists, 1968- to date; National Wildlife Federation, 1968- to date; Oklahoma Association for Undergraduate Education in Biology, 1971- to date; Oklahoma Academy of Science, 1969- to date.


[^0]:    * Significant effect at 0.05 probability.

