

K-268

~~NOV 1 1978~~

S
~~MAY 1 1981~~ 0065

~~VII 1 1984~~

JAN 12 1986

d

n

d

t

m

t

a.

a.

o.

l.

af

ac

na

ir.

3-7-68

ABSTRACT

THE EFFECT OF INTRASPECIFIC INTERACTIONS ON THE GROWTH AND FEEDING BEHAVIOR OF ANAX JUNIUS (DRURY) NAIADS

By

Quentin Everett Ross

A consistent but unexplained pattern of significant differences in the mean size of final instar, dragonfly naiads was observed in a set of ponds whose naiad and prey densities had been experimentally manipulated. The objective of the present study was to find the behavioral mechanism which had generated the size differences among the naiads.

The relative importance of four variables known to affect the feeding behavior of predators, the prey density and distribution, the predator's own density and the amount of environmental complexity, was determined in a series of laboratory studies.

In the first of the laboratory studies, the variables affecting the intensity and outcome of intraspecific interactions were manipulated. Final and penultimate instar naiads were used in this experimental series because these instars represented the largest and most strongly interacting

s

i

t

i

a

E

t

s

t

r

n

s

n

t

e

r

t

F

c

i

o

w

i

size classes. The experimental procedure consisted of manipulating the size and hunger of two large groups of naiads; then, two naiads were randomly selected and placed together in a large plastic pan. The behavior of the two interacting naiads was recorded for a thirty minute period. Eight independent pairs of naiads were observed at each treatment combination. The intensity and frequency of intra-specific interactions increased with the hunger and size of the naiads. Because of their greater aggressiveness and reactive distance, larger naiads completely dominated smaller naiads.

In the second laboratory study, the effect of prey consumption on predator activity was determined. Individual naiads were placed in experimental activity chambers where their activity was continuously monitored by means of photo-electric cells whose outputs fed into an Esterline Angus event recorder. Predator activity decreased when the prey consumption exceeded 25% of the normal, total prey consumption. Furthermore, although hungry naiads were capable of moving considerable distances, solitary naiads were generally quite inactive.

In the next laboratory study, the relative importance of the variables affecting the feeding behavior of the naiads was determined. Naiad and prey densities were manipulated in the presence and absence of physical structure in the

large plastic pans. Within the restricted area of the pans, intraspecific interactions interfered with feeding behavior and determined the number of prey eaten by the naiads. Because of the intraspecific interference the observed prey consumption was dependent upon the number of discrete prey clumps available relative to the number of interacting naiads and not on the number of prey available in each prey clump. When there was an abundance of prey clumps, intraspecific interactions increased the feeding rate of the naiads by increasing their level of activity.

Because of the restricted size of the large plastic pans (19" x 17" x 4"), the effect of intraspecific interactions on the feeding behavior of the naiads in a structurally patterned environment was studied in a plastic pool, five feet in diameter. In this study, the size distribution of three, interacting naiads and the number and spatial distribution of structured prey clumps were manipulated. The least interference with feeding behavior occurred when the number of structured clumps was equal to the total number of naiads present. The most interference with feeding behavior occurred when the number of structured clumps was less than the number of large naiads present.

The final laboratory study demonstrated that interruptions in feeding could generate significant size differences within an instar and that intraspecific interactions did

affect the growth of interacting naiads. The mean size of the naiads decreased when the naiad density increased and intraspecific interactions interfered with feeding.

The analysis of the feeding behavior of naiads in the experimental ponds demonstrated that the frequency of intraspecific interactions and the relative abundance of prey determined the diversity of the prey consumed; and the comparison of size differences among the final instar naiads demonstrated that the intensity of the intraspecific interactions determined the growth of the naiads under natural conditions.

THE EFFECT OF INTRASPECIFIC INTERACTIONS
ON THE GROWTH AND FEEDING BEHAVIOR
OF ANAX JUNIUS (DRURY) NAIADS

By
Quentin Everett Ross

A THESIS

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

DOCTOR OF PHILOSOPHY

Department of Zoology

1971

ACKNOWLEDGEMENTS

Especial thanks are given to Dr. William E. Cooper for his generous assistance and support in the laboratory and for providing critical ancillary data from his own study. I wish also to thank Drs. M. Balaban, J. E. Cantlon, J. I. Johnson and S. N. Stephenson for their comments and suggestions and their patience. Finally, I wish to thank Mrs. Bodil Burke for relieving some of the drudgery entailed in this study.

This study was supported by a National Science Foundation graduate fellowship and the Animal Behavior Training Grant 5T01 GM01751-04BHS from the National Institutes of Health. Additional support was provided by National Science Foundation Grants GB-15665-Coherent Area Research Project in Freshwater Ecosystems and GI-20-The Design and Management of Environmental Systems.

TABLE OF CONTENTS

	Page
LIST OF TABLES	ix
LIST OF FIGURES.	xii
INTRODUCTION	1
METHODS.	4
Culture Techniques.	4
<u>Anax junius</u> Naiads	4
<u>Chironomus tentans</u> Larvae.	4
Apparatus	5
Experimental Lighting System	5
Activity Chambers.	6
Experimental Arenas.	7
Artificial Prey Clumps	8
Experimental Design and Analysis.	8
The Relative Importance of the Variables Affecting the Feeding Behavior of the Naiads	8
Variables Affecting the Intensity of Intraspecific Interactions.	8
The effect of hunger on the interactions between naiads in the same instar.	10
The effect of hunger on the interactions between naiads in different instars.	10

TABLE OF CONTENTS--continued

Page

The Relation Between the Activity of Final Instar Naiads and the Amount of Prey Eaten.	10
The Relative Importance of the Naiad Density, Prey Density, and the Presence of Environmental Structure on the Number of Prey Eaten	11
The feeding behavior of solitary naiads: the effect of naiad size and prey density on the feeding behavior over a three day period	12
The feeding behavior of inter- acting naiads: the effect of naiad size and density	12
The effect of naiad size and the presence of environmental struc- ture	12
The effect of prey density and the presence of environmental structure.	13
The Effect of the Instar Distribution and the Pattern of Environmental Structure on the Feeding Behavior of Interacting Naiads.	13
The Relation Between the Feeding Behavior and the Instar Growth of the Naiads.	14
The Effect of Different Feeding Pat- terns on the Instar Growth of Iso- lated Naiads.	14
Feeding continuous but restrict- ed in amount	15
Feeding interrupted but unre- stricted in amount	16
The Effect of Different Naiad and Prey Clump Densities on Instar Growth	17
Feeding Behavior and Growth of the Naiads Under Natural Conditions	19

TABLE OF CONTENTS--continued

Page

The Effect of the Relative Abundance of Prey and the Density of Naiads on the Diversity of the Prey Eaten. . .	19
The Size Differences Observed Among the Final Instar Naiads in the Ex- perimental Ponds	20
RESULTS	22
The Relative Importance of the Variables Affecting the Feeding Behavior of the Naiads .	22
The Variables Affecting the Intensity of Intraspecific Interactions.	22
The Effect of Hunger on the Inter- actions Between Naiads in the Same Instar	22
Avoidance responses	22
(F) Naiads	22
(F-1) Naiads	22
Total activity.	24
Stalking distance	24
Total complete stalks	24
Total strikes	27
The Effect of Hunger on the Inter- actions Between Naiads in Different Instars.	27
Comparison of aggressive be- havior.	27
Aggressive behavior of the larger naiad.	27
Avoidance behavior of the small- er naiad.	27
The Relation Between the Activity of Final Instar Naiads and the Amount of Prey Eaten.	32
The duration of the digestive pause	32
The total distance traveled during the period of activity following the digestive pause .	32

TABLE OF CONTENTS--continued

Page

The Relative Importance of the Naiad Density, Prey Density, and the Presence of Environmental Structure on the Number of Prey Eaten.	32
The feeding behavior of solitary naiads	32
The feeding behavior of interacting naiads.	37
The effect of naiad size and density	37
The effect of naiad size and the presence of environmental structure.	37
The effect of prey density and the presence of environmental structure.	37
The Effect of the Instar Distribution and the Pattern of Environmental Structure on the Feeding Behavior of Interacting Naiads.	37
The Relation Between the Feeding Behavior and the Instar Growth of the Naiads.	40
The Effect of Different Feeding Patterns on the Instar Growth of Isolated Naiads.	40
Feeding continuous but restricted in amount	40
Differences in instar growth.	40
Differences in instar duration.	40
Feeding interrupted but unrestricted in amount	44
The number of feeding bouts per instar.	44
The amount (grams) of prey consumed per feeding bout	44
The amount (grams) of prey consumed per instar	44
Differences in instar growth.	48

TABLE OF CONTENTS--continued	Page
Effect of Different Naiad and Prey Clump Densities on Instar Growth. . .	48
Differences in instar growth . .	48
Differences in instar duration .	48
The Feeding Behavior and Growth of Naiads Under Natural Conditions	51
The Effect of the Relative Abundance of Prey and the Density of Naiads on the Diversity of the Prey Eaten by the Naiads in the Experimental Ponds.	51
The effect of the prey density .	51
The effect of the naiad density.	51
The Size Differences Observed Among the Final Instar Naiads in the Experimental Ponds.	51
The size differences observed among the overwintering naiad populations.	51
The size differences observed among the summer naiad popula- tions.	54
DISCUSSION	55
The Relative Importance of the Variables Affect- ing the Feeding Behavior of the Naiads.	55
The Variables Affecting the Intensity of Intraspecific Interactions	55
The Effect of Hunger on the Interactions Between Naiads in Different Instars. . . .	59
The Relation Between the Activity of Final Instar Naiads and the Amount of Prey Eaten	59
The Relative Importance of the Naiad Dens- ity, Prey Density and Presence of Environ- mental Structure on the Number of Prey Eaten.	60

TABLE OF CONTENTS--continued	Page
The Effect of the Instar Distribution and the Pattern of Environmental Structure on the Feeding Behavior of Interacting Naiads.	61
The Relation Between the Feeding Behavior and the Instar Growth of the Naiads.	64
The Effect of Different Naiad and Prey Clump Densities on Instar Growth.	66
The Feeding Behavior and Growth of the Naiads Under Natural Conditions	68
The Effect of the Relative Abundance of Prey and the Density of Naiads on the Diversity of Prey Eaten by the Naiads in the Experimental Ponds.	68
The Size Differences Observed Among the Final Instar Naiads in the Experimental Ponds	71
SUMMARY	76
BIBLIOGRAPHY.	78
APPENDIX.	80

LIST OF TABLES

TABLE	Page
1. The Effect of Hunger and Size on the Avoidance Responses of (F) and (F-1) Naiads.	23
2. The Effect of Differences in the Hunger Levels, the Maximum Hunger Level and the Size of Two Interacting Naiads on Their Total Activity During the Experimental Observation Period ($\log_{10}$ cm).	25
3. The Effect of Hunger and Size on the Mean ($\pm$ Standard Error) Stalking Distance (cm) of Interacting Naiads	26
4. The Effect of Differences in the Hunger Levels, the Maximum Hunger Level, and the Size of Two Interacting Naiads on the Frequency of Aggressive Behaviors	28
5. A Comparison of the Aggressive Behaviors Exhibited by Interacting Naiads that were Different in Size	29
6. The Effect of Hunger on the Aggressive Behavior of the Larger of Two Interacting Naiads. .	30
7. The Effect of Hunger on the Mean ($\pm$ Standard Error) Avoidance Response (cm) of the Smaller of Two Interacting Naiads.	31
8. The Effect of the Amount of Prey Eaten on the Duration of the Digestive Pause and the Distance Traveled During the Period of Activity Following the Digestive Pause.	33
9. The Effect of Naiad Size and Prey Density on the Number of Prey Eaten: Feeding Behavior Over Successive Days without the Replacement of Prey.	34
10. The Relative Importance of the Naiad Density, Prey Density, and the Presence of Environmental Structure on the Number of Prey Eaten .	38

LIST OF TABLES--continued	Page
11. The Effect of the Number of Large Naiads and the Spatial Distribution of Structured Prey Clumps on the Pattern of Feeding by Interacting Naiads.	39
12. The Instar Duration (days) Means ($\pm$ S.E.) for the Naiads Reared on the Continuous but Restricted Feeding Treatments	43
13. The Differences in the Number of Feeding Bouts Per Instar Generated by the Interruptions in Feeding	45
14. The Differences in the Amount (grams) of Prey Consumed per Feeding Bout Generated by the Interruptions in Feeding.	46
15. The Differences in the Amount (grams) of Prey Consumed per Instar Generated by the Interruptions in Feeding.	47
16. The Differences in Instar Growth (the increase in labium length-measured in optical micrometer units) Generated by the Interruptions in Feeding	49
17. The Differences in Instar Growth and Duration Generated by Different Naiad and Prey Clump Densities	50
18. The Differences in the Mean Diversity ($\pm$ S.E.) of Naiad Gut Contents Generated by Different Naiad and Prey Densities in the Experimental Ponds	52
19. The Differences in the Labium Length (mm) Means Observed Among the Final Instar Naiads in the Experimental Ponds.	53
20. The Comparison of the Size Differences Observed Among the Final Instar Naiads in the Experimental Ponds with the Differences in the Prey Distributions Generated by the Experimental Manipulations	74

APPENDIX TABLES

1. Analysis of Variance of the Transformed ($\log_{10}$) Total Activity Data.	81
2. Analyses of Variance for Prey Consumption and Naiad Activity Date.	82
3. Analyses of Variance for the Data on the Feeding Bouts per Instar ($\log_{10}$ Days).	83
4. Analyses of Variance for the Data on the Prey Consumption (grams) per Feeding Bout	84
5. Analyses of Variance for the Data on the Prey Consumption (grams) per Instar	85
6. Analyses of Variance for the Data on the Growth of Isolated Naiads (Labium Increment Data) . . .	86
7. Analyses of Variance for the Data on the Growth of Interacting Naiads.	87
8. Analyses of Variance for the Data on Naiad Growth Under Natural Conditions.	88

LIST OF FIGURES

FIGURE	Page
1. The spatial distribution of the structured and unstructured prey clumps in the plastic pool.	36
2. The instar means for the transformed ($\log_{10}$ mm) labium length and labium increment data from the naiads reared on the continuous but restricted feeding treatments	42
3. The percentage composition of the pre- and post-emergence gut analysis samples taken from the low naiad x high prey density ponds.	70

INTRODUCTION

A consistent but unexplained pattern of significant differences in the mean size of the final instar, dragonfly naiads was observed in a set of ponds (Ross, 1967) whose naiad and prey densities had been experimentally manipulated (Hall et al., 1970). The objective of the present study was to find the behavioral mechanism which had generated the size differences among the naiads. The feeding behavior of individual predators (Holling, 1965; 1966) and populations of weakly interacting predators (Griffiths, 1969; Holling and Griffiths, 1969) is determined by the density of prey under laboratory conditions. However, with more strongly interacting predators, the feeding rate is determined by the predator density (Ivlev, 1961). Within a natural community, additional variables may affect the feeding behavior of strongly interacting predators. Ivlev (1961) reported that the effect of the distribution of prey overweighed the effect of prey density under both field and laboratory conditions. Many experimenters have also observed that the physical complexity of the environment has a significant effect on the feeding behavior of predators in the laboratory (Gause, 1934; Gause et al., 1936; Huffaker, 1958; Huffaker et al., 1963; Flanders, 1968; Glass, 1971).

Ivlev (1961) did not suggest a behavioral mechanism to account for the effect of the prey distribution on the feeding behavior of his predators, but it may have been a functional response (Holling, 1965, 1966) to the density of prey in each local aggregation within his experimental arena. If so, the effect of the prey distribution would increase as the activity of the predator decreased (a less active predator would be more likely to react to the local prey density rather than the overall prey density). Aeschnid naiads are not very active and do react to the relative abundance of prey (Pritchard, 1964). Anax junius naiads interact very strongly (cannibalism is not uncommon under laboratory conditions) and are primarily visual predators (Corbet, 1962); and the intensity of intraspecific interactions under field conditions are probably influenced by the distance between individual naiads imposed by the local distribution of prey and the degree to which the visual field of each naiad is restricted by the amount of physical structure present in its vicinity.

Because all or some combination of the above factors could have influenced the feeding behavior of the dragonfly naiads in the experimental ponds, the first series of laboratory experiments were designed to determine the relative importance of these variables on the feeding behavior of the Anax junius naiads. The second series of laboratory experiments were designed to determine the effect of

different feeding behaviors on the instar growth of the naiads. The results of the growth experiments were then used to interpret the size differences observed among the naiads in the experimental ponds.

METHODS

Culture Techniques

Anax junius Naiads

Unless otherwise noted, the naiads used in the following experiments were collected during late summer, brought into the laboratory, cooled gradually down to 16° C and maintained in B.O.D. boxes (Precision Scientific Model 805) under a 16:8 (light:dark) photoperiod. The naiads were fed 6-10 fourth instar chironomus larvae once each week. Mortality was less than one percent under these conditions.

The naiads selected for a given experiment were warmed gradually (one degree per day) to room temperature. They were fed ad libidum until they molted; then, they were placed under the particular experimental conditions.

At 16° C, the naiads were kept individually in disposable plastic drinking cups filled with filtered (charcoal) tap water to a depth of 1½ inches. At room temperature, the naiads were kept in green, plastic pint cottage cheese containers filled to a depth of one inch.

Chironomus tentans Larvae

Permanent chironomus cultures were maintained in two large (47" x 22" x 13½") screen-covered aquaria. Fertilized

adult female chironomus were collected daily from these two cultures. The females were placed in a small glass (two gallon), screen-covered aquarium filled to a depth of $1\frac{1}{2}$ inches. After the females had oviposited, the egg masses were collected from the water. Two egg masses were placed in each of the two gallon, glass aquaria that were used as the initial culture vessels. A one-half inch layer of blended toilet paper was maintained as the substrate for the chironomus larvae, and 0.25-0.50 cc (instars 1 and 2) or 1-2 cc (instars 3 and 4) of blended chicken mash was added daily for food. All culture vessels were aerated vigorously to prevent bacterial fouling. As soon as fourth instar larvae appeared in the glass aquaria, all larvae were transferred to large plastic pans (19" x 17" x 4"). Fourth instar larvae were picked out of these pans and were used to feed the naiads. At least 1,000 fourth instar larvae were available daily under these culture methods.

Apparatus

Experimental Lighting System

The experiments were conducted in two 8'x 8' rooms under a controlled, 16:8 (light:dark) photoperiod. Each pan in the experimental rooms was lighted by a single 10 watt incandescent light (placed 15 inches above the pan). The lights were turned on and off gradually over an 80 minute period by means of a reversing motor connected to an autotransformer.

To increase the length of the on-off transitions, a pair of time delay relays supplied one second of current at five minute intervals to the reversing motor. Under these conditions, the motor turned 6.25 percent of the total on-off distance every five minutes.

Activity Chambers

Naiad activity was measured automatically in activity chambers. The chambers consisted of two concentric, circular, opaque green plexiglass strips glued to a clear plexiglass plate to form a circular channel $5/8$ " wide, 1" deep and approximately 46" in circumference. A $3/8$ " wide strip of fiberglass screening was glued down the center of the channel to provide purchase for the naiads (they could not walk on the smooth surface of the plexiglass). At regular intervals, five, focused pen lights were mounted above the center of the channel. Opaque mounts for the lights were constructed by boring a $3/8$ " hole in No. 5 black rubber stoppers. A circular piece of a Wratten gelatin filter (No. 27) was cemented over the open end of the bored stopper. This provided a focused beam of red light that was not readily visible to the naiads (Autrum and Kolb, 1968).

The channel plate was mounted on a base of $3/8$ " plywood cut to fit and painted flat black to reduce the background light intensity. Beneath each light beam, a $1/16$ " hole was drilled completely through the plywood. The $1/16$ " holes were re-drilled to $3/8$ " in diameter from below to within

1/4" from the upper surface of the plywood. Photocells were then inserted in these 3/8" holes and connected, using shielded leads, to Heathkit photoelectric relays. The outputs of the relays were connected to a 20 channel Esterline Angus event recorder. The activity chambers recorded directional and temporal data every time a naiad moved 9.2 inches.

The activity chambers were filled to a depth of 3/4 inches. The water was changed daily. The naiads were fed in the activity chambers by dropping opaque green partitions down in front of and behind the naiads. All of the chironomus larvae were then placed in this enclosed space with the naiad. After the larvae had been consumed, the water in the chamber was siphoned out and replaced. Only after these maintenance activities had been completed were the partitions removed. This procedure minimized the disturbance of the naiad.

The activity chambers were isolated from each other within one of the light-controlled rooms that was well-insulated from the noise and activity of the rest of the laboratory.

Experimental Arenas

Large, blue plastic pans (19" x 17" x 4") were used in the behavioral studies. The bottoms of these pans were roughened by lightly sanding them with rough sandpaper in order to provide purchase for the naiads. The bottoms were also gridded in 10 centimeter squares with a black, felt-tip pen. A circular wading pool, five feet in diameter, was similarly roughened and gridded.

Artificial Prey Clumps

Easily moveable prey clumps were created by using the lids of disposable plastic petri dishes. The "bottom" of the lid was covered with a disk of fiberglass screening to provide purchase of the naiads. The contrast in color between new blended toilet paper and the chironomus larvae was reduced by blending a 1:2 mixture of old (strained from an old culture) and new substrate. Five to six cc of this brown substrate were poured into the petri dish lid, and then, the chironomus larvae were added. The petri dishes were allowed to sit, undisturbed, overnight in the experimental arenas. Any larvae that had moved out of the dishes during this time were found beside or beneath their respective dishes. These larvae were returned to their dishes; and after an additional 15-30 minute wait for these larvae to settle down, the naiads were added to the pans.

Experimental Design and Analysis

The Relative Importance of the Variables Affecting the Feeding Behavior of the Naiads

Variables Affecting the Intensity of Intraspecific Interactions

Hoppenheit (1964) demonstrated that the size of the prey and the hunger of the attacking naiad were major factors in determining the intensity of aggressive behavior by large aeschnid naiads. Consequently, the size and hunger levels of

Anax junius naiads were manipulated in order to determine their effect on the frequency and intensity of intraspecific interactions. Pairs of naiads were placed in unstructured pans and observed for a thirty minute period. Eight pairs of naiads were observed at each treatment combination. The individual members of each pair were randomly selected from two large groups of final (F) and penultimate (F-1) instar naiads and were run only once each day. Individual naiads did appear in more than one treatment combination over successive days. However, all individual responses were recorded separately, and no consistent individual trends through time were observed. As a result, it was concluded that individual behavior was not affected by the interactions occurring on the preceding day. Any naiads injured during the interactions were not used again. The average length and weight of the (F) naiads were 39.3 mm and 1.00 grams. The respective values for the (F-1) naiads were 32.0 mm and 0.58 grams.

Total activity, stalking, striking and avoidance behavior were recorded. χ^2 tests were used to analyze the frequency data. An analysis of variance was performed on the total activity data (the combined distance moved by both naiads). The means and variances for these data were significantly related, and a logarithmic (base 10) transformation was used to remove this relationship before proceeding with the analysis. A five percent significance level was

used throughout this study. Differences among treatment means in the analysis of variance were analyzed with Duncan's New Multiple Range test (Steel and Torrie, 1960).

The means and standard errors for the treatment combinations were presented to illustrate behavior trends in the data on the avoidance responses and stalking distances.

The effect of hunger on the interactions between naiads in the same instar.--A 2^n factorial design ($n=3$) was used to determine the effects of naiad size, the contrast between the hunger levels of the interacting naiads and the maximum hunger level represented in the interaction on the frequency and intensity of interactions between naiads similar in size. (F) and (F-1) naiads were used in this study. The hunger levels were either equal or unequal, and the maximum hunger levels were either 48 or 72 hours of food deprivation.

The effect of hunger on the interactions between naiads in different instars.--A 3×3 factorial design was used to determine the effects of size and hunger of the individual naiads interacting on the frequency and intensity of interactions between naiads that were not similar in size. (F) and (F-1) naiads were deprived of food for 24, 48 and 72 hours.

The Relation Between the Activity of Final Instar Naiads and the Amount of Prey Eaten

In pilot studies using the activity chambers, the level of individual activity was found to be affected by the size,

time within an instar, past feeding history and present feeding history of the individual naiad. However, in context of the studies on intraspecific interactions, it was decided that it was more important to determine when a naiad would become active rather than the level of activity (activity of any intensity released stalking and striking responses). As a result, the effect of the amount of prey consumed on the activity of the naiads was studied.

To remove the effect of individual differences in the level of activity, a randomized, complete block design was used. Seven, (F) instar naiads (the final instar naiads were studied because they dominated the intraspecific interactions) were placed in the activity chambers and were fed fixed amounts of prey at 48 hour intervals. The food levels (0.03, 0.06, 0.09, 0.12 grams wet weight) represented 12.5, 25.0, 37.5 and 50.0 percent of the prey consumption normally exhibited by (F) naiads on a 48 hour feeding schedule. In terms of fourth instar chironomus larvae, the food levels represented 2, 4, 6, and 8 larvae.

The digestive pause and the total distance traveled during the first period of activity following feeding were recorded. Duncan's New Multiple Range test was used to analyze differences among the treatment means.

The Relative Importance of the Naiad Density,
Prey Density, and the Presence of Environmental
Structure on the Number of Prey Eaten

In the following series of experiments, 2 x 2 factorial designs with three replicates per treatment combination were

used. An artificial prey clump was placed in each corner of the pans. Environmental structure was generated by placing 18 inverted, disposable, plastic drinking cups in the pans. The naiads were deprived of food for 24 hours prior to being placed in the pans. The total number of prey consumed in the three pans was recorded, and χ^2 tests were performed on the resulting 2 x 2 contingency tables.

The feeding behavior of solitary naiads: the effect of naiad size and prey density on the feeding behavior over a three day period.--Solitary (F) and (f-1) naiads were used in this study. The prey densities were 15 and 25 chironomus larvae per clump. The experiment was run for three consecutive days without replacing the prey that had been consumed. Once each day, the naiads were removed from the pans, and the prey remaining in each clump were counted. The clumps were returned to their original positions; and after the prey had settled down in the clumps (15-30 minutes), the naiads were returned to their respective pans.

The feeding behavior of interacting naiads: the effect of naiad size and density.--(F) and (F-1) naiads were used in this study. One or two naiads were placed in unstructured pans. The prey density was fixed at 15 chironomus larvae per clump. The experiment was terminated after 24 hours.

The effect of naiad size and the presence of environmental structure.--(F) and (F-1) naiads were used in this

study. Two naiads were placed in structured and unstructured pans. The prey density was fixed at 15 chironomus larvae per clump.

The effect of prey density and the presence of environmental structure.--Two (F-1) naiads were placed in structured and unstructured pans. Prey densities of 15 and 25 chironomus larvae per clump were used.

The Effect of the Instar Distribution
and the Pattern of Environmental
Structure on the Feeding Behavior of
Interacting Naiads

In order to determine the effect of the interaction between the pattern of environmental structure and the intensity of intraspecific interactions on the feeding behavior of interacting naiads, naiads in groups of three were placed in a circular pool five feet in diameter. Five clumps of 25 prey each were placed in the pool at regular distances from each other. Structured clumps were generated by gluing two opaque green strips ($1\frac{1}{2}$ " x $5\frac{1}{2}$ ") of plexiglass together to form a right angle and placing the prey clump within the arms of the right angle. The naiads were deprived of food for 24 hours prior to being placed in the pool. After 24 hours, the naiads were removed from the pool. The number of prey consumed from each clump were counted, and the experiment was terminated.

A 4 x 3 factorial design with one replicate per treatment combination was used in this study. Four size

distributions of (F) and (F-1) naiads, 3(F), 2(F)1(F-1), 1(F)2(F-1) and 3(F-1), and three spatial arrangements of structured clumps, three adjacent, two adjacent and two separated by an unstructured clump, were selected (see Figure 1 on page 36). Within each treatment combination, the difference in prey consumption between the structured and unstructured clumps was tested with a χ^2 test. The pattern of the resulting significant differences was then used to judge the intensity of intraspecific interactions with respect to the number of large naiads and the number and spatial relationships of structured clumps.

The Relation Between the Feeding Behavior and the Instar Growth of the Naiads

The limited duration of the preceding studies precluded the interpretation of the significance of the differences in prey consumption with respect to naiad growth. The following studies were designed to determine the effect of disturbances in feeding behavior on naiad growth.

The Effect of Different Feeding Patterns on the Instar Growth of Isolated Naiads

The prey consumption by individual naiads was not monitored in the instar distribution studies, and as a result, the behavioral details of the interference phenomenon were not recorded. However, the results of the studies on intraspecific interactions suggested two possible explanations for the reduction in prey consumption. During the observation

periods in the interaction studies, the naiads spent as long as 25 minutes watching each other without moving. Similar behavior during the predation studies would have reduced the number of prey consumed per feeding bout without necessarily reducing the number of feeding bouts. On the other hand, intraspecific interactions resulted in considerable avoidance behavior; and if there were a limited number of prey clumps in a large area, the avoidance responses would move naiads away from clumps and decrease the number of feeding bouts without necessarily reducing the number of prey consumed per feeding bout. The effects of these two different disturbances in feeding behavior, continuous feeding with restricted prey consumption and discontinuous feeding with unrestricted prey consumption, were investigated in the following studies.

Feeding continuous but restricted in amount.--The naiads used in this study were collected from the field in October and November. In order to determine whether size differences among naiads could be reversed by feeding differences, the naiads were grouped according to their size within an instar, generating an initial size difference between the two food levels. The smaller naiads were put on a high food level (10 chironomus larvae per day), and the larger naiads were put on a low food level (5 chironomus larvae per day). Both groups were maintained at these food levels in the B.O.D. boxes at $24 \pm 2^{\circ}$ C until metamorphosis.

Individual molting dates and labium lengths (measured from the preserved exuviae) were recorded. The variances for the labium length data were heterogeneous, and the data were transformed using common logarithms (the individual measurements were multiplied by 100 to generate whole numbers and simplify the transformation). The instar differences were tested with Student's t statistic, using a two-tailed test with a five percent significance level.

Feeding interrupted but unrestricted in amount.--Since the time at which an interruption in feeding occurred within an instar could be important because of the molting cycle (the sensitivity to disturbances in feeding would increase if both instar growth and molting processes overlapped late within an instar), single, long interruptions (72 hours in duration) in feeding were made during the beginning (day 2), middle (day 5) or end (day 7) of the instar. In contrast to these single interruption treatments, multiple interruption treatments were also run where the naiads were fed every 48 or every 72 hours. In the control treatment, the naiads were fed every 24 hours. When fed, the naiads were given more prey than they could consume in 24 hours.

Since temperature also influences growth in invertebrates, the six feeding treatments were run at 24⁰ and 27⁰ C. Six naiads were reared at each treatment combination.

The total prey consumption per individual naiad per day (grams wet weight), molting dates and labium length (measured

from preserved exuviae) were recorded. The experiment was terminated when the naiads molted into the last instar.

Instar growth, instar duration and prey consumption data were analyzed using a 2 x 6 factorial analysis of variance. The instar duration variances were heterogeneous and not independent of the means. Consequently, these data were transformed using common logarithms. Differences among treatment means were analyzed with Duncan's New Multiple Range Test.

The Effect of Different Naiad and Prey Clump Densities on Instar Growth

In the preceding growth studies, the feeding behavior was manipulated directly by the experimenter. In the following study, the densities of naiads and prey clumps were manipulated; and the resulting intraspecific interactions determined the growth and feeding behavior of the naiads. The naiads were reared for two complete instars in structured pans under a 16:8 photoperiod with a twilight transition. Twelve, inverted, disposable plastic drinking cups were placed in the pans to generate the structure. The temperature was not controlled and ranged from 24° to 28° C. The naiad densities (one and three naiads per pan) and the clump densities (two and 12 clumps per pan) were manipulated according to a 2 x 2 factorial design. The prey density was fixed at 27 chironomus larvae per clump. Five and six individual naiads per treatment combination were started at the low and

high naiad densities, respectively, but cannibalism and irregularities in molting reduced the replication to four naiads per treatment combination.

Two identical sets of pans were used in the study. While the naiads were in one set, the water and prey were replaced in the duplicate set. The inverted drinking cups were placed over the replenished prey clumps (the petri dish lids were not used in this study because of the lack of space at the high clump density), and the pans sat overnight with the prey under the cups.

The next morning, at 9:00 A.M., the cups were moved to one side, exposing the prey clumps. After waiting 15-30 minutes for the prey to settle down, the naiads were transferred to the replenished pans. In the pans with only two prey clumps exposed, four prey clumps (one in each corner) were placed in the pan. At 3:00 P.M., the alternate set of diagonal clumps was exposed, and the two diagonal clumps that had been initially exposed at 9:00 A.M. were covered again with the inverted drinking cups.

The naiads used in this study were reared ab ovo. Prior to the start of the experiment, the naiads were measured, and a group equal in size were selected for the experiment. Thus, at the start of the experiment, there were no significant differences in size among the treatment combinations. Each individual naiad was uniquely marked on the dorsal surface of the abdomen with a black felt-tipped pen. A unique

combination of abdominal spines was also clipped in order to identify newly molted individuals for re-marking purposes (the abdominal spines required two molts to grow back completely).

Individual molting dates and labium length measurements (from preserved exuviae) were recorded. The instar duration and growth data were analyzed according to the 2 x 2 factorial design. Differences among the treatment combination means were analyzed with Duncan's New Multiple Range Test.

The Feeding Behavior and Growth of the Naiads Under Natural Conditions

Because the spatial dimensions and structural complexity of the laboratory arenas did not begin to approximate the actual area and complexity of the predator's natural habitat, data on growth and feeding behavior were collected from the field. Of critical importance for the comparison of the laboratory and field results was the fact that the field data was collected from a group of ponds, identical in size and depth and whose predator and prey densities had been experimentally manipulated (see Hall et al., 1970, for a complete description of the experimental manipulations).

The Effect of the Relative Abundance of Prey and the Density of Naiads on the Diversity of the Prey Eaten

Using a 6 x 100 foot seine, samples consisting of 25-30 large naiads were collected from selected ponds every two weeks during August and once a month during September and

October. All samples were collected at night.

The gut contents were identified by comparing the prey remains with a complete collection of the potential prey organisms present in the ponds. The gut analyses for each pond sample were grouped on the basis of the emergence period (the pre-emergence samples were collected prior to the emergence of the principal prey species in August; the post-emergence samples were collected after the August emergence period), prey density (high or low) and naiad density (high or low), and the percentage composition and diversity for each sample within the group were calculated. Simpson's D (Pielou, 1970) was selected for the calculation of the sample diversity. In the instances where the number of pond samples was greater than one, the mean of the sample indices was calculated. The standard error for this mean diversity index was calculated in both of the following ways, by using the variance about the mean index or by using the mean variance calculated from the variances of the sample indices (Simpson, 1949). The standard error appearing in Table 18 is the larger of these two values.

The Size Differences Observed Among the
Final Instar Naiads in the Experimental
Ponds

Differences in naiad growth among the ponds were assessed in both overwintering and summer populations by collecting (F) instar exuviae from the ponds during the emergence periods in June and August. Sixteen exuviae were collected from each

pond. Using data on the prey densities supplied by Dr. Cooper, the ponds were classified in terms of the actual prey densities when the large naiads were present in the ponds. Using exuviae density (from Dr. Cooper's emergence traps)/Chironomus tentans density (fourth instar larvae only) ratios, the ponds were classified in terms of naiad densities (high and low). This determination of naiad density was based on the potential intensity of intraspecific interactions. Sixteen ponds could be unequivocally classified using the fall benthos data (four replicates per treatment combination). Because of the nutrient manipulations, the ponds changed during the summer; and only twelve ponds could be unequivocally classified using the summer benthos data (three replicates per treatment combination).

The ponds were the experimental units, and the labium length means for the exuviae collected from each pond were used in the 2 x 2 factorial design. Differences among the treatment combination means were analyzed with Duncan's New Multiple Range Test.

RESULTS

The Relative Importance of the Variables Affecting the Feeding Behavior of the Naiads

The Variables Affecting the Intensity of Intraspecific Interactions

The Effect of Hunger on the Interactions Between Naiads in the Same Instar

Avoidance responses (Table 1)

(F) Naiads.--The interaction between the hunger level of the naiad being attacked and the strike intensity had a significant effect on the avoidance responses of (F) naiads. At the low hunger level, the mean avoidance response decreased as the strike intensity increased. At the high hunger level, the mean avoidance response increased as the strike intensity increased.

(F-1) Naiads.--The strike intensity had a significant effect on the avoidance responses of (F-1) naiads. The mean avoidance response increased as the strike intensity increased.

Table 1. The Effect of Hunger and Size on the Avoidance Responses* of (F) and (F-1) Naiads

Avoidance Responses by (F) Naiads:

		Strike Intensity	
		Low	High
Hunger of the Naiad Attacked	Low	23±6 N=18	7±2 N=26
	High	14±3 N=30	25±5 N=27

Avoidance Responses by (F-1) Naiads:

		Strike Intensity	
		Low	High
Hunger of the Naiad Attacked	Low	11±3 N=14	15±2 N=25
	High	11±2 N=22	19±2 N=48

*These data are the mean distances (cm) ± the standard errors, traveled by naiads in response to a strike by another naiad (the strike initiates the avoidance behavior). The strike intensity is determined by the hunger level of the attacking naiad.

Total activity (Table 2).--The main effect of Naiad Size and the effects of the interactions between Hunger Contrast and the Naiad Size and among Hunger Contrast, Maximum Hunger Level and Naiad Size were significant. The total activity of the (F) naiads was less than that of the (F-1) naiads. The significant interaction among the Hunger Contrast, Maximum Hunger Level and Naiad Size treatments was caused by a difference in the responses of (F) and (F-1) naiads to the 72 Hour, Hunger contrast treatment combination. Under these conditions, (F) naiads increased their total activity while (F-1) naiads decreased their total activity.

The significant interaction between the Hunger Contrast and Naiad Size was caused by the response of (F) and (F-1) naiads to differences in the hunger levels of interacting naiads. In the presence of a contrast in hunger levels, (F) naiads increased their total activity while (F-1) naiads decreased their total activity.

Stalking distance (Table 3).--The mean stalking distance of both (F) and (F-1) naiads was not affected by hunger. However, the mean stalking distance did increase significantly with the size of the naiad.

Total complete stalks (Table 4).--The contrast in hunger levels had a significant effect (significant χ^2 results are indicated on Tables 4, 5, 6, 9 and 10 by the presence of the corresponding row, column or grand totals) on the number of stalks completed by (F) and (F-1) naiads. The frequency

Table 2. The Effect of Differences in the Hunger Levels, the Maximum Hunger Level and the Size of Two Interacting Naiads on Their Total Activity During the Experimental Observation Period ($\log_{10}$ cm)

First-Order Interactions:

Hunger Level Contrast x Naiad Size

Treatment

Hunger Contrast	Abs.	Pres.	Pres.	Abs.
Naiad Size	(F)	(F)	(F-1)	(F-1)
Mean	<u>1.78</u>	<u>2.06</u>	<u>2.24</u>	<u>2.50</u>

Second-Order Interactions:

Hunger Level Contrast x Maximum Hunger Level x Naiad Size

Treatment

Hunger Contrast	Abs.	Pres.	Abs.	Pres.	Pres.	Abs.	Pres.	Abs.
Maximum Hunger	48	48	72	72	72	48	48	72
Naiad Size	(F)	(F)	(F)	(F-1)	(F)	(F-1)	(F-1)	(F-1)
Mean	<u>1.76</u>	<u>1.79</u>	<u>1.80</u>	<u>2.08</u>	2.32	2.40	2.40	2.60

Means subtended by the same line are not significantly different at the five percent level.

Table 3. The Effect of Hunger and Size on the Mean ($\pm$ Standard Error) Stalking Distance (cm) of Interacting Naiads

		HUNGER CONTRAST			
		Absent		Present	
Maximum Hunger Level		48	72	48	72
Naiad Size	(F)	33 $\pm$ 2 N = 20	31 $\pm$ 2 N = 25	31 $\pm$ 2 N = 16	30 $\pm$ 2 N = 48
	(F-1)	23 $\pm$ 2 N = 36	21 $\pm$ 2 N = 43	23 $\pm$ 2 N = 25	22 $\pm$ 2 N = 29

of completed stalks increased when the hunger levels of interacting naiads were different.

Total strikes (Table 4).--The contrast in hunger levels and the size of the predator both had a significant effect on the total number of strikes. The frequency of strikes increased with both naiad size and the presence of hunger contrasts.

The Effect of Hunger on the Interactions
Between Naiads in Different Instars

Comparison of aggressive behavior (Table 5).--(F) naiads stalked and struck more than (F-1) naiads.

Aggressive behavior of the larger naiad (Table 6).--The total number of stalks and strikes by (F) naiads was significantly affected by hunger. The frequency of these behaviors increased as the hunger of the (F) naiad increased.

Avoidance behavior of the smaller naiad (Table 7).--The mean avoidance response of the (F-1) naiads increased as the hunger of the (F) naiads increased. The mean avoidance response at the (F)-24 x (F-1)-24 treatment combination was the smallest observed, and it was significantly different from the next to the smallest avoidance response at the (F)-24 x (F-1)-48 treatment combination.

Table 4. The Effect of Differences in the Hunger Levels, the Maximum Hunger Level, and the Size of Two Interacting Naiads on the Frequency of Aggressive Behaviors

Total Complete* Stalks

		HUNGER CONTRAST			
		Absent		Present	
Maximum Hunger Level		48	72	48	72
Naiad Size	(F)	22	19	34	42
	(F-1)	31	34	35	37
		106		148	

Total Strikes

		HUNGER CONTRAST			
		Absent		Present	
Maximum Hunger Level		48	72	48	72
Naiad Size	(F)	24	31	39	54
	(F-1)	23	29	31	30
		107		154	

*In a complete stalk, the attacking naiad confronts the naiad being stalked. In an incomplete stalk, the attacking naiad turns away and does not confront the naiad being stalked.

**Table 5. A Comparison of the Aggressive Behaviors Exhibited
by Interacting Naiads that were Different in Size**

		Naiad	Size	
		(F)	(F-1)	
Aggressive Behavior	Total Stalks	257	62	319
	Total Strikes	195	46	241
		452	108	

Table 6. The Effect of Hunger on the Aggressive Behavior of the Larger of Two Interacting Naiads

Total Stalks

		(F) NAIAD HUNGER LEVEL		
		24	48	72
(F-1) Naiad Hunger Level	24	29	30	39
	48	27	27	28
	72	13	27	37
		69	84	104

Total Strikes

		(F) NAIAD HUNGER LEVEL		
		24	48	72
(F-1) Naiad Hunger Level	24	17	27	32
	48	16	21	21
	72	12	21	28
		45	69	81

Table 7. The Effect of Hunger on the Mean ($\pm$ Standard Error) Avoidance Response (cm) of the Smaller of Two Interacting Naiads

		(F) NAIAD HUNGER LEVEL		
		24	48	72
(F-1) Naiad Hunger Level	24	14 $\pm$ 3 N = 22	21 $\pm$ 4 N = 22	22 $\pm$ 2 N = 35
	48	20 $\pm$ 2 N = 23	26 $\pm$ 3 N = 23	30 $\pm$ 5 N = 25
	72	24 $\pm$ 6 N = 14	21 $\pm$ 2 N = 26	31 $\pm$ 5 N = 33

The Relation Between the Activity of Final
Instar Naiads and the Amount of Prey Eaten

The duration of the digestive pause (Table 8).--The duration of the digestive pause was significantly affected by the amount of prey consumed. The length of the inactive period immediately following feeding increased when the prey consumption exceeded 25 percent of the unrestricted prey consumption.

The total distance traveled during the period of activity following the digestive pause (Table 8).--The total distance traveled during the activity bouts following feeding was significantly affected by the amount of prey consumed. The total distance traveled increased as the prey consumption dropped below 37.5 percent of the unrestricted prey consumption.

The Relative Importance of the Naiad Density,
Prey Density, and the Presence of Environ-
mental Structure on the Number of Prey Eaten

The feeding behavior of solitary naiads (Table 9).--Prey consumption was significantly affected by both naiad size and prey density. Prey consumption increased with both naiad size and prey density.

The total prey consumption varied significantly over the three successive days of feeding. The total prey consumption was the highest on the first day and the lowest on the second day. There was also a significant interaction between naiad size and prey density on the second day.

Table 8. The Effect of the Amount of Prey Eaten on the Duration of the Digestive Pause and the Distance Traveled During the Period of Activity Following the Digestive Pause

DIGESTIVE PAUSE

Treatment

Food Level 12.52%* 25% 37.5% 50%

Mean

(Minutes) 105.7 239.9 494.2 433.8

TOTAL DISTANCE TRAVELED

Treatment

Food Level 50% 37.5% 25% 12.5%

Mean

(Feet) 7.7 9.2 18.4 35.3

Means subtended by the same line are not significantly different at the five percent level.

* Percent of the unrestricted prey consumption for a 48 hour feeding schedule.

Table 9. The Effect of Naiad Size and Prey Density on the Number of Prey Eaten; Feeding Behavior Over Successive Days without the Replacement of Prey

<u>Day 1</u>		Prey Density/Clump		
		15	25	
Naiad Size	(F)	54	72	126
	(F-1)	35	51	86
			89	123
<u>Day 2</u>		15	25	
	(F)	24	25	49
	(F-1)	9	26	35
<u>Day 3</u>		15	25	
	(F)	36	49	85
	(F-1)	13	28	41
			49	77

* The interaction between naiad size and prey density was significant.

Figure 1. The spatial distribution of the structured and unstructured prey clumps in the plastic pool.

A = Two adjacent, structured clumps.

B = Two separated, structured clumps.

C = Three adjacent, structured clumps.

(F) naiads did not increase their prey consumption as the prey density increased, while the (F-1) naiads ate fewer prey than expected at the low prey density.

The feeding behavior of interacting naiads (Table 10).

The effect of naiad size and density.--The effects of both naiad size and density were significant. Prey consumption increased with naiad size and decreased with naiad density.

The effect of naiad size and the presence of environmental structure.--The effect of naiad size was significant. Prey consumption increased with naiad size.

The effect of prey density and the presence of environmental structure.--None of the treatment effects were significant.

The Effect of the Instar Distribution and the Pattern of Environmental Structure on the Feeding Behavior of Interacting Naiads (Table 11)

Large naiads not present (row 4 in Table 11).

No significant differences in the intensity of predation on the structured and unstructured prey clumps were observed.

Large naids present (the remaining cells in columns 1-3 in Table 11).

When the number of structured prey clumps was equal to the total number of interacting naiads (column 1 in Table 11), the feeding intensity was greater on the structured prey clumps.

Table 10. The Relative Importance of the Naiad Density, Prey Density, and the Presence of Environmental Structure on the Number of Prey Eaten

The Effect of Naiad Size and Density

		Naiad	Density	
		1	2*	
Naiad Size	(F)	53	25	78
	(F-1)	35	16	51
		88	41	

The Effect of Naiad Size and the Presence of Environmental Structure

		Structure		
		Absent	Present	
Naiad Size	2*(F)	25	24	49
	2*(F-1)	16	17	33

The Effect of Prey Density and the Presence of Environmental Structure (2*(F-1) naiads were present)

		Structure		
		Absent	Present	
Prey Density/Clump	15	16	17	
	25	17	22	

*One half the total prey consumption is shown to adjust for the increase in naiad density.

Table 11. The Effect of the Number of Large Naiads and the Spatial Distribution of Structured Prey Clumps on the Pattern of Feeding by Interacting Naiads

The Number and Proximity of Structured Prey Clumps				
		3 Adjacent	2 Adjacent	2 Separated
Number of Large Naiads Present	3	S > U*	NS	S < U**
	2	S > U*	NS	NS
	1	S > U*	NS	NS
	0	NS	NS	NS

*The predation was greater on the structured prey clumps.

**The predation was greater on the unstructured prey clumps.

When the number of adjacent, structured prey clumps was less than the total number of interacting naiads (column 2 in Table 11), no significant differences in the intensity of predation on the structured and unstructured prey clumps were observed.

When the number of separated, structured prey clumps was less than the total number of interacting naiads (column 3 in Table 11), the feeding intensity was greater on the unstructured clumps when all of the interacting naiads were large.

The Relation Between the Feeding Behavior and the Instar Growth of the Naiads

The Effect of Different Feeding Patterns on the Instar Growth of Isolated Naiads

Feeding continuous but restricted in amount.--

Differences in instar growth (Figure 2).--Significant growth differences were observed in all of the instars represented in this study. Instar growth was greater at the high food level, and the initial size difference was reversed after two molts.

Differences in instar duration (Table 12).--Significant differences in instar durations were observed in all of the instars represented in this study. The naiads spent at least twice as long in a given instar at the low food level (5 chironomus larvae) as at the high food level (10 chironomus larvae).

Figure 2. The instar means for the transformed ($\log_{10}$ mm) labium length and labium increment data from the naiads reared on the continuous but restricted feeding treatments.

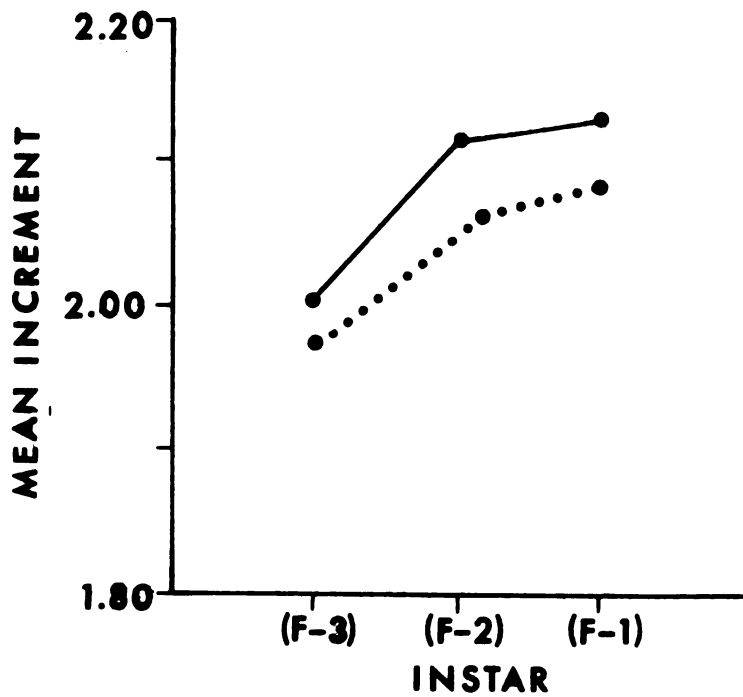
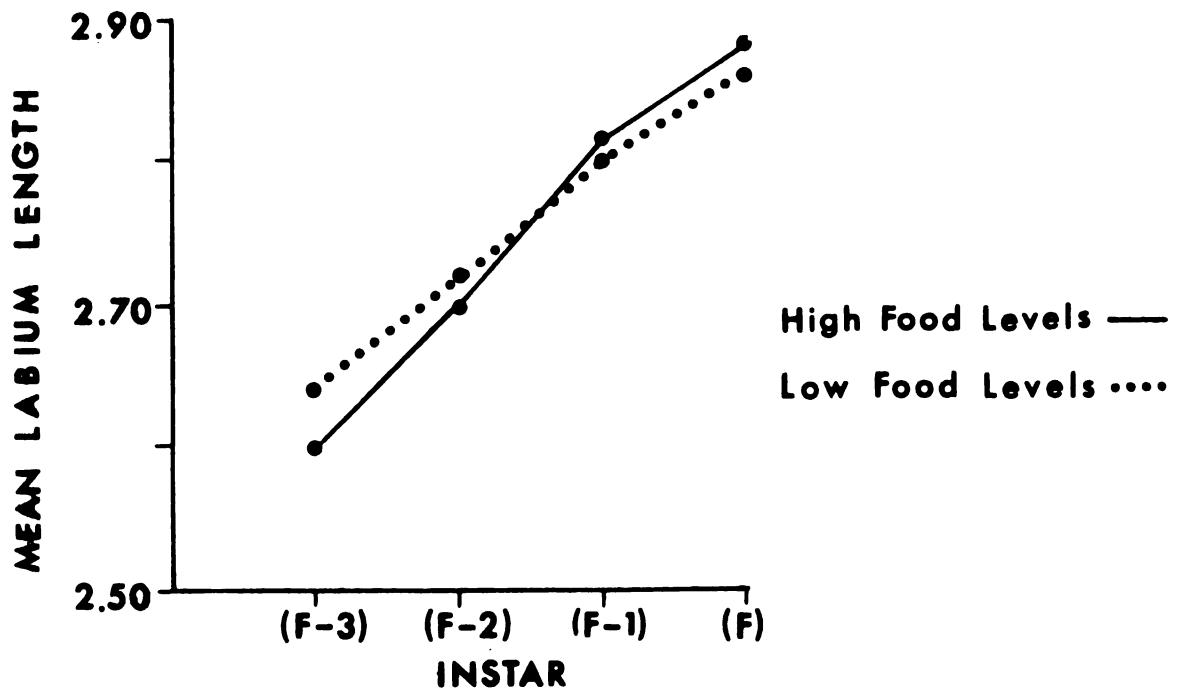


Figure 2

Table 12. The Instar Duration (days) Means ($\pm$ S.E.) for the Naiads Reared on the Continuous but Restricted Feeding Treatments

		Food Level	
		High	Low
Instar	(F-3)	9 ± 1 $N = 15$	24 ± 1 $N = 27$
	(F-2)	11 ± 1 $N = 23$	28 ± 2 $N = 27$
	(F-1)	14 ± 1 $N = 39$	30 ± 1 $N = 24$
	(F)	23 ± 1 $N = 34$	43 ± 1 $N = 27$

Feeding interrupted but unrestricted in amount.--

The number of feeding bouts per instar (Table 13).--

In both instars, the feeding treatments had a significant effect on the number of feeding bouts per instar. Multiple interruptions in feeding caused a decrease in the number of feeding bouts. No significant differences were observed among the means for the multiple interruption treatments in both instars or among the means for the single interruption treatments in instar (F-1). Significant differences among the means for the single interruption treatments were observed in instar (F-2). A single interruption in feeding at the end of the instar caused an increase in the number of feeding bouts.

The amount (grams) of prey consumed per feeding bout (Table 14).--In both instars, the feeding treatments had a significant effect on the amount of prey consumed per feeding bout. Multiple interruptions in feeding caused an increase in the prey consumption. The means for the multiple interruption treatments were significantly different, and an increase in the duration of the multiple interruption caused an increase in the prey consumption. No differences were observed among the means for the single interruption treatments.

The amount (grams) of prey consumed per instar (Table 15).--No significant differences were observed in instar (F-2).

Table 13. The Differences in the Number of Feeding Bouts Per Instar Generated by the Interruptions in Feeding (m = multiple interruptions; s = single interruptions; c = no interruptions)

Instar (F-2)					
Treatment					
Feeding Pattern					
72 _m	48 _m	72 _s Beginning	72 _s Middle	24 _c	72 _s End
Mean					
7.0	8.4	10.9	12.0	12.7	13.2

Instar (F-1)					
Treatment					
Feeding Pattern					
72 _m	48 _m	24 _c	72 _s Beginning	72 _s End	72 _s Middle
Mean					
9.0	10.3	16.6	16.9	17.3	17.6

Means subtended by the same line are not significantly different at the five percent level.

Table 14. The Differences in the Amount (grams) of Prey Consumed per Feeding Bout Generated by the Interruptions in Feeding (m = multiple interruptions; s = single interruption; c = no interruptions)

Instar (F-2)						
Treatment						
Feeding Pattern						
72 _s Middle	72 _s End	24 _c	72 _s Beginning	48 _m	72 _m	
Mean						
0.08	0.09	0.09	0.09	0.12	0.15	

Instar (F-1)						
Treatment						
Feeding Pattern						
72 _s End	72 _s Middle	24 _c	72 _s Beginning	48 _m	72 _m	
Mean						
0.12	0.12	0.13	0.14	0.18	0.21	

Means subtended by the same line are not significantly different at the five percent level.

Table 15. The Differences in the Amount (grams) of Prey Consumed per Instar Generated by the Interruptions in Feeding (m = multiple interruptions; s = single interruption; c = no interruptions).

Instar (F-1) *					
Treatment					
Feeding Pattern					
48 _m	72 _m	72 _s End	24 _c	72 _s Middle	72 _s Beginning
Mean					
1.88	1.89	1.93	2.09	2.12	2.24
Temperature		24° C	27° C		
Mean		<u>2.09</u>	<u>1.96</u>		

Means subtended by the same line are not significantly different at the five percent level.

*No significant differences were observed in Instar (F-2).

The instar (F-1), both feeding and temperature treatments had significant effects. The prey consumption decreased as the temperature increased. The prey consumption also decreased when the feeding interruptions were multiple or occurred at the end of the instar.

Differences in instar growth (Table 16).--No significant differences were observed in instar (F-1).

In instar (F-2), the feeding treatment had a significant effect. Instar growth decreased when the feeding interruptions were multiple or occurred at the end of the instar. Instar growth also decreased as the duration of multiple interruptions increased.

The Effect of Different Naiad and Prey
Clump Densities on Instar Growth

Differences in instar growth (Table 17).--Only the naiad density had a significant effect on the growth of the naiads. The instar growth of solitary naiads was greater than that of interacting naiads.

Differences in instar duration (Table 17).--The interaction between naiad density and clump density had a significant effect on the instar duration. At the low clump density, the instar duration increased as the naiad density increased. At the high clump density, the instar duration decreased as the naiad density increased.

Table 16. The Differences in Instar Growth (the increase in labium length-measured in optical micrometer units) Generated by the Interruptions in Feeding (m = multiple interruptions; s = single interruption; c = no interruptions)

INSTAR (F-2)					
Treatment					
Feeding Pattern					
72 _m	72 _s End	48 _m	72 _s Middle	72 _s Beginning	24 _c
Mean					
14.6	15.3	15.6	15.9	16.0	16.4

Means subtended by the same line are not significantly different at the five percent level.

Table 17. The Differences in Instar Growth and Duration Generated by Different Naiad and Prey Clump Densities

Labium Length Data (mm): Instar (F)

Treatment

Naiad Density	One Naiad	Three Naiads
Mean	<u>8.43</u>	<u>8.11</u>

Instar Duration Data (Days)

Treatment

Naiad Density				
Prey Clump ^x Density	(3 x 12)	(1 x 2)	(1 x 12)	(3 x 2)
Mean	7.8	9.5	10.3	11.5

Means subtended by the same line are not significantly different at the five percent level.

The Feeding Behavior and Growth of Naiads
Under Natural Conditions

The Effect of the Relative Abundance of
Prey and the Density of Naiads on the
Diversity of the Prey Eaten by the Naiads
in the Experimental Ponds (Table 18)

The effect of the prey density.--Within the pre- and post-emergence samples, the diversity of the gut contents increased as the total prey density decreased.

At high prey densities, the diversity of the gut contents decreased after the major summer emergence of the prey species.

The effect of the naiad density.--At high prey densities, the diversity of the gut contents increased as the naiad density increased.

The Size Differences Observed Among
the Final Instar Naiads in the
Experimental Ponds (Table 19)

The size differences observed among the overwintering naiad populations.--The interaction between the naiad and prey manipulations had a significant effect on the size of the final instar naiads. The main effect of the prey manipulation was also significant. In general, the size of the final instar naiads increased as the prey density decreased. At the low prey density, the mean size decreased as the naiad density increased. At the high prey density, the mean size increased as the naiad density increased.

Table 18. The Differences in the Mean Diversity ($\pm$ S.E.) of Naiad Gut Contents Generated by Different Naiad and Prey Densities in the Experimental Ponds (N refers to the number of ponds sampled)

Pre-Emergence Samples

Experimental Manipulation

High Prey Density	Low Prey Density
Low Naiad Density	Low Naiad Density
0.70 ± 0.01	0.83 ± 0.03
(N = 7)	(N = 3)

Post-Emergence Samples

Experimental Manipulation

High Prey Density	High Prey Density	Low Prey Density
Low Naiad Density	High Naiad Density	High Naiad Density
0.48 ± 0.03	0.71 ± 0.04	0.83 ± 0.02
(N = 4)	(N = 1)	(N = 3)

Table 19. The Differences in the Labium Length (mm) Means Observed Among the Final Instar Naiads in the Experimental Ponds

Overwintering Naiad Populations

Experimental Manipulation

Naiad Density	Low	High	High	Low
x	x	x	x	x
Prey Density	High	High	Low	Low
Mean	<u>8.14</u>	<u>8.28</u>	<u>8.40</u>	<u>8.56</u>

Summer Naiad Populations

Experimental Manipulation

Prey Density	High	Low
Mean	<u>8.21</u>	<u>8.50</u>

Means subtended by the same line are not significantly different at the five percent level.

The size differences observed among the summer naiad populations.--Only the prey manipulation had a significant effect on the size of the final instar naiads. The mean size increased as the prey density decreased.

DISCUSSION

The Relative Importance of the Variables Affecting the Feeding Behavior of the Naiads

The Variables Affecting the Intensity of Intraspecific Interactions

The avoidance responses (the distance moved by a naiad immediately after it has been struck) were affected by three factors: the intensity of the strike, which was governed by the hunger level of the attacking naiad; the readiness of the naiad being attacked to move in response to a strike, which was governed by the hunger level of the naiad being attacked; and the frequency of successive strikes, which was governed by the difference in the individual activity levels of the interacting naiads. The intensity of the strike increased with hunger. The readiness to move in response to a strike increased with hunger and the number of successive strikes. However, successive strikes also inhibited the general activity of the naiad being struck, and the difference in individual activity levels which led to the successive strikes usually disappeared by the end of the thirty minute observation period.

When the hunger levels of two interacting, large naiads were low, the individual differences in the general activity

levels were marked (usually some activity versus no activity at all), and the more active naiad was usually struck several times in succession (in the restricted area of the plastic pans the active naiad often moved past the inactive naiad and elicited a strike without causing the other naiad to move). The successive strikes caused the increase in the mean avoidance responses of the large naiads in the Low Hunger x Low Strike Intensity trials (Table 1).

The increase in the mean avoidance responses of the large naiads between the Low Hunger x High Strike Intensity and High Hunger x Low Strike Intensity trials indicated that at low hunger levels the large naiads were more sensitive to their own hunger level than to the intensity of the strike. However, the increase in the mean avoidance response in the High Hunger x High Strike Intensity trials indicated that the intensity of the strike did become important when the hunger level (and the readiness to move) of the naiad being attacked was high.

The small naiads were generally more active than the large naiads, and the individual differences in the activity levels of the small naiads in the Low Hunger trials were not marked. As a result, series of successive strikes did not occur. The increase in the mean avoidance response within both hunger levels in response to an increase in the strike intensity indicated that the small naiads were always more sensitive to the intensity of the strike than their own hunger level.

The activity of solitary large and small naiads increased with hunger in pilot studies, but no significant differences in the total activity of interacting naiads were observed between the 48 and 72 hour hunger levels in the absence of hunger level contrasts (Table 2). The increase in the intensity of the strikes in the 72 hour treatment combinations probably inhibited the general activity of the interacting naiads.

In the presence of hunger level contrasts, significant differences in the total activity of the interacting naiads were observed between the 48 and 72 hour hunger levels. Large naiads increased their total activity while small naiads decreased theirs. This difference in the behavior of the naiads can be explained by the difference in the sensitivity of large and small naiads to their own hunger levels and the intensity of a strike. The large naiad at the lower hunger level within the hunger contrast was relatively insensitive to the intensity of the strike by the hungrier naiad, as long as the strikes did not occur in succession; and the attacks increased the activity of the less hungry naiad. Furthermore, the lower intensity of the strikes by the less hungry naiad did not inhibit the activity of the hungrier naiad as much as a strike by a naiad equally as hungry as the hungrier naiad. The difference in the sensitivity to the strike intensity and the difference in the strike intensities led to a lower inhibition of the

total activity among the large naiads when their hunger levels differed; and as the hunger levels increased within the hunger level contrast treatments, the total activity increased.

On the other hand, small naiads were more sensitive to the intensity of the strike than to their own hunger level; and the difference in the intensities of strikes between the small naiads, when they differed in their hunger levels, inhibited the general activity of the less hungry naiad. This effect increased as the hunger levels of the interacting small naiads increased and generated the significant decrease in total activity between the 48 and 72 hour hunger contrasts.

The lower general activity levels of the large naiads were caused by the fact that the (F) naiads spent most of the time within an observation period watching or stalking each other. This was partially due to their greater reactive distance (Table 3), but the large naiads were also more persistent in following up a stalk with a strike (and the fact that strikes did not always occur immediately after the completion of a successful stalk used up more of the time within an observation period). The totals for the number of stalks conducted by large and small naiads were comparable, but the (F) naiads completed a greater number of strikes than the (F-1) naiads (Tables 4 and 5). This difference in aggressiveness also accounted for the significant

increase in the total number of strikes by the large naiads as the activity increased within the hunger contrast treatments (Table 4).

The Effect of Hunger on the Interactions
Between Naiads in Different Instars

(F) naiads completely dominated (F-1) naiads, and the aggressive behavior of the large naiads increased with hunger. However, the avoidance behavior of the small naiads was determined by both the readiness to move (their own hunger level) and the strike intensity (the hunger level of the attacking naiad) (compare the results of the (F-1)-24 x (F)-24 and (F-1)-49 x (F)-24 treatments and the (F-1)-24 x (F)-24 and (F-1)-24 x (F)-72 treatments in Table 7).

The Relation Between the Activity of Final
Instar Naiads and the Amount of Prey Eaten

Although the naiads did spend long periods of time searching for prey and traveled considerable distances relative to their own size, they became quite inactive for almost as long once feeding occurred. As a result, the distribution of undisturbed naiads approximated the distribution of the clumps of prey. However, the actual distribution and feeding behavior of interacting naiads depended upon the number and size of the interacting naiads and the distance between prey clumps. The activity data (Table 8) indicated that the clumps had to be at least nine feet apart in order to minimize the intraspecific interactions

among well-fed naiads and at least 35 feet apart for hungry naiads, but this could not be checked in the laboratory and has to be determined in future field studies.

The Relative Importance of the Naiad Density;
Prey Density and Presence of Environmental
Structure on the Number of Prey Eaten

As was expected (Holling, 1966), prey consumption increased as the prey density increased. Prey consumption also increased as the size of the naiad increased. However, within the limited area of the pans, intraspecific interactions interfered with feeding behavior and decreased the prey consumption of all naiads even at the high prey density in the presence of environmental structure (Table 10). The slight increase in prey consumption when structure was present at the high prey density (Table 10) suggested that the presence of environmental structure might become an important factor at prey densities higher than were used in this study.

In the study of the feeding behavior of individual naiads over three days, the decrease in prey consumption on the second day was apparently due to the inactivity of well-fed naiads which caused the second feeding bout to occur in the same area as the first feeding bout. Prey consumption decreased because of the lower local prey density, but the activity of the naiads did not increase because the prey clumps still held more than six chironomus larvae (which, if eaten, were enough to localize well-fed naiads).

As the naiads became more hungry (because of the even lower local prey density) and more active on the third day, they moved away from the area on which they had fed for the first two days and began feeding on the remaining undisturbed prey clumps. The higher local prey density in the previously undisturbed area caused the prey consumption to increase relative to that for the second day. The prey consumption of the small naiads did not increase on the third day, and this was probably due to the fact that the lower daily prey consumption by the (F-1) naiads decreased the local prey density at a lower rate than that for the large naiads. This allowed the small naiads to remain in a given area longer than the large naiads before the local prey density decreased to the point where the naiads became hungry enough to move to another area. However, it should be emphasized that the relation between the local prey density and the feeding behavior of well-fed naiads disappeared when the activity of the naiads increased because of intra-specific interactions.

The Effect of the Instar Distribution and
the Pattern of Environmental Structure on
the Feeding Behavior of Interacting Naiads

Within the restricted area of the plastic pans, dragonfly naiads fed primarily on structured prey clumps whenever they were given a choice between structured and unstructured prey clumps. The absence of a preference in the feeding behavior when three (F-1) naiads were placed in the plastic

pool was probably due to the fact that the adjacent prey clumps were 40 centimeters apart, and the small naiads did not react to objects at that distance. Consequently, the relative abundance of the structured and unstructured clumps, which were approximately equal in number, determined the feeding behavior of the small naiads.

Large naiads did react to objects 40 centimeters away; and when at least one large naiad was present and the number of structured clumps was equal to the total number of naiads in the pool, predation was greater on the structured prey clumps. The abundance of structured clumps relative to the number of interacting naiads reduced intraspecific interference with feeding on the preferred clumps when two or more large naiads were present. When only one large naiad was present, the greater predation on the structured clumps probably resulted from the equal number of structured and unstructured prey clumps available to the two small naiads after the large naiad had monopolized one of the three structured clumps. The feeding behavior of the single large naiad generated the significant difference in predation under these conditions.

When only one large naiad and two structured prey clumps were present, the large naiad fed primarily on the structured prey clumps; but the two small naiads fed primarily on the unstructured prey clumps because of their greater relative abundance. The difference in the feeding behavior of

the large and small naiads equalized the predation on the structured and unstructured prey clumps.

When two or more large naiads and two adjacent, structured prey clumps were present, the intraspecific interactions among the large naiads centered about the structured clumps and interfered with feeding behavior. This interference equalized the predation on the structured and unstructured prey clumps.

When two large naiads and two separated, structured prey clumps (80 centimeters apart) were present, the large naiads were no longer immediately aware of both structured clumps; and the feeding behavior was determined by the local abundance of structured and unstructured prey clumps. Unstructured prey clumps were locally more abundant which equalized the predation on the structured and unstructured prey clumps (the single structured clump was still preferred but only one naiad could feed on it at a time; the others fed on the adjacent, unstructured prey clumps).

When two large naiads and two separated, structured prey clumps were present, the repeated interactions between the large naiads on the structured clumps (one naiad was always moving around the pool) interfered with feeding and caused most of the feeding to occur on the less preferred but unoccupied unstructured prey clumps.

The results of these experiments and the ones in the plastic pans demonstrated that intraspecific interactions

determine the intensity and pattern of predation by dragonfly naiads. Differences in prey densities were of secondary importance and determined how long an individual naiad would remain in a given area. In an open-field situation, the presence of limited amounts of environmental structure intensified the intraspecific interactions by increasing the aggregation of the large naiads. A limited number of prey clumps would bring about the same effect.

The Relation Between the Feeding Behavior and
the Instar Growth of the Naiads

When feeding was uninterrupted but continuously restricted throughout an instar, growth differences were generated in each of the last four instars. Multiple interruptions in feeding decreased the number of feeding bouts per instar and increased the amount of prey consumed per feeding bout in both instar (F-2) and (F-1). Although the relative size of the compensatory increase in the amount of prey consumed per feeding bout was equivalent in the two instars (53 versus 54 percent), the relative decrease in the number of feeding bouts by the larger naiads was greater than that for the smaller naiads (43 versus 37 percent). This difference in the response of the larger naiads to the multiple interruptions in feeding generated the significant differences in the total prey consumption within instar (F-1)--Table 15.

Contrary to the differences in the total prey consumption by the large and small naiads, the only significant growth differences generated by interruptions in feeding were observed among the small naiads. Multiple interruptions or a single, long interruption in feeding at the end of instar (F-2) caused a decrease in instar growth (Table 16). Growth and molting processes both occurred during the last half of an instar. Since both of these processes required food, interruptions in feeding generated competition between these two processes. Because most of the instar growth requirements are completed before the onset of the molting process is triggered (Wigglesworth, 1959), most of the food assimilated can be channeled into the molting process without seriously affecting the functioning of the naiad in the next instar. The generation of a decrease in growth is dependent upon the length of the interruption in feeding relative to the time interval over which the two processes co-occur. Although the length of the feeding interruptions were fixed in this study, the difference in the durations of instars (F-2) and (F-1) caused the length of the time interval over which the two processes co-occurred to vary and generated differences in the amount of competition between the two processes in the two instars. The 72 hour deprivation period interrupted feeding for 50 percent of the last half of instar (F-2) and 36 percent of the last half of instar (F-1). The absence of growth differences between multiple and single

interruption treatments in instar (F-1) and the presence of a significant difference between the multiple interruption treatments in instar (F-2) demonstrated that naiads could compensate for limited interruptions in feeding during the last half of the instar by increasing the amount of prey consumed per feeding bout.

The results of this laboratory study suggested a mechanism by which interruptions in feeding caused by intraspecific interactions could generate significant differences in the mean size of interacting naiads.

The decrease in the total prey consumption per instar observed among the (F-1) naiads at the higher temperature level was probably due to a slight temperature stress. In pilot studies using the pint containers, mortality began to occur among the larger naiads in the 28-30° C temperature range.

The Effect of Different Naiad and Prey Clump Densities on Instar Growth

The pattern of the instar duration and growth differences observed in this study were not unexpected given the relation between intraspecific interactions and the activity and feeding behavior of naiads and the effect of interruptions in feeding on instar growth. Solitary (F-1) naiads are quite inactive and tend to remain on or near a single clump. Consequently, one would not expect the instar duration or growth to be affected by differences in the number

of clumps available as long as the number of prey per clump was maintained (as it was in this experiment).

The activity of the naiads increases as the naiad density increases. At high naiad and clump densities the number of clumps was four times the number of naiads; and the intraspecific interactions only increased the number of prey encountered, causing the feeding rate to increase relative to that of a solitary naiad. The pilot studies which preceded the experimental manipulation of the variables affecting the intraspecific interactions indicated that toward the end of an instar, naiads became much more sensitive to the presence of other naiads and increased their avoidance behavior. This change in behavior increased the activity and frequency of intraspecific interactions toward the end of the instar and decreased the feeding rate during a critical period in the instar with respect to instar growth. Because the normal intraspecific interactions increased the feeding rate during most of the instar, the duration of the instar decreased; but the decrease in the feeding rate toward the end of the instar caused by the heightened avoidance responses generated a significant decrease in the instar growth.

At the High Naiad and Low Clump densities, there were fewer prey clumps than naiads; and the intraspecific interactions interfered with feeding behavior, causing the prey consumption to decrease relative to that of a solitary naiad.

The lower prey consumption throughout the instar caused the instar duration to increase and the instar growth to decrease.

The results of this laboratory study demonstrated that the relative abundance of the prey clumps determined the intensity of intraspecific interactions and that intraspecific interactions could generate significant differences in the mean size of final instar naiads.

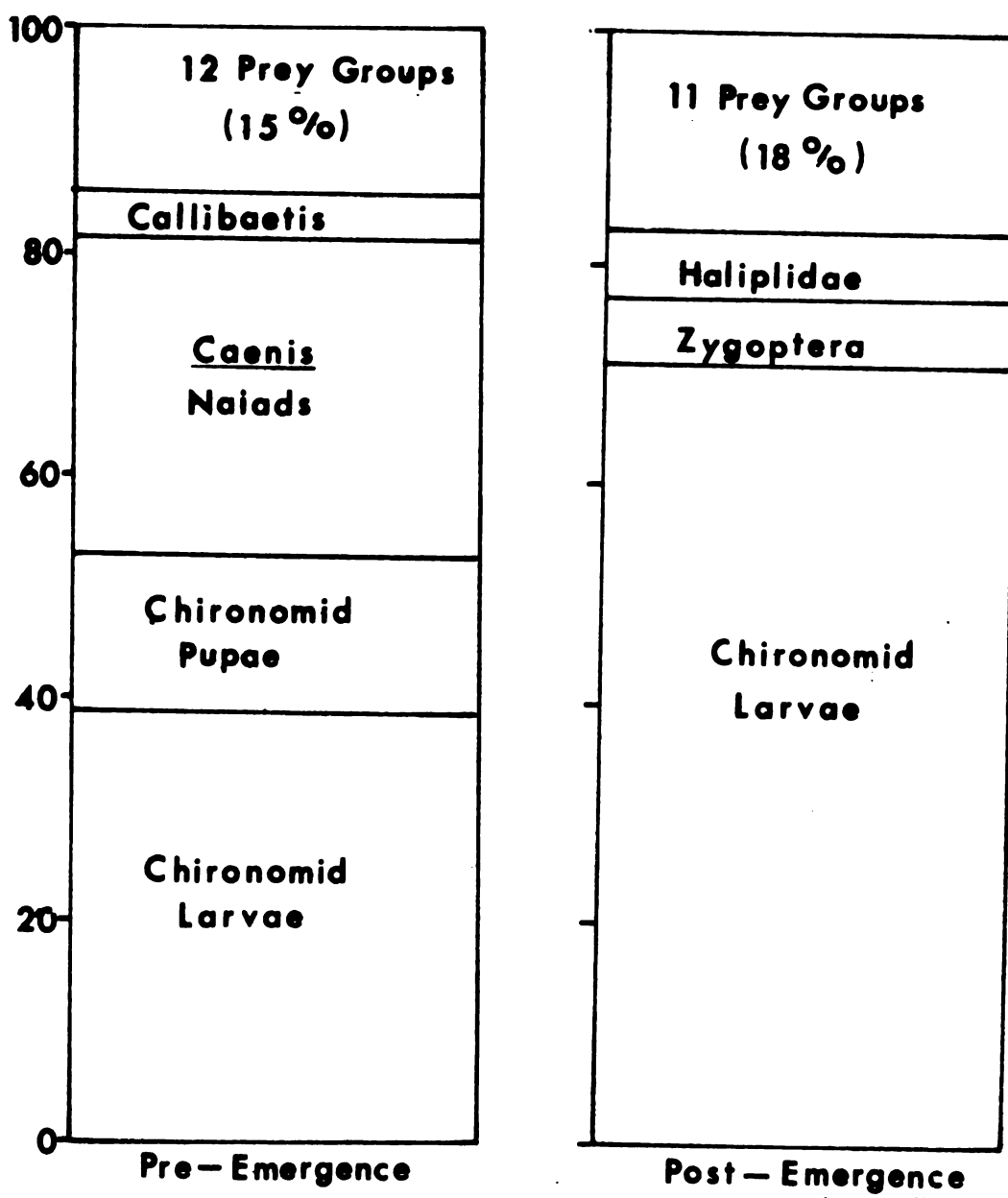
The Feeding Behavior and Growth of the Naiads Under Natural Conditions

The Effect of the Relative Abundance of Prey and the Density of Naiads on the Diversity of Prey Eaten by the Naiads in the Experimental Ponds

An examination of the gut contents indicated that under natural conditions, large Anax junius naiads selected the larger individuals from the prey array. After the emergence of the larger instars within each prey species, the diversity of large prey was limited in the high prey ponds; and the naiads fed primarily on chironomid larvae (Figure 3).

The prey diversity was higher in the low prey ponds during both the pre- and post-emergence periods (Hall et al., 1970), and the diversity of the gut contents increased accordingly. Pritchard (1964) reported similar effects of the relative abundance of prey on the feeding behavior of the naiads of ten other anisopteran dragonfly species.

Figure 3. The percentage composition of the pre- and post-emergence gut analysis samples taken from the low naiad x high prey density ponds.

**Figure 3**

In the high prey ponds, increasing the level of intraspecific interactions (through the manipulation of the naiad densities) increased the activity of the naiads and increased the probability of encountering large prey other than chironomid larvae. As a result, the diversity of the gut contents increased.

In the low prey ponds, the much lower abundance of all prey species caused the effect of the increase in the level of intraspecific interactions to be much less conspicuous.

These results demonstrated that the feeding behavior of the naiads under natural conditions was affected by both intraspecific interactions and the relative abundance of prey.

The Size Differences Observed Among the Final Instar Naiads in the Experimental Ponds

The increased growth in the low prey ponds was opposite to what one would have predicted strictly on the basis of the differences in the prey densities. However, the laboratory studies demonstrated that relative abundance of naiads and prey clumps determined the growth and feeding behavior of interacting naiads. The laboratory studies also indicated that the distance between prey clumps was an extremely important factor in reducing the intensity of intraspecific interactions. Although the Eckman dredge samples had been taken randomly from the pond bottoms, an estimate of the prey distribution characterizing each treatment combination

was obtained by pooling all of the dredge samples from the ponds within each treatment combination over all of the sampling dates in June through August for the summer populations and August through October for the overwintering populations. Then, the larger prey organisms (greater than one milligram dry weight) within each dredge sample were summed. From these data, the frequency distribution of the samples containing given numbers of prey (0-5, 6-10, 11-15, etc.) was generated for each treatment combination. In the laboratory, Anax junius naiads consumed between 50 and 80 percent of prey clumps containing ten chironomus larvae, causing their activity to decrease markedly. Consequently, the percentage of the dredge samples containing ten or more prey organisms was calculated for the prey distribution at each treatment combination. The estimates of the probability of not encountering prey based on the prey distribution data (Table 20) indicated that the prey clumps in the high prey density ponds were either larger or closer together than those in the low prey ponds. In either case, the difference in the distribution of the prey between the high and low prey density ponds would increase the aggregation of the naiads in the high prey ponds, increasing the frequency of intraspecific interactions and the interference with feeding.

The size differences observed among the final instar naiads in the experimental ponds can be explained by comparing them with the differences in the distributions of prey

among the treatment combinations and considering the effect of the differences in prey distribution on the frequency of intraspecific interactions and the interference with feeding behavior (Table 20). The experimental manipulations generating the low prey densities also increased the distance between adjacent prey clumps. This increased the distance between naiads and decreased the frequency of intraspecific interactions and the interference with feeding behavior.

During the overwintering generation, the number of prey clumps were apparently limited in the low prey ponds; and the increase in the number of naiads in the high naiad ponds increased the interference with feeding and decreased the instar growth. During the summer generation, the distribution of prey changed in the low prey ponds, erasing the limitation in the number of prey clumps; and the increase in the number of naiads in the high naiad ponds did not increase the interference with feeding. The increase in the amount of environmental structure during the summer generation caused by the seasonal increase in the amount of vegetation may have also played a role in decreasing the interference with feeding in the high naiad ponds.

However, in both generations, the significant differences between the high and low prey ponds were caused by differences in the distribution of prey not differences in the density of prey. Furthermore, the significant difference between the high and low naiad means in the high prey

Table 20. The Comparison of the Size Differences Observed Among the Final Instar Naiads in the Experimental Ponds with the Differences in the Prey Distributions Generated by the Experimental Manipulations

Overwintering Naiad Populations:

Experimental Manipulations				
Naiad Density	Low	High	High	Low
x	x	x	x	x
Prey Density	High	High	Low	Low
Mean Labium Length (mm) *	<u>8.14</u>	<u>8.28</u>	<u>8.40</u>	<u>8.56</u>
The Differences among the Prey Distributions**	0.16	0.43	0.90	0.93

Summer Naiad Populations:

Experimental Manipulations				
Naiad Density	High	Low	High	Low
x	x	x	x	x
Prey Density	High	High	Low	Low
Mean Labium Length (mm) *	<u>8.17</u>	<u>8.25</u>	<u>8.48</u>	<u>8.52</u>
The Differences among the Prey Distributions**	0.49	0.56	0.73	0.73

*The means subtended by the same line are not significantly different at the five percent level.

**The probability of not encountering prey calculated from the prey distributions derived from the pooled dredge samples.

ponds during the overwintering generation was probably caused by the difference in the prey distributions rather than the naiad densities. If the difference in the mean size of the final instar naiads had been caused by the difference in naiad densities, one would have observed the opposite results; the naiads in the low density ponds would have been larger than the naiads in the high density ponds.

SUMMARY

1. The intensity and frequency of intraspecific interactions increased with the hunger and size of Anax junius naiads. Because of their greater aggressiveness and reactive distance, larger naiads completely dominated smaller naiads.

2. Although the prey consumption did increase as the number of prey per clump increased, the frequency of intraspecific interactions determined the feeding behavior of interacting naiads. When the number of prey clumps was limited, intraspecific interactions interfered with feeding behavior, and the feeding rate decreased as the naiad density increased. When there was an abundance of prey clumps, the feeding rate increased with the naiad density as the intraspecific interactions increased the activity and the number of prey encountered by the interacting naiads.

3. Although hungry naiads were capable of moving considerable distances, solitary naiads were generally quite inactive. The activity of individual naiads increased with hunger and through intraspecific interactions.

4. Prolonged interruptions in feeding late in an instar decreased instar growth significantly. The avoidance behavior of the naiads increased toward the end of an instar

which increased the interruptions in feeding caused by intraspecific interactions and decreased the instar growth among interacting naiads.

5. The frequency of intraspecific interactions and the relative abundance of prey determined the diversity of prey consumed by the naiads under natural conditions.

6. The frequency of intraspecific interactions which was determined by the number of naiads and the distribution of the prey controlled the growth of the naiads under natural conditions.

BIBLIOGRAPHY

BIBLIOGRAPHY

- Autrum, H. and G. Kolb. 1968. Spektrale Empfindlichkeit einzelner Sehzellen der Aeschniden. Z. vergl. Physiol. 60(4):450-477.
- Corbet, P. S. 1962. A biology of dragonflies. H. F. and G. W. Witherby Ltd., London.
- Flanders, S. E. 1968. Mechanisms of population homeostasis in Anagasta ecosystems. Hilgardia 39:367-404.
- Gause, G. F. 1934. The Struggle for Existence. Williams and Wilkins, Baltimore, Maryland.
- Gause, G. F., N. P. Smaragdora and A. A. Witt. 1936. Further studies of interaction between predators and prey. J. Anim. Ecol. 5:1-18.
- Glass, N. R. 1971. Computer Analysis of Predation Energetics in the Largemouth Bass in Systems Analysis and Simulation in Ecology, Vol. I (B. C. Patten, ed.), Academic Press, New York, pp. 325-363.
- Griffiths, K. J. 1969. The importance of coincidence in the functional and numerical responses of two parasites of the European Pine Sawfly, Neodiprion sertifer. Can. Ent. 101:673-713.
- Griffiths, K. J. and C. S. Holling. 1969. A competition submodel for parasites and predators. Can. Ent. 101: 785-818.
- Hall, D. J., W. E. Cooper and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15(6):839-928.
- Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45.
- Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48.

- Hoppenheit, M. 1964. Untersuchungen uber den Einfluss von Hunger und Sattigung auf das Beutefangverhalten der Larve von Aeschna cyanea. Mull. (Odonata). Z. wissen. Zool. 170 (3/4):309-322.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.
- Huffaker, C. B., K. P. Shea, and S. G. Herman. 1963. Experimental studies on predation: complex dispersion and levels of food in an acarine predator-prey interaction. Hilgardia 34:305-330.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Conn.
- Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York.
- Pritchard, G. 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in ponds in northern Alberta. Can. J. Zool. 42(50):785-800.
- Ross, Q. E. 1967. The Effect of Different Naiad and Prey Densities on the Feeding Behavior of Anax junius Drury Naiads. M. S. Thesis, Cornell University, Ithaca, New York.
- Simpson, E. H. 1949. Measurement of diversity. Nature, 163:688.
- Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York.
- Wigglesworth, V. B. 1959. The control of growth and form: a study of the epidermal cell in an insect. Cornell University Press, Ithaca, New York.

APPENDIX

Table 1. Analysis of Variance of the Transformed (Log_{10})
Total Activity Data

Source	DF	MS	F-Test Results
Hunger Level Contrast	1	0.00200	NS
Maximum Hunger Level	1	0.19799	NS
Naiad Size	1	3.27017	$P(F \geq 24.50) < 0.001$
Contrast x Size	1	1.14553	$0.005 < P(F \geq 8.58) > 0.001$
Contrast x Hunger	1	0.00064	NS
Hunger x Size	1	0.47127	NS
Contrast x Hunger x Size	1	1.01614	$0.01 < P(F \geq 7.61) > 0.005$
Error	56	0.13349	

Table 2. Analyses of Variance for Prey Consumption and Naiad Activity Data

Digestive Pause Data:

Source	DF	MS	F-Test Results
Food Level	3	223,080	$P(F \geq 11.43) < 0.001$
Naiad	6	32,610	NS
Error	18	19,502	

Data for the Total Distance Traveled:

Source	DF	MS	F-Test Results
Food Level	3	1902	$P(F \geq 16.58) < 0.001$
Naiad	6	600	$0.005 > P(F \geq 5.23) > 0.001$
Error	18	115	

Table 3. Analyses of Variance for the Data on the Feeding Bouts per Instar (Log₁₀ Days)

Instar (F-2) Data:			
Source	DF	MS	F-Test Results
Feeding Pattern	5	0.06629	$P(F \geq 16.67) < 0.001$
Temperature	1	0.00365	NS
F x T	5	0.00190	NS
Error	60	0.00398	

Instar (F-1) Data:			
Source	DF	MS	F-Test Results
Feeding Pattern	5	0.05384	$P(F \geq 9.57) < 0.001$
Temperature	1	0.00621	NS
F x T	5	0.00145	NS
Error	60	0.00562	

Table 4. Analyses of Variance for the Data on the Prey Consumption (grams) per Feeding Bout

Instar (F-2) Data:

Source	DF	MS	F-Test Results
Feeding Pattern	5	0.0086	$P(F \geq 43) < 0.001$
Temperature	1	0.0007	NS
F x T	5	0.0002	NS
Error	60	0.0002	

Instar (F-1) Data:

Source	DF	MS	F-Test Results
Feeding Pattern	5	0.0165	$P(F \geq 27.5) < 0.001$
Temperature	1	0.0000	NS
F x T	5	0.0013	NS
Error	60	0.0006	

Table 5. Analyses of Variance for the Data on the Prey Consumption (grams) per Instar

Instar (F-2) Data:			
Source	DF	MS	F-Test Results
Feeding Pattern	5	0.0595	NS
Temperature	1	0.0672	NS
F x T	5	0.0274	NS
Error	60	0.0256	

Instar (F-1) Data:			
Source	DF	MS	F-Test Results
Feeding Pattern	5	0.2617	$0.005 < P(F \geq 3.92) >$ 0.001
Temperature	1	0.2725	$0.005 < P(F \geq 4.08) >$ 0.001
F x T	5	0.0512	NS
Error	60	0.0668	

Table 6. Analyses of Variance for the Data on the Growth of Isolated Naiads (Labium Increment Data)

Instar (F-2) Data:			
Source	DF	MS	F-Test Results
Feeding Pattern	5	4.78	$P(F \geq 8.39) < 0.001$
Temperature	1	2.00	NS
F x T	5	1.02	NS
Error	60	0.57	

Instar (F-1) Data:			
Source	DF	MS	F-Test Results
Feeding Pattern	5	3.82	NS
Temperature	1	1.84	NS
F x T	5	0.91	NS
Error	60	1.89	

Table 7. Analyses of Variance for the Data on the Growth of Interacting Naiads

Labium Length Data: Instar (F)			
Source	DF	MS	F-Test Results
Naiad Density	1	56.25	$0.01 < P(F \geq 11.35) > 0.005$
Clump Density	1	0.25	NS
N x C	1	0.00	NS
Error	12	4.96	

Instar Duration Data: Instar (F-1)			
Source	DF	MS	F-Test Results
Naiad Density	1	0.25	NS
Clump Density	1	9.00	$0.025 < P(F \geq 6.91) > 0.01$
N x C	1	20.25	$0.005 < P(F \geq 15.68) > 0.001$
Error	12	1.29	

Table 8. Analyses of Variance for the Data on Naiad Growth Under Natural Conditions

Labium Length Data: Instar (F)

Overwintering Populations

Source	DF	MS	F-Test Results
Naiad Density	1	0.01	NS
Prey Density	1	11.71	$P(F \geq 61.63) < 0.001$
N x P	1	3.56	$P(F \geq 18.70) < 0.001$
Error	8	0.19	

Summer Populations

Source	DF	MS	F-Test Results
Naiad Density	1	0.31	NS
Prey Density	1	8.43	$0.005 < P(F \geq 14.81) > 0.001$
N x P	1	0.03	NS
Error	8	0.57	