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EARLY INSTAR GROWTH AND SURVIVORSHIP IN THE COMMON
BASKETTAIL DRAGONFLY *EPITHECA CYNOSURA*
(ANISOPTERA: CORDULIIDAE).

A Thesis

Presented to

the Faculty of the Department of Biological Sciences

East Tennessee State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science in Biological Sciences

by

Bryan Arthur Reece

August 2000

APPROVAL

This is to certify that the Graduate Committee of

Bryan Arthur Reece

met on the

11th day of July, 2000.

The committee read and examined his thesis, supervised his defense of it in an oral examination, and decided to recommend that his study be submitted to the Graduate Council, in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences.

Dr. Dan Johnson
Chair, Graduate Committee

Dr. Karl Joplin

Dr. Foster Levy

Signed on behalf of
the graduate school

Dr. Wesley Brown
Dean, School of Graduate
Studies

ABSTRACT

EARLY INSTAR GROWTH AND SURVIVORSHIP IN THE COMMON BASKETTAIL DRAGONFLY *EPITHECA CYNOSURA*

(ANISOPTERA: CORDULIIDAE).

by

Bryan Arthur Reece

Egg masses of *Epitheca cynosura* were collected from Bays Mountain Park, Tennessee, USA, in June, 1999. Newly hatched individuals were placed into enclosures and sampled at scheduled time intervals throughout the summer. Enclosures were exposed to combinations of high and low densities and presence/absence of a second-year class *E. cynosura* predator. Survivorship, mean head widths, and mean dry masses were compared across treatments. Due to poor recovery of early-instar larvae, survivorship showed no significant differences in mortality among treatments. The predator present treatment caused significantly smaller head widths and dry masses only on days 42 and 55. The density treatment had a significant effect on larval growth from day 28 through day 86 (end of the experiment). Larvae from low density treatments had larger head widths and dry masses. The effects observed within the density treatments were likely to have resulted in a cohort split. Those individuals in the low density treatment followed a univoltine life history, and high density individuals followed a semivoltine life history. Density is probably a very important factor influencing the voltinism of *E. cynosura* at Bays Mounain Lake.

ACKNOWLEDGMENTS

I would like to thank the Department of Biological Sciences at ETSU for providing such a diverse and rewarding environment in which to work. I thank the members of my committee: Dr. Dan Johnson, Dr. Karl Joplin and Dr. Foster Levy for guidance and assistance with revisions. Statistical advice was provided by Dr. John Kalbfleisch and Dr. Robert Price Jr.. I would also like to thank the Dr. Denise I. Pav Research Award for providing partial funding for this work. I also thank Bays Mountain Park for allowing access to such an incredible research location. I would like to thank Karol Lynn Johnson for her valued assistance with construction of enclosures. I would also like to thank Jennifer Smith for her assistance in the field and for her relentless competitive attitude that expedited the production of this document.

In addition to his assistance and guidance as chair of my committee, I would like to thank Dr. Dan Johnson for allowing me the opportunity to work with him on the ecology of the Odonata. His insight and mastery of the subject have enriched my understanding and fascination with the order. I thank him heartily for his assistance in the field at which time not only did he provide valuable physical assistance, but his stories of previous adventures as a young grad student and subsequent stories as a world renowned expert of the Odonata were greatly valued.

Finally, I would like to thank my friends and family who have provided me with encouragement and support in all that I do.

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CHAPTER 1

INTRODUCTION

A fundamental aspect of population ecology is to be able to accurately depict the status of a given species at a specific time. In any given population, such things as fecundity, mortality, life cycle length, sex ratio, habitat status, frequency of stochastic events, and many other factors are needed to predict the status of a population (Akçakaya *et al.* 1999). These factors must be assembled and presented in a logical way that enables the researcher to make predictions. Models are constructed to predict population dynamics of a species. Accurate data on life history parameters of any given organism are required to construct useable models.

In some situations, however, it is not possible to gather all of the needed information to construct a realistic model. For example, rare and endangered species may be locally common or protected from collection and manipulation. Therefore, it is difficult to get a large enough sample or enough observations to construct a model. Secondly, legislative protection makes it illegal to conduct some types of experiments. It is ironic that these impediments make modeling especially difficult for the very organisms for which good population models are most needed to facilitate proper management decisions. It may be possible, however, to formulate a model based on

similar species (within family) to gain a picture of population dynamics that would be better than simple speculation.

In the case of the Hine's emerald dragonfly (*Somatochlora hineana*)(Anisoptera: Corduliidae), for example, such a model would be quite useful in determining possible critical periods (times of high or low growth/survivorship) of development for the endangered species (U.S. Fish and Wildlife Service 2000). Due to its endangered status, any collecting of specimens for life history studies is prohibited; however, several other species of corduliid dragonflies are widespread across North America. Controlled experimentation with these species might be used to determine some of the critical factors of corduliid life histories that could be used to create a model of *S. hineana*. One of the most studied and widespread corduliid dragonflies is the common baskettail, *Epitheca cynosura* (Needham and Westfall 1955: 372).

Corbet and Hoess (1998) compiled sex ratios of emerging dragonflies by reviewing and analyzing published and unpublished records from an array of dragonfly species to compare sex ratios at emergence. It may be possible to construct a 'typical' larval dragonfly life history by a similar approach, summarizing and analyzing past and current works concerning larval dragonfly population dynamics. This model of 'typical' larval survivorship may be useful where information on an individual species is limited. Depending on genetics and environmental factors (both biotic and abiotic), dragonflies

develop from egg to emergence in a range from a few months to 5 years.

Univoltine species are those that emerge in 1 year (Corbet 1999: 585-587). In some populations of some species, 2 years are required for development (semivoltine), and for others, more than 2 years (partivoltine). Gresens *et al.* (1982) showed that temperature affected the feeding rate of larval *Celithemis fasciata*. Lower latitudes (warmer habitats) may induce shorter development times and higher latitudes (cooler habitats) may induce longer development times. Elevation may also affect the temperature of a system and could have similar effects on development rates.

Within 1 population, a cohort split may occur (Johnson 1986), when a proportion of individuals from a single year's egg hatch emerge in 1 year but others take 2 or more years to emerge. Norling (1984) explained how 2 phenomena influence this partitioning: within a population, expression of certain genes may be induced by environmental factors such as photoperiod and temperature, causing either continued growth or delayed diapause; or biotic interactions among organisms may induce either continued growth or diapause.

Because *E. cynosura* has a relatively brief flight period from May-June, reproductive success requires that individuals emerge together. The cohort split acts to synchronize emergence of 'spring' species such as *E. cynosura* by preventing emergence at times other than spring (Corbet 1958, Kormondy and Gower 1965).

Previous researchers provided detailed descriptions of the life histories of several species of corduliid dragonfly populations. However, due to the differences in larval and adult ecology, many researchers have focused primarily on a single aspect of odonate development: either adults or larvae. Benke and Benke (1975) examined a multiple species assemblage of dragonflies in a eutrophic pond community containing fish near Aiken, South Carolina. The corduliid examined (*Epitheca cynosura*) showed heavy mortality (91% - 93%) in a univoltine population with a significant amount (48.7%) of mortality occurring in the early instars (from hatch through August). The data used to construct the survivorship curve were based on densities of larvae collected at each sampling date.

Wissinger (1988) explained the problems inherent with using density data alone to construct survivorship curves. Wissinger suggested that spatial and temporal variation necessitated an examination of changes in total population size. By incorporating densities with habitat area, Wissinger constructed a survivorship curve based on total population size estimates from a small fishless pond in Tippecanoe County, Indiana. Wissinger observed ~84% larval mortality in *E. cynosura* with ~50% mortality in the early instars (from hatch through August). By examining long-term data (8 consecutive years), Johnson (1986) constructed a 'typical' life history of *E. cynosura* for Bays Mountain Lake, Tennessee. Unlike the studies cited above, *E. cynosura* of Bays

Mountain Lake exhibit cohort splitting and take one or two years to emerge. Again, heavy larval mortality was observed (~97%) and early instar mortality was high (~60% from hatch through August).

One of the first egg to adult survivorship curves constructed for odonata was that of *Cordulia aenea amurensis* (Anisoptera: Corduliidae) by Ubukata (1981) from a dystrophic pond containing fish near Sapporo, Hokkaido, Japan. By compiling data collected from each life stage, Ubukata was able to construct a very complete survivorship curve. Ubukata observed nearly 99% larval mortality of early instars in the first year. Ubukata reported mortality rates of 99.83% and 99.80% respectively for cohorts that hatched in 1970 and 1971 during a 5-year aquatic larval period. Only 0.066% (1970) and 0.077% (1971) of the initial population survived to reproductive maturity.

A model of survivorship in *E. cynosura* was constructed from data in Benke and Benke (1975) and Johnson (1986) data (Figure 1). Note the apparent heavy early mortality and subsequent leveling off of mortality through the progression of the seasons. Summer mortality was the greatest followed by fall, spring, and winter respectively. Unfortunately, it is the very earliest life stages that are based on the fewest data points. Therefore, a more detailed dissection of the early phase could yield much needed information.

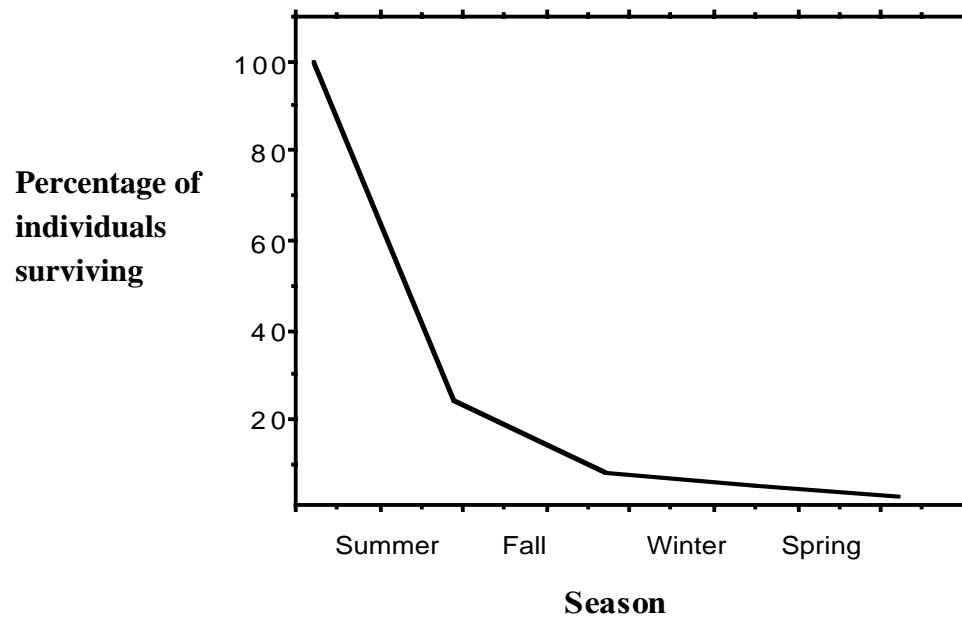


FIGURE 1. SEASONAL SURVIVORSHIP OF *E. CYNOSURA* FROM BENKE AND BENKE (1975) AND JOHNSON (1986).

The population of *E. cynosura* at Bays Mountain Lake is a population that exhibits the cohort-split phenomenon (Johnson 1986). Martin *et al.* (1991) described how competition from redear sunfish (*Lepomis microlophus*) decreased univoltine emergence in field enclosures. Johnson *et al.* (1995) concluded that intraspecific predation (especially within-cohort cannibalism) may be critical in the early survivorship of larval odonates. However, because of the difficulty in determining such interactions, more studies of this phenomenon should be conducted.

Hopper *et al.* (1996) examined within-cohort cannibalism in laboratory studies and determined that when asynchronous hatching occurs within close proximity cannibalism can decrease population size and reduce competition. It can also tend to synchronize cohorts of larvae by removing smaller individuals from the population. These findings once again show the importance of the early-instar stages of development.

Attempts have been made to observe the early larval mortality of *E. cynosura* (Johnson *et al.* 1995). However, because of the small size of early instar larvae, sampling has been very inefficient. I used a modification of the experimental design in Johnson *et al.* (1995) to describe the larval mortality and growth of early instar individuals. By stocking field enclosures with known densities of *E. cynosura* larvae and then removing entire enclosure replicates at several times, it was possible to more accurately determine both larval mortality and growth rates. Because *E. cynosura* is within the same family

(Corduliidae) as *Somatochlora hineana* and has a similar life cycle with multi-year larval development, the data generated for this early developmental period in *E. cynosura* may be useful in modeling aspects of that endangered corduliid. Based on the findings presented above, a field study was constructed and executed over the Summer of 1999 to examine mortality and growth rates of early instar *E. cynosura*. Samples were taken at weekly intervals for the first month, bi-weekly intervals for the second month, and a final sample 1 month after the last bi-weekly sample. This design was intended to acquire data on survivorship and growth during the early stages of development of larval corduliids.

Because of the cohort split for *E. cynosura* at Bays Mountain Lake, hatchlings may be eaten both by other hatchlings and by 1-year-old semivoltine individuals. Therefore, the experimental treatments contained both high or low density of hatchlings and presence or absence of a predator of 2nd year class *E. cynosura*. Table 1 lists the treatments and potential interactions of treatment factors that were tested. I expected Low Density treatments to exhibit high survivorship and high growth rates because of decreased interaction with other individuals. High Density treatments were expected to show lower survivorship and/or slower growth rates. The presence of a predator was expected to decrease survivorship through consumption of smaller individuals. Crowley *et al.* (1987) observed that in the presence of a 2nd year class predator, 1st year individuals exhibited lowered activity levels. Therefore, with predators present, growth rates were

expected to decrease either through a behavioral modification (lowered activity) of the hatchlings or because the active individuals responsible for acquiring larger masses and head widths within the treatment are eaten by the 2nd year class predator.

TABLE 1. LIST OF POSSIBLE INTERACTIONS AND HYPOTHESES FOR EACH TREATMENT FACTOR.

-
- 1) H_o : Mean response is the same at all 8 times ($\mu_{t1}=\mu_{t2}=\mu_{t3}=\mu_{t4}=\mu_{t5}=\mu_{t6}=\mu_{t7}=\mu_{t8}$).
 H_A : Mean is not the same at all 8 times (difference somewhere).
 - 2) H_o : Mean response is the same in both high (H) and low (L) densities ($\mu_H=\mu_L$).
 H_A : Mean response is not the same in both high (H) and low (L) densities ($\mu_H\neq\mu_L$).
 - 3) H_o : Mean response is the same in the presence (P) and absence (A) of a predator ($\mu_P=\mu_A$).
 H_A : Mean response is not the same in the presence (P) and absence (A) of a predator ($\mu_P\neq\mu_A$).
 - 4) H_o : Differences in mean responses in time are independent of the density of larvae (A x B interaction).
 H_A : Differences in mean responses in time are not independent of the density of larvae.
 - 5) H_o : Differences in mean response in time are independent of the presence or absence of a predator (A x C interaction).
 H_A : Differences in mean response in time are not independent of the presence or absence of a predator.
 - 6) H_o : Differences in mean response of density are independent of presence or absence of a predator (B x C interaction).
 H_A : Differences in mean response of density are not independent of presence or absence of a predator.
 - 7) H_o : Differences in mean response of all time treatments are independent of the other two factors (A x B x C interaction).
 H_A : Differences in mean response of all time treatments are not independent of the other two factors.
-

The response variable was either mean head width (mm) or mean dry mass (mg).
 The 3 factors tested were A = time, B = density, C = predator.

CHAPTER 2

MATERIALS AND METHODS

Study Area

Field research was conducted from 10 June through 4 September, 1999, at Bays Mountain Lake in Bays Mountain Park, Kingsport, Sullivan Co., Tennessee, USA (82° 37' W, 36° 31' N). Bays Mountain Lake is a shallow eutrophic lake with a surface area of 15 ha at an elevation of 550 meters (Johnson and Crowley 1980, 1989). The study site was the Schoolhouse Cove section of the lake (see Figure 2). Because the odonate assemblage and larval ecology had been heavily studied since 1977 and the water table is maintained fairly constant, Bays Mountain Lake is an excellent study location (Johnson *et al.* 1980, Johnson *et al.* 1984, Johnson *et al.* 1985, Crowley *et al.* 1987, Johnson *et al.* 1987, Johnson *et al.* 1995).

Experimental Design

Enclosures were used to allow manipulations of *E. cynosura* larval density as well as the presence or absence of a 2nd year class *E. cynosura* predator. Enclosures consisted of cylinders similar to those described by Crowley *et al.* (1987) except with sewn continuous bottoms of nylon netting (Nitex HC 3-500) with 0.5-mm mesh. Each

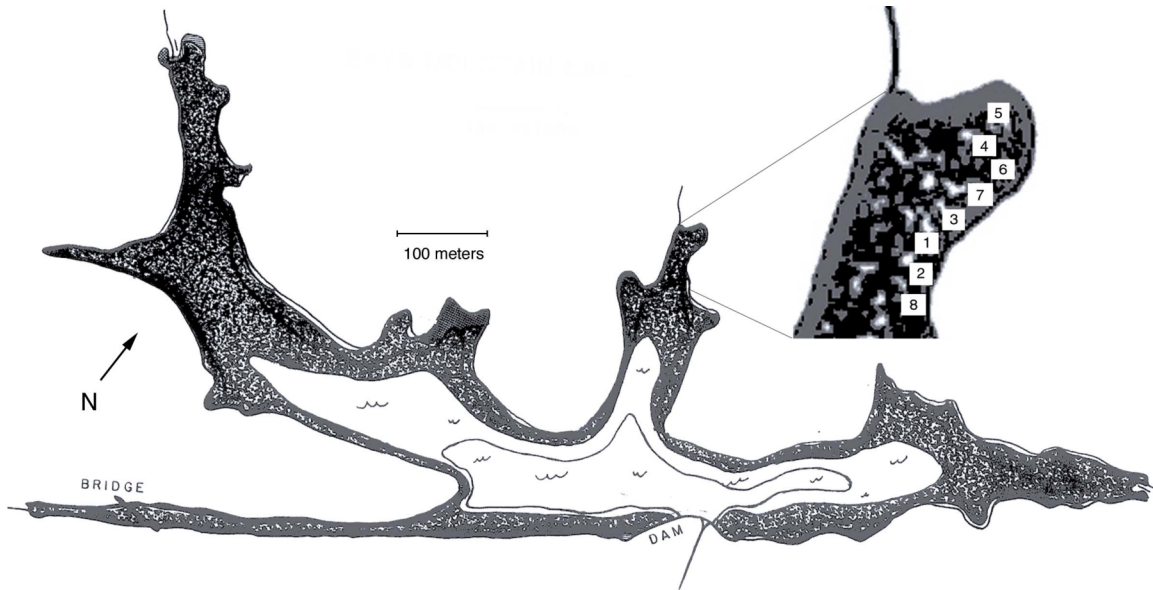


FIGURE 2. MAP OF BAYS MOUNTAIN LAKE WITH DETAILED ENLARGEMENT OF SCHOOLHOUSE COVE. Modified from Johnson and Crowley (1984 Figure 1). Blocks represent the eight sample units removed at each time interval. The number within each block represents the order of samples taken.

cylinder was 30.5 cm tall and the enclosed bottom of 25.5 cm in diameter formed an area of 0.051 m² per enclosure. A cylinder of heavy plastic mesh supported the netting tied to a 1-meter oak stake. A 25.5-cm diameter clear plastic dish was placed into the base of the enclosures to provide a circular rigid base. Enclosures were placed into the lake at a depth of 20.5 cm on May 18. To ensure randomized replication and interspersion (Hulbert 1984), treatments and replications was assigned randomly (Figure 3).

Approximately 0.25 liter of leaf litter from the surrounding terrestrial habitat was placed into each enclosure providing substrate for prey populations to colonize.

Egg masses of *E. cynosura* were collected on June 3, 1999. These eggs were placed into several 12" x 7.5" x 2" enamel trays each filled with lake water. Aeration was provided by 50 gallon aquarium pumps (Aquarium Equipment E114229). Trays were housed in a temperature-controlled room at Bays Mountain Park Nature Center. Hatching began on June 6.

From June 6-8 2nd year class individuals of *E. cynosura* were captured and placed into predator treatments (1 per designated enclosure resulting in an approximate density of 20/m²). On June 10, hatchlings were placed into enclosures at either low density (4 per enclosure for an approximate density of 70/m²) or high density (40 per enclosure for an approximate density of 700/m²). The density values of 70/m² and 700/m² bracket the average hatch density of 175.25/m² ± 40.23 (standard deviation) (Benke and Benke

1975). The 20/m² density of second year age class dragonfly predator is close to that used by Johnson *et al.* (1985 and 1995) to approximate natural densities.

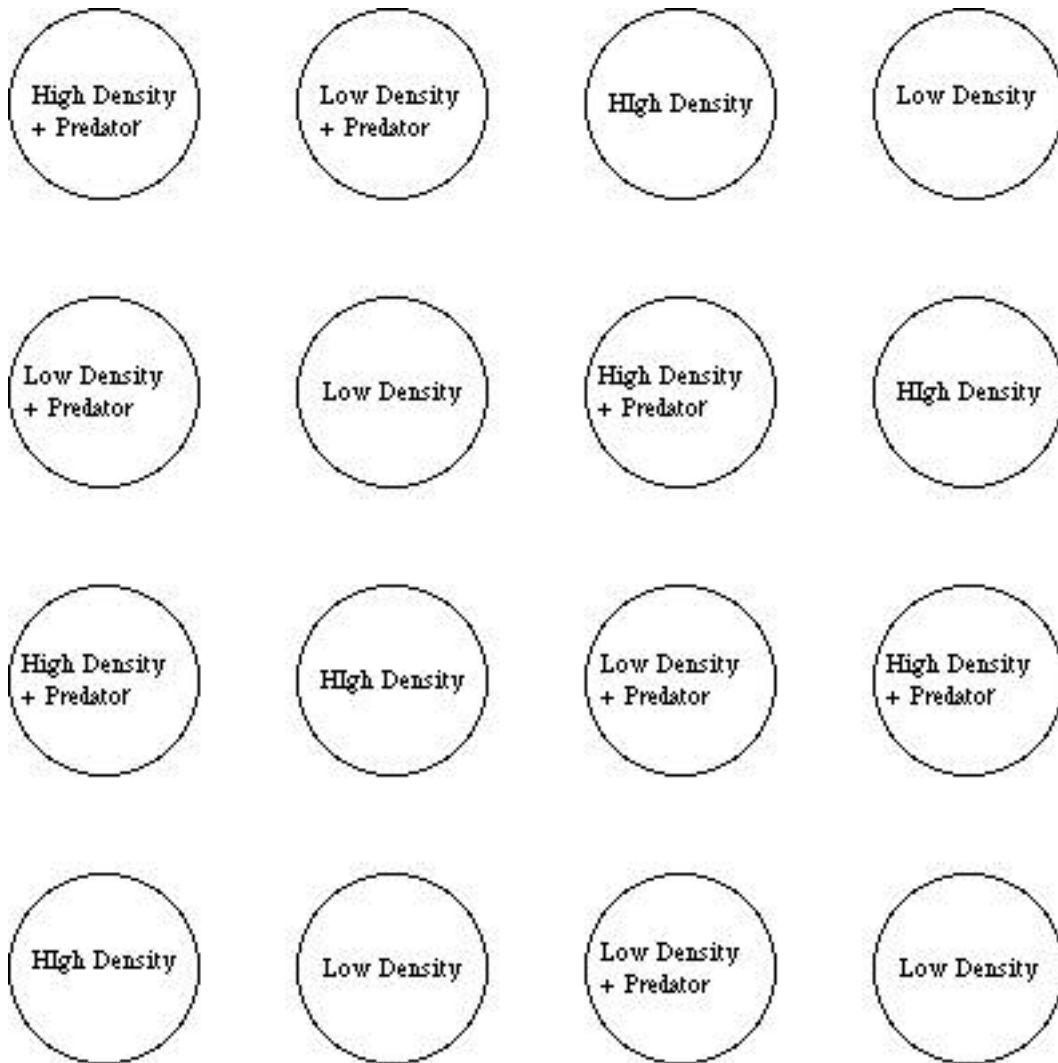


FIGURE 3. EXAMPLE ASSIGNMENT OF TREATMENTS AND REPLICATES FOR AN INDIVIDUAL SAMPLING TIME.

Sample Processing

To obtain early estimates of survivorship and growth, a sampling regime was produced that provided for several early samples to be taken (table 2). At the time of sampling, entire enclosures were raised out of the lake allowing the water to drain out through the 0.5 mm mesh. The entire contents of the enclosure were transferred to a storage container containing 95% ethanol as preservative. In the laboratory, individual leaves were rinsed in the storage alcohol and transferred into a bowl containing distilled water. The remaining material was filtered through a #60 (250 micron) sieve. The material was then suspended in a sugar solution to facilitate particle separation (Anderson 1959). The osmolarity of the sugar solution induces animal material to float and plant material to sink. The surface of the sugar solution containing sample material was examined with a Wild Heerbrugg M5A dissecting microscope at 25-50 x magnification. Dragonfly larvae were transferred into a vial containing 95% ethanol. The solution was then filtered through the sieve and contents transferred into a container of distilled water. The leaves were then rinsed in distilled water and discarded. The remaining material from the leaf portion was then filtered with the sieve. After filtration, the contents were floated in sugar solution and scanned under the dissecting microscope. After this scan, the contents of the leaf portion were discarded. The original residue was then filtered and transferred back into sugar solution. Then both a surface and substrate scan were run on

TABLE 2. SAMPLING AND CONSTRUCTION DATES OF FIELD ENCLOSURES DURING SUMMER 1999.

<u>ACTIVITY</u>	<u>DATE</u>
Field enclosures constructed	18 May 1999
Collection of egg strands	3 June 1999
Introduction of 2 nd year class predator	8 June 1999
Introduction of hatchling dragonflies	10 June 1999
Sample 1	10 June 1999
Sample 2	17 June 1999
Sample 3	24 June 1999
Sample 4	1 July 1999
Sample 5	8 July 1999
Sample 6	22 July 1999
Sample 7	4 August 1999
<u>Sample 8</u>	<u>4 September 1999</u>

each sample. After all specimens were collected from a sample, entire residues were disposed of. Each individual larva was measured for head capsule width to the nearest 0.04 mm using a calibrated ocular micrometer. Dry mass was measured to the nearest 0.00001 g using a Denver Instrument A-200DS electrobalance after drying to constant weight in a GCA-Precision Scientific Group gravity convection oven at 65°C.

Statistical Analysis

In some instances, fish had jumped into enclosures and, therefore, could have affected both survivorship and growth. Any such occurrence was noted and all replicates with fish present were removed from all analyses.

Because survivorship data were calculated as a proportion, values were limited within the range of 0 – 1 and were not normally distributed, the following transformation of proportions was used to normalize the data (Zar 1996: 283):

$$p' = \frac{1}{2} \left[\arcsin \sqrt{\frac{X}{n+1}} + \arcsin \sqrt{\frac{X+1}{n+1}} \right]$$

Where p' = transformed estimate of the proportion, X = number of larvae successfully recovered from treatment, n = total number of larvae initially present in treatment.

The square root transformation acts to reduce the dependence of high means with high variance. That is, after transformation, variances are independent of the mean. The

arcsine transformation acts to normalize the binomial distribution. It is important to note that the arcsine transformation must be in degrees not radians. A Tukey-type multiple comparison test was performed on the transformed data (Zar 1996: 561). After finding the difference between 2 transformed proportions ($p'_A - p'_B$), the result was divided by the appropriate denominator standard error term calculated by 1 of the following equations:

$$SE = \sqrt{\frac{820.70}{n + 0.5}} \qquad SE = \sqrt{\frac{410.35}{n_A + 0.5} + \frac{410.35}{n_B + 0.5}}$$

The first of these equations was used when the samples were the same size. The second was used when comparing different sized samples. The result of this division was the calculated value of q that was then compared to critical q values from Zar (1996; Appendix Table B.5).

Dry mass and head width are both continuous variables. A 3-way ANOVA was performed on these data testing for direct factor effects [age (A), density (B), and predator (C)] as well as first (A x B, A x C, B x C) and second (A x B x C) order interactions (Sokal and Rohlf 1995). Plots of the residuals did not fit a straight line and therefore were not normally distributed (Figure 4, panel A). Therefore, natural log (ln) transformations were used to normalize both dry mass and head width prior to analysis

(Figure 4, panel B). After performing the 3-way ANOVA, subsequent 2-way ANOVA's were performed within each time of sampling. These analyses determined the significance of direct factor effects (density and predation) in addition to first order interactions of density x predator.

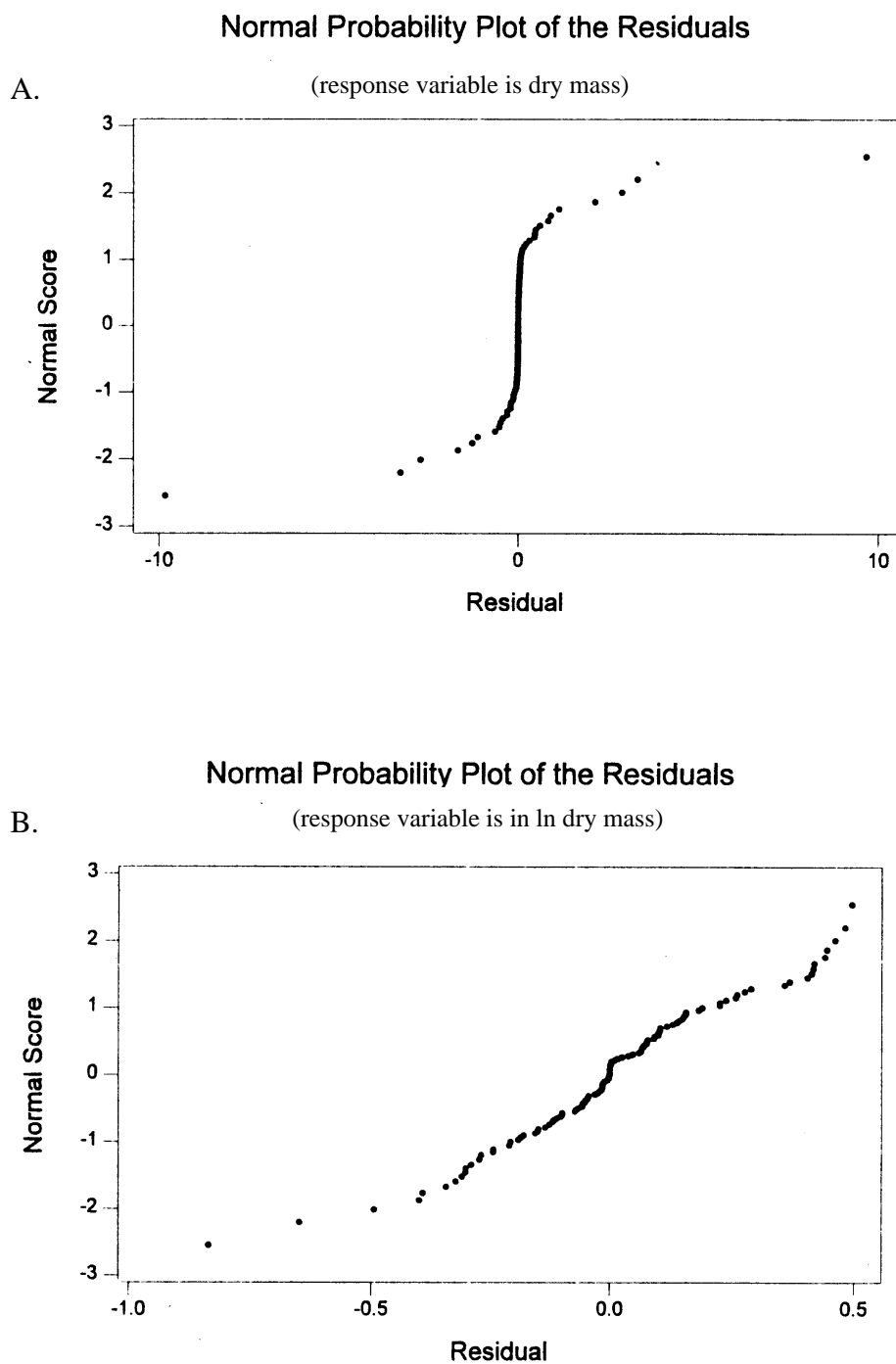


FIGURE 4. RESIDUAL PLOTS OF DRY MASS DATA. Panel A contains the residual plot of raw data, panel B contains the residual plot of the natural log transformed data.

CHAPTER 3

RESULTS

Survivorship

Data for proportions of *E. cynosura* recovered at each sampling date are presented in table 3. Proportions of individuals found at each time interval were plotted and the transformed values compared for significance (Figure 4). Very few of the points were significantly different from each other, most likely due to either low sample size or high variance among samples. At day 55, the High Density, Predator Absent treatment showed significantly higher survivorship than the High Density, Predator Present treatment. At day 86, the Low Density, Predator Absent treatment showed significantly higher survivorship than the High Density, Predator Present treatment. A possible explanation for the poor ability to determine significant differences within times may be that the small larvae were very difficult to recover. Exhaustive searches failed to recover many individuals believed to be present. As time progressed and larvae became larger, individuals became easier to find. This may partly explain why significant differences were observed only near the end of the experiment. However, of the individuals recovered, both dry mass and head width provided data that were very useful in determining critical periods of larval growth.

TABLE 3. PROPORTIONS OF INDIVIDUAL *E. CYNOSURA* RECOVERED FOR EACH SAMPLING DATE.

Treatment	Day 0	Day 7	Day 14	Day 21	Day 28	Day 42	Day 55	Day 86
Low Density, Predator Absent	7/16 0.4275	9/16 0.4375	10/16 0.3750	9/16 0.5625	11/16 0.6875	11/16 0.6875	14/16 0.8750	15/16 0.9375
High Density, Predator Absent	107/160 0.6688	135/16 0.8438	123/160 0.7688	116/160 0.7250	129/160 0.8062	89/120* 0.7417	130/160 0.8130	72/120* 0.6000
Low Density, Predator Present	11/16 0.6875	12/16 0.7500	10/16 0.6250	10/16 0.6250	12/16 0.7500	9/16 0.5625	13/16 0.8125	8/16 0.5000
High Density, Predator Present	71/160 0.4438	128/16 0.8000	121/160 0.7563	59/80* 0.7375	105/160 0.6563	93/160 0.5813	94/160 0.5875	71/160 0.4438

Top value represents count found over count possible. Bottom value is the calculated proportion. Asterisks (*) designate the presence of a fish in at least one of the replicate samples. If a fish was present, the entire replicate was discarded from statistical analyses thus resulting in a reduction of the value of total possible.

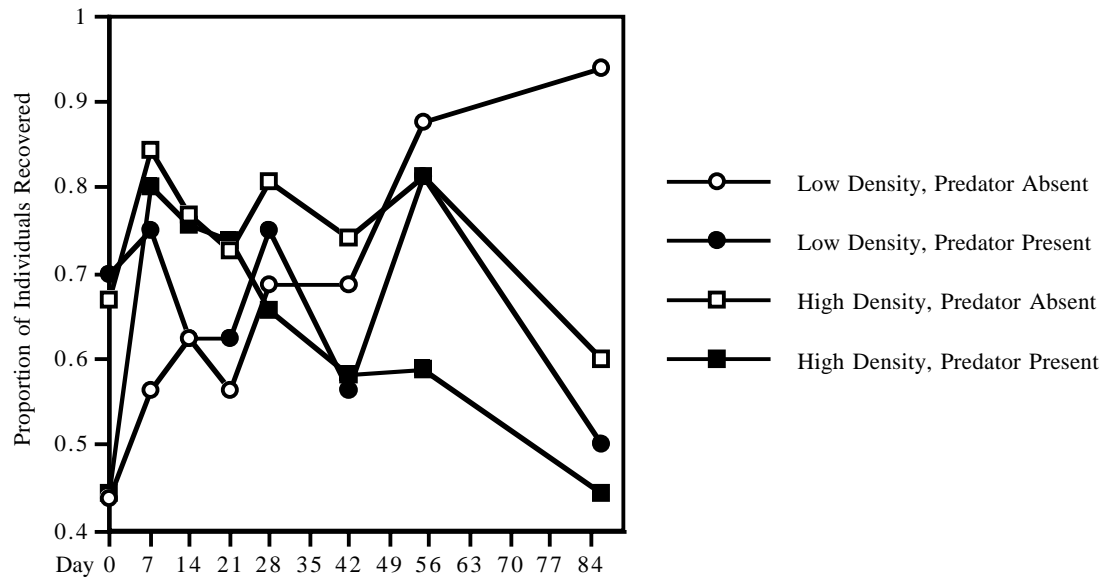


FIGURE 4. PLOT OF PROPORTION OF INDIVIDUALS RECOVERED FOR EACH OF THE 8 SAMPLING TIMES. At day 55, survivorship within High Density, Predator Absent treatments was significantly higher than survivorship within High Density, Predator Present treatments $p < 0.05$. At day 86, survivorship within Low Density, Predator Absent treatments was significantly higher than survivorship within High Density, Predator Present treatments $p < 0.05$.

Larval Growth

Dry Mass

Mean dry-masses were calculated and plotted for each sampling time (Figure 6). In Figure 6, significant factor effects are signified by asterisks below the x-axis. Three-factor model I ANOVA indicated that Age, Density, Age x Density, Age x Predator, and Density x Predator were all significant factors (Appendix A, Table 4). A 2-factor model I ANOVA was performed for each time period to determine the temporal occurrence of significant effects of Density, Predator or Density x Predator. Density was a significant factor at day 14, then again from day 28 through the remainder of the experiment. The mean dry-masses for the Low Density treatments were significantly larger than the mean dry-masses obtained for the High density treatments from day 28 on.

Head Width

Mean head widths were calculated and plotted for each sampling time (Figure 7). In Figure 7, significant factor effects are signified by asterisks beneath the x-axis. Three-factor model I ANOVA indicates that Age, Density, Predation, and Age x Density are all significant factors (Appendix A, Table 5). A 2-factor model I ANOVA was performed within all time periods to determine when significant effects of Density, Predator, or Density x Predator were observable. Density was a significant factor from day 28 through the remainder of the experiment. Individuals exposed to the Low Density

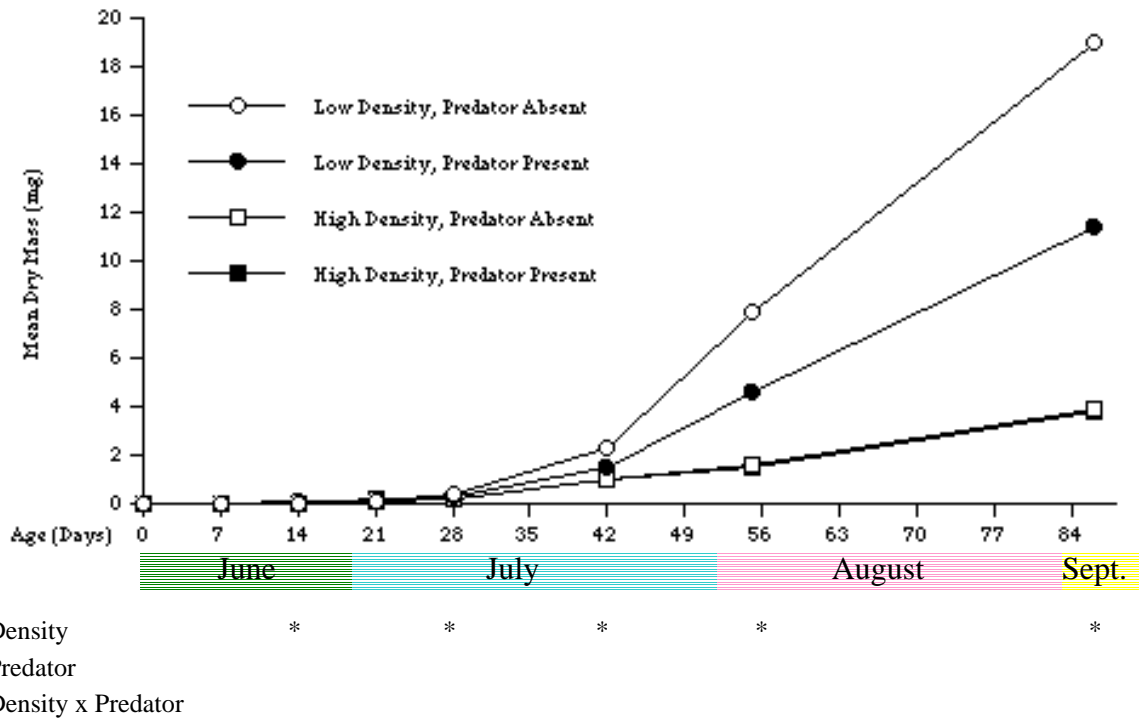


FIGURE 6. MEAN DRY MASS OVER ALL SAMPLING TIMES. Asterisks (*) indicate significant differences obtained from 2-way ANOVAs (see Appendix B. Table 6).

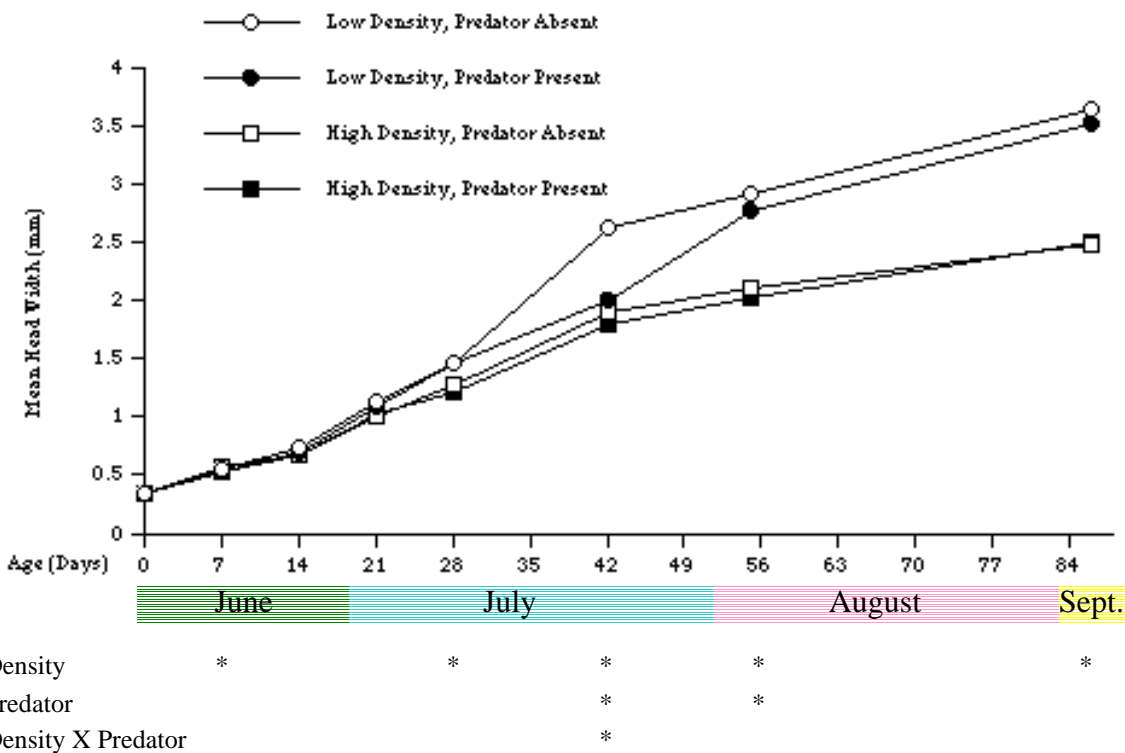


FIGURE 7. MEAN HEAD WIDTH OVER ALL SAMPLING TIMES. Asterisks (*) indicate significant differences obtained from 2-way ANOVAs (see Appendix C. Table 7).

treatments achieved significantly larger head-widths than individuals exposed to the High Density treatments at these times. The effect of a predator was discontinuous and was significant at days 7, 42, and 55. At these times, the head widths observed in the presence of a predator were significantly smaller than those observed in the absence of a predator. Only on day 42 was the Density x Predator interaction significant.

CHAPTER 4

DISCUSSION

Effects of Density on Larval Growth

Individuals at high densities showed significantly lower dry masses and smaller head widths than individuals exposed to the low density treatments from day 28 throughout the remainder of the experiment (Figures 6 and 7). The fact that both of these factors become significant and remain significant at the same times suggests that density is a very important population parameter for larval *Epitheca cynosura*. Density may affect growth of larval odonates in many ways.

Increasing population size within a confined area may increase competition. Food resources are important for any organism to grow and, therefore, variation in food availability should be examined. Although no direct analysis of prey items was performed, prey items appeared to have been plentiful in all samples upon visual examination. In an extensive analysis of similar enclosures, Johnson *et al.* (1987) reported that 3 types of larval odonate prey categories were consistently reduced in numbers, but that these three prey categories consisted of less than one-third of the typical larval odonate diet. There was no difference in total benthic prey resource attributable to differences in density of odonate larvae. Exploitative competition

(consumption of an individual's food source by a competitor) did not seem to be an important factor in those studies. Because the present study had a similar design, with similar odonate densities in the High Density treatment, it is not likely that the significant differences in larval odonate growth observed between density treatments were caused by prey depletion.

Another effect of increasing the density of individuals is an increased rate of direct interaction. For larval odonates, interactions with one another are potentially fatal. From a study on newly hatched *E. cynosura* larvae collected from Bays Mountain Lake, Hopper *et al.* (1996) found that a difference of 1 instar resulted in 20 - 100% cannibalism out of 30 trials depending on hunger level of the individuals. A difference of 2 instars resulted in 100% cannibalism in all 11 trials.

As the larvae grew in each of the treatments in the current study, it was likely that all individuals were not in the same instar. As density increased, it is possible that an increase in instances of cannibalism occurred. Survivorship data should have been able to detect an increase in mortality attributable to cannibalism. Unfortunately, due to the inability to find small larvae, these data were inconclusive.

Even if we were able to determine if cannibalism occurred, it would not explain why lower dry masses and head widths were obtained from high density treatments. We would expect that if cannibalism occurred, a mean head width or dry mass measurement

would be based on successful cannibals and the smaller individuals would no longer be in the population. This could yield a mean equal to or higher than the mean obtained from the low density treatments. Because such a pattern did not occur, another aspect of the density effect must be explored.

Crowley *et al.* (1987) reported that when first and second year class *E. cynosura* were together, the smaller year class moved less frequently than when reared without the second year class. As we have shown above, intracohort variation as little as 1 instar increased the probability of cannibalism. Therefore, increasing density could have a similar effect (lowered activity) as observed by Crowley *et al.*. Such a decrease in movement could lower the encounter rate with other larvae and therefore reduce the chances of being eaten. Coupled with decreased movement is also the decrease in encounter rate with prey items. Therefore, by reducing the risk of encountering other individuals, the larva also reduces its encounter rate with prey items. This decrease in encounter with prey items would be manifested as a lowered dry mass and subsequent delay in molting (observable via head width measurement). This hypothesis is consistent with the findings in the present study that an increase in density decreased both the mean dry mass and the mean head width of *E. cynosura* larvae.

Head width reveals an interesting separation between high and low density treatments. Not only is the difference statistically significant after day 28, but this

difference has a very important biological significance as well. Johnson (1986) suggested that individuals that exceeded 3.0 mm head width by September may continue growing slowly throughout the winter and emerge the following spring (univoltine). Those individuals with head widths below 3.0 mm head width enter diapause, continue growing the following summer, and emerge 2 years after hatching (semivoltine). In the present experiment, mean head widths of low density treatments reached over 3.0 mm by September; we may assume that these larvae were exhibiting univoltine growth. Mean head widths from high density treatments however, were less than 3.0 mm by September; these would be expected to experience slower growth, diapause, and a semivoltine life history emergence.

Effects of Predation on Larval Growth

The presence or absence of a 2nd year class predator showed a significant effect on mean head width on days 42 and 55 (Figure 5). At these 2 times, individuals exposed to the 2nd year class predator showed lower average head widths than individuals free of the potential predation by the 2nd year class predator. Because the statistical significance of this effect did not continue throughout the experiment, we must interpret the results speculatively, keeping in mind that the predator effect was only significant during 2 sampling times.

A potential explanation for the difference observed in head width may again be

the decrease in activity induced by the presence of the predator. Reduced activity would have decreased the chance of individuals' being eaten by lowering the encounter rate with the predator. Reduced activity also could have led to fewer interactions with prey items and thus potentially lowered growth rates.

Another possible explanation is that within all treatments, more active and less active individuals were present. The more active individuals would have encountered prey items more frequently and, therefore, could have potentially grown more rapidly. However, being more active in the presence of a predator could have increased that individual's risk of being eaten. If the more active individuals were eaten in the predator present treatments, we would have expected a decrease in the mean head width when compared to the mean head width of the Predator Absent treatments where the more active individuals would have grown rapidly free of predation.

Advantages of the Cohort Split

For odonate species with relatively short adult flight seasons, it is critical that synchronous emergence occurs. If larvae emerge outside of this flight window, reproduction is not possible due to the absence of potential mates (Corbet 1983:95-97). *Epitheca cynosura* is an excellent example of a 'spring' species of dragonfly with the adult flight season occurring from late April through June (Johnson *et al.* 1980).

The cohort split phenomenon observed for *E. cynosura* at Bays Mountain Lake is

an example of 1 of the ways in which synchronous emergence is maintained by a larval population. When a larva grows rapidly, it will be able to emerge the following spring. However, if the larva is not growing as rapidly, it is unlikely that this individual will emerge early enough in the following year. Instead, the slow growing larva will enter diapause, continue growth during the next summer, and emerge a year later in the spring.

Based on the findings of this research, the density of larvae in an area appear to have a strong influence on the growth rate and subsequent voltinism of those individuals. Potentially, regions of high density would tend to be semivoltine whereas areas of low density would tend to be univoltine. For the population of *E. cynosura* at Bays Mountain Lake, this could promote synchronized emergence by allowing those individuals that have acquired a particular size to proceed to grow and emerge the following spring, or to prevent individuals from growing that would be unable to reach a large enough size to emerge the following spring.

Implications For Future Studies

A goal of the experiment was to be accurately determine the survivorship of early instars of *E. cynosura*. In light of all of the effort afforded to recovering every individual present in a sample, I feel that many were missed. This is not promising for researchers wishing to estimate early instar mortality when non-lethal measures are the only method

allowed. Collecting, sorting, identifying, and counting early instar individuals in the field is a task that must be looked at as a loose interpretation of the actual population's dynamics.

Although the presence of a 2nd year class predator showed very little effect on the growth of hatchlings, only one density of predator was tested. In some instances, natural densities are concentrated during periods of environmental stress (*ie.*), during periods of drought, when some species, such as *Somatochlora hineana* find refuge in active crayfish burrows (Pintor and Soluk 2000). This leads to high densities of many different instars that have a wide array of potential interactions with each other or with the crayfish inhabitant. Situations such as this may yield important predator effects that this study was unable to determine.

It is very likely that within the family Corduliidae, high density may cause delayed growth rates. Van Buskirk (1993) found that under high densities, growth rates of an aeshnid dragonfly were delayed in natural populations. Because this phenomena is observed across these families it is likely that density dependent growth is an important aspect of larval odonate ecology and should be considered in any study focused on determining critical aspects of life history.

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APPENDICES

APPENDIX A:
THREE-WAY ANOVA TABLES
FOR DRY MASS AND HEAD WIDTH

THREE-WAY ANOVA TABLE FOR DRY MASS. Analysis performed with natural log transformed data using general linear model in Minitab version 12.1. All replicates containing fish were excluded from analysis. Asterisks (*) indicate p values less than 0.05.

Source	DF	SS	MS	F	p
Age (A)	7	536.24	76.60	1110.1	0.000*
Density (B)	1	5.30	5.30	76.85	0.000*
Predator (C)	1	0.14	0.14	1.98	0.163
A x B	7	8.74	1.25	18.09	0.000*
A x C	7	1.07	0.15	2.22	0.040*
B x C	1	0.32	0.32	4.57	0.035*
A x B x C	7	0.32	0.05	0.67	0.698
Error	86	5.94	0.07		

THREE-WAY ANOVA TABLE FOR HEAD WIDTH. Analysis performed with natural log transformed data using general linear model in Minitab version 12.1. All replicates containing fish were excluded from analysis. Asterisks (*) indicate p values less than 0.05.

Source	DF	SS	MS	F	p
Age (A)	7	57.97	8.28	1779.4	0.000*
Density (B)	1	0.61	0.61	131.6	0.000*
Predator (C)	1	0.06	0.06	12.42	0.001*
A x B	7	0.48	0.07	14.71	0.000*
A x C	7	0.06	0.01	1.96	0.071
B x C	1	0.01	0.01	2.16	0.146
A x B x C	7	0.04	0.01	1.24	0.288
Error	85	0.40	0.00		

APPENDIX B:

TWO-WAY ANOVA TABLE FOR DRY MASS
AT EACH TIME PERIOD SAMPLED

TWO-WAY ANOVA TABLE FOR DRY MASS AT EACH TIME PERIOD SAMPLED. Analysis performed with natural log transformed data using general linear model in Minitab version 12.1. All replicates with fish present were removed from analysis. Asterisks (*) indicate p values less than 0.05.

Source	DF	SS	MS	F	p
Age 0 days					
Density	1	0.00	0.00	0.00	0.967
Predator	1	0.00	0.00	0.15	0.705
Density x Predator	1	0.00	0.00	0.74	0.409
Error	11	0.05	0.05		
Age 7 days					
Density	1	0.18	0.18	1.61	0.228
Predator	1	0.00	0.00	0.00	0.979
Density x Predator	1	0.06	0.06	0.58	0.461
Error	12	1.34	0.11		
Age 14 days					
Density	1	0.48	0.48	8.17	0.014*
Predator	1	0.28	0.28	4.75	0.050
Density x Predator	1	0.01	0.01	0.22	0.647
Error	12	0.71	0.06		
Age 21 days					
Density	1	0.11	0.11	1.85	0.211
Predator	1	0.07	0.07	1.21	0.304
Density x Predator	1	0.04	0.04	0.64	0.446
Error	8	0.49	0.06		

APPENDIX B. CONTINUED.

Source	DF	SS	MS	F	<i>p</i>
<hr/> <u>Age 28 days</u> <hr/>					
Density	1	0.43	0.43	7.09	0.022*
Predator	1	0.13	0.13	2.13	0.173
Density x Predator	1	0.01	0.01	0.19	0.674
Error	11	0.66	0.06		
<hr/> <u>Age 42 days</u> <hr/>					
Density	1	1.35	1.35	16.23	0.002*
Predator	1	0.25	0.25	3.00	0.111
Density x Predator	1	0.10	0.10	1.25	0.288
Error	11	0.91	0.08		
<hr/> <u>Age 55 days</u> <hr/>					
Density	1	6.53	6.53	77.59	0.000*
Predator	1	0.33	0.33	3.88	0.072
Density x Predator	1	0.28	0.28	3.26	0.096
Error	12	1.01	0.08		
<hr/> <u>Age 86 days</u> <hr/>					
Density	1	5.04	5.04	58.71	0.000*
Predator	1	0.16	0.16	1.86	0.206
Density x Predator	1	0.12	0.12	1.39	0.268
Error	9	0.77	0.09		

APPENDIX C:

TWO-WAY ANOVA TABLE FOR HEAD WIDTH
AT EACH TIME PERIOD SAMPLED

TWO-WAY ANOVA TABLE FOR HEAD WIDTH AT EACH TIME PERIOD SAMPLED. Analysis performed with natural log transformed data using general linear model in Minitab version 12.1. All replicates with fish present were removed from analysis. Asterisks (*) indicate p values less than 0.05.

Source	DF	SS	MS	F	p
Age 0 days					
Density	1	0.00	0.00	0.13	0.721
Predator	1	0.00	0.00	2.21	0.168
Density x Predator	1	0.00	0.00	0.50	0.498
Error	10	0.01	0.00		
Age 7 days					
Density	1	0.00	0.00	0.51	0.489
Predator	1	0.01	0.01	12.03	0.005*
Density x Predator	1	0.00	0.00	0.32	0.584
Error	12	0.01	0.00		
Age 14 days					
Density	1	0.01	0.01	0.99	0.339
Predator	1	0.00	0.00	0.32	0.582
Density x Predator	1	0.00	0.00	0.14	0.717
Error	12	0.14	0.01		
Age 21 days					
Density	1	0.02	0.02	4.34	0.071
Predator	1	0.00	0.00	0.24	0.639
Density x Predator	1	0.00	0.00	0.38	0.554
Error	8	0.04	0.00		

APPENDIX C. CONTINUED.

Source	DF	SS	MS	F	<i>p</i>
<hr/> <i>Age 28 days</i> <hr/>					
Density	1	0.08	0.08	8.45	0.014*
Predator	1	0.00	0.00	0.18	0.677
Density x Predator	1	0.00	0.00	0.27	0.616
Error	11	0.11	0.01		
<hr/> <i>Age 42 days</i> <hr/>					
Density	1	0.17	0.17	38.49	0.000*
Predator	1	0.10	0.10	22.63	0.001*
Density x Predator	1	0.04	0.04	9.37	0.011*
Error	11	0.05	0.00		
<hr/> <i>Age 55 days</i> <hr/>					
Density	1	0.40	0.40	464.45	0.000*
Predator	1	0.01	0.01	8.54	0.013*
Density x Predator	1	0.00	0.00	0.03	0.859
Error	12	0.01	0.00		
<hr/> <i>Age 86 days</i> <hr/>					
Density	1	0.40	0.40	113.05	0.000*
Predator	1	0.00	0.00	0.11	0.744
Density x Predator	1	0.00	0.00	0.38	0.551
Error	9	0.03	0.00		

VITA

BRYAN ARTHUR REECE

- Personal Data: Date of Birth: 19 February, 1974
Place of Birth: St. Joseph, MO
- Education: Missouri Western State College, St. Joseph, MO. B.S. degrees in
Biology and Natural Science, *cum laude*, 1996.
University of South Florida, Tampa, FL.
East Tennessee State University, Johnson City, TN. M.S.
Biological Sciences, 2000.
- Professional
Presentations: Ashley, David C., Bryan Reece, and Rodney Yager. 1995. Using
miniprojects in an invertebrate zoology course. Seminar
presented to members of the Idalia Society of Mid-
American Lepidopterists. Kansas City, MO.
- Reece, Bryan A. 1999. Modeling larval dragonfly seasonal
mortality. Poster presented at the 1999 International
Congress of Odonatology and the first Symposium of the
Worldwide Dragonfly Association. Hamilton, NY.
- Reece, Bryan A, 1999. Survivorship of *Epithea cynosura*
(Odonata: Corduliidae) during their first three months.
Seminar presented at The Insect/Arthropod Symposium.
Boone, NC.
- Reece, Bryan A. 2000. Early instar growth and survivorship in
the common baskettail dragonfly *Epithea cynosura*
(Anisoptera: Corduliidae). Oral Thesis Defense, Johnson
City, TN.

Reece, Bryan A. and David C. Ashley. 1995. Studies on the ecology of larval dragonflies in an ephemeral pond in northwest Missouri. Seminar presented at the district meeting of Beta Beta Beta, National Biological Honor Society. Steeleville, MO.

Reece, Bryan A. and David C. Ashley. 1995. Preliminary studies on the emergence ecology of larval dragonflies in an ephemeral pond in northwest Missouri. Seminar presented at the annual meeting of the Missouri Academy of Science. Maryville, MO.

Honors and
Awards:

1992-1994	President's Academic Scholarship
1992-1995	William Tobin King Scholarship
1994-1996	Regent's Scholarship
1995-1996	Sonnenmoser Biology Scholarship
1995-1996	Rushin-Ashley Biology Scholarship
1996	John Yancey Biology Award for Outstanding Achievement in Biology
1996	Beta Beta Beta National Biological Honor Society Scholar of the Year
1999	Dr. Denise I. Pav Research Award
2000	Inducted into Sigma Xi, The Professional Research Society