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Interference Competition between Odonata Larvae at Modified Densities

Abstract

Ladona and Cordulia larvae coexist in Bay Lake at UNDERC in Gogebic County, Michigan. A field enclosure experiment was conducted during June and July of 1998 in order to determine if density has an effect on interference competition. The data indicate that there is no statistically significant relationship between the two variables but experimental error was high and the results are, most likely, an inaccurate representation of the true relationship between density and interference competition.

Introduction

Insecta Odonata are among the most abundant macroinvertebrate predators in freshwater littoral-zone habitats; thus, it seems plausible that interactions among them (both competitive and predatory) exert an important influence on community structure (Benke 1978, Benke et al. 1982, cited in Johnson et al. 1985). Consequently, it is important to study these interactions in order to gain valuable insight on both odonate behavior and the impact of this behavior on the entire ecological system.

This particular experiment investigated the effects of odonata density on interference, particularly competitive interference. Odonata density of larvae is of specific interest because, while adult dragonflies can disperse and select low density habitats, larval dragonflies live in and are restricted to discrete aquatic habitats, often at high densities (Ball and Hayne 1952; Gerking 1962; Macan 1964; Benke 1976, cited in Van Buskirk 1987). Thus, a positive correlation between the two variables, density and interference, would indicate the existence of an important relationship that affects both the odonata community as well as the entire macroenvironment in which they are present.

In this experiment, odonata density was manipulated in field enclosures, thus remaining under the control of the experimenter. Therefore, interference competition was the variable measured in response to the controlled density. To demonstrate the presence of competition, two features are necessary and sufficient. First, it must be shown that the presence of an individual negatively influences the numbers (or some other measure of performance) of its competitors. Second, it must show that alteration of the hypothesized critical resource (density) does in fact change the interaction between individuals predictable from and consistent with the competitive process. Thus, to demonstrate a positive relationship between density and competition, it must be shown that an increase in the population density has a negative effect on the individuals within this population and that a decrease in the size of this population will correspondingly alleviate the negative effect imposed by an increased density. The task of this experiment, then, was to show that each individual in a population is not competitively oblivious to the presence of the others, indicating that competitive interference does in fact occur. It appears that competition is most strongly felt by individuals if it leads to their death but competition may also be expressed through the alteration of biomass produced, without change in survivorship (DeBenedictis 1974). Therefore, the average change in mass of the individuals over time and the proportion of survivors at the conclusion of the experiment can be utilized as response variables to modified densities, and consequently, indicators of competitive interference.

A decrease in biomass over the duration of the experiment can result if their is competition for a limited resource. The failure of an individual to acquire this resource can lead to a lower growth rate or death, and thus a sub par increase, no change, or a decrease in biomass. This change in biomass, however, can inaccurately reflect a change in mass due to death when cannibalism is practiced in the population because the victim's mass is recycled by the cannibal, and the loss of one individual is not clearly represented by the loss of that individual's mass from the population. Thus, a change in average biomass can only indicate the effects of density on growth rate in a cannibalistic society.

In the odonata community, cannibalism is a common practice and the killing of one odonate by another can be considered an extreme expression of interference competition (e.g., Benke 1978; Crowley et al. 1987; McPeak and Crowley 1987, cited in Crowley et al. 1987) because (1) killing obviously denies the victim access to resources, and does so via the same sort of aggressive behavior as in less extreme forms of interference (Baker 1980, 1981; Rowe 1980, 1985; Pierce et al. 1985; McPeek and Crowley 1987, cited in Crowley et al. 1987); and also (2) other odonates, though consistent contributors to odonate diets (Merrill and Johnson 1984; Moore 1985, cited in Crowley et al. 1987), may sometimes be killed by an odonate without being completely or even partially eaten (P.H. Crowley, laboratory observations, cited in Crowley et al. 1987). Thus, as an expression of interference competition, cannibalism can serve as a measurable variable in response to differing densities. The proportion of the population that is missing at the conclusion of the experiment comprises a good estimate of the proportion cannibalized because (1) it is well-known that odonates rarely starve to death at low fod levels in the laboratory, (2) no other predators will be present in the field enclosures, (3) cool water temperatures will prevent decomposition, (4) it will not be possible for the larvae to crawl out of the enclosures during the experiment, and (5) final instars will not be used so no individuals will be missing due to emergence (Van Buskirk 1989). Therefore, the proportion of survivors can be determined by subtracting the final number of survivors from the initial number of larvae and then dividing this number by the initial number of larvae used in the experiment.

The individuals in an odonata population that are most vulnerable to cannibalism are the smaller, younger larvae. In a study done by Fox, she reported that cannibalism occurred when there was physical proximity between different age classes even if alternative food was abundant (1975). Therefore, it appears that cannibalism is a mechanism of interference competition that aids in population regulation by stabilizing population numbers and thereby reducing the exploitative pressures on the food resources (Fox 1975). Additionally, cannibalism alters the size distributions of the larvae, which leads to an increase in population synchrony by exerting size-specific mortality on smaller individuals throughout development (Hopper et al. 1996). Thus, a density-dependent population that employs cannibalism as a mechanism of population regulation also promotes Darwinian fitness in the sense that the survivors will make a greater contribution for future generations because they were better fed as juveniles and are likely to grow faster, survive better, breed earlier, and/or produce more young (Fox 1975).

Previous studies done on odonata density and competitive interference provide additional support for a proposal suggesting that an increase in density will cause an increase in competitive interference. Van Buskirk reported that the principle effect of increasing density was to lower the growth rates and reduce the proportion of larvae that emerged during one of his experiments. In such species, larval growth and survival were shown to be inversely related (1987). In another study, Van Buskirk reported that individuals in crowded pools were developmentally delayed and survived less well than individuals in sparsely populated pools, suggesting a casual link between crowding and reduced larval performance (1993). In a similar study, Hopper et al. suggested that an increase in density will increase competition because elevated density both increases encounter probabilities between conspecifics and reduces per capita food availability. Low food availability typically increases hunger levels and foraging activities and may force organisms to expand their diets to include previously overlooked items such as conspecifics (1996). Fox provides additional evidence that cannibalism is density-dependent when she reports that the rates of cannibalism are consistent with simple encounter models in which the probability of attack is proportional to the probability of encountering a vulnerable individual (1975). Thus, an increased density leads to an increased cannibalistic interference between individuals because physical proximity is reduced, food availability decreases and hunger increases, and the probability of a hungry individual encountering a vulnerable individual is increased.

Materials and Methods

Experimental Organisms

In order to determine if intraspecific and interspecific competition vary with modified densities, two species of odonate larvae were used in this experiment: Odonata Anisoptera Libellulidae Ladona and Odonata Anisoptera Corduliidae Cordulia. Ladona and Cordulia were chosen in particular because of their relative abundances in Bay Lake. Their ample numbers allowed for both ease in collection of larvae as well as an indication of a suitable environment in which to carry out the field experiment.

Ladona and Cordulia larvae are also fairly easy to identify with the naked eye. The Cordulia nymph is stocky, somewhat cylindrical, and the abdomen is broadly oval with lateral spines on segments 8 and 9 only, small and slender and nearly equal; cerci longer than mid-dorsal length of 9, straight, acute; epiproct straight, longer than cerci; paraprocts a little longer than epiproct (*The Odonata of Canada and Alaska).* In contrast, the Ladona nymphs are slender and thin-legged, with a long taper to the end of the abdomen. The caudal appendages are very long, fully as long as segments 9 and 10 together, and very sharp. The end segments of the abdomen tend to a triquetral form (*Dragonflies of North America*). Thus, the distinguishing characteristics most often used for identification between the two species were the shape of the body (stocky or slender) along with the posterior of the abdomen (broad or pointed).

The larvae were collected from Bay Lake using dip nets. The most effective collecting areas tended to be near the shoreline in muddy substrates, with a substantial covering of leaves. The odonates were gathered from the lake and placed in oxygenated fish tanks with strips of screening for support in order to reduce stress prior to the experiment. A total of 180 Cordulia and 180 Ladona were used in this experiment. Preceding the actual experiment, the head widths of all the larvae were measured and the initial dry mass of each larva was determined based on this head width.

Experiment Locale

The area chosen for study was the University of Notre Dame Environmental Research Center (UNDERC) located on both sides of the state line between Wisconsin and Michigan's Upper Peninsula in Vilas County (Wisconsin) and Gogebic County (Michigan). It includes a land area of 6135 acrea (2485 ha) and 30 lakes and bogs with a combined surface area of 1210 acres (490 ha). The center of the UNDERC site is at 46 13' North by 89 32' East. The altitude of the area ranges between 640 ft (500 m) and 1700 ft (520 m).

The specific site chosen for this experiment was Bay Lake. This lake was chosen based on its abundance of larvae, indicating that it is a productive mircoenvironment for odonata. This was important to the project not only for the acquisition of the experimental animals but also for the conduction of the field experiment within a successful habitat. The shoreline is also conducive to the placement of the cages used for this experiment.

Experimental Design

In order to determine the effects of density on interference competition, this experiment utilized nine different density treatments of odonate larvae with four replicates of each treatment. Therefore, the total number of treatment cages that were stationed in Bay Lake was thirty-six. The nine different treatments used were: (1) zero larvae (used as the control), (2) five Ladona, (3) five Cordulia, (4) five Ladona and five

Cordulia, (5) five Ladona and ten Cordulia, (6) ten Ladona and five Cordulia, (7) ten Ladona, (8) ten Cordulia, and (9) ten Ladona and ten Cordulia.

The treatment cages were constructed of plastic planter bottoms 40.64 centimeters in diameter and wire screening covered in 0.5 mm nylon mesh 25 centimeters high. This gave the cylindrical enclosures a bottom area of 1297.17 cm^2 and a total volume of 32,429.28 cm^3. The top of the cylinder was covered with a square piece of wire screening in order to prevent any odonata from escaping and also to prevent any odonates or other animals from entering the cages. The mesh around the cages also aided in retaining the experimental animals while still allowing movement of water and small invertebrates through the enclosures. These cages were attached to metal stakes for stability in the water.

The bottoms of the enclosures were prepared for odonate inhabitation with a combination of Bay Lake mud and leaves, placed on a piece of mesh for extra support. On June 7th, 1998, odonata were randomly assigned and placed into treatments and the cages were submerged along the shoreline of Bay Lake in approximately 20 centimeters of water. The enclosures were randomly distributed and spaced approximately 1 meter apart.

The cages were left undisturbed until July 14th, 1998, when they were removed from the water. The contents of each cage was brought back to the lab and the surviving larvae were retrieved. The head width of each larva was measured and then each individual dry mass was also measured. Data analysis followed.

Results

In order to determine if interference occurred and competition increased as odonata larvae density increased, the data from this experiment was analyzed using two different measures — change in mass over time and proportion of survivors. If interference does in fact increase with density, the change in mass should decrease with increasing density and the proportion of survivors should also decrease with increasing density.

Change in mass over time, or mass difference, was determined by subtracting the initial mass mean from the final mass mean for each treatment. The initial mass mean was obtained by summing all of the individual larva's extrapolated initial dry masses used in the treatment and dividing that number by the number of individuals in the treatment. The final mass mean was obtained by summing all of the weighed final dry masses of the larvae that were recovered from that treatment at the conclusion of the experiment and dividing that number by the number of individuals recovered. The results of the mass difference calculations for each treatment are presented in Table 1A. The average of the mass differences of the four replicates of each treatment is also provided in Table 1A and illustrated in bar graph form in Figure 1A. The mean difference data for each treatment was entered into a One Way Repeated Measure Analysis of Variance (ANOVA). The differences in the mean values among the treatment groups were not great enough to exclude the possibility that the difference was due to random sampling variability; there was not a statistically significant difference (P=0.684).

The average mass difference for each density was also calculated and these results are presented in Table 1B and displayed in line graph form in Figure 1B. The line graph indicates that as the density of larvae increased, the mass difference also increased. These results are opposite of what would be expected if an increased density led to an increase in interference and competition.

The proportion of survivors was determined by subtracting the final number of larvae that were recovered at the conclusion of the experiment from the initial number of larvae in each treatment and then dividing that number by the initial number of larvae. The results of these calculations for each replicate of each treatment are provided in Table 2A along with the mean of all of the replicates for each treatment. The means of the proportion of survivors for each treatment are presented in bar graph form in Figure 2A. The mean proportion data for each treatment was entered into a One Way Repeated Measures Analysis of Variance (ANOVA). The differences in the mean values among the treatment groups were not great enough to exclude the possibility that the difference was due to random sampling variability; there was not a statistically significant difference (P=0.637).

The mean proportion of survivors for each density was also calculated and these results are featured in Table 2B and also displayed in line graph form in Figure 2B. The line graph indicates that at larval densities of 5 and 15, survivorship was highest and at densities of 10 and 20 larvae, survivorship was lowest. These results do not coincide with the results that would be expected if an increase in density caused an increase in interference. The anticipated results would have been a direct negative correlation between density and the proportion of survivors.

Table and Bar Graph of Mass Difference (Final Dry Mass - Initial Dry Mass)

Table 1A

Treat-ments	**5 Ladona**	**5 Cordulia**	**10 Ladona**	**10 Cordulia**	**5 Ladona + 5 Cordulia**	**10 Ladona + 5 Cordulia**	**5 Ladona + 10 Cordulia**	**10 Ladona + 10 Cordulia**
Rep. 1	-0.0008092	-0.0082141	0.0066358	-0.0068116	0.0139238	0.0013574	0.0086465	0.0054944
Rep. 2	0.0053769	0.0024179	0.0080072	0.0143313	0.0037511	0.0125521	0.0114393	0.0079261
Rep. 3	0.0106658	0.0217618	0.0010106	0.0087527	0.0035484	0.0064317	0.010405	0.0048512
Rep. 4	-0.0126028	0.0035132	-0.0059056	0.0058252	0.017697	0. 1000403	0.0064026	0.015192
Avg. Diff.	0.0006577	0.0048697	0.002437	0.0055244	0.0097301	0.0060926	0.0092233	0.0083659

Figure 1A

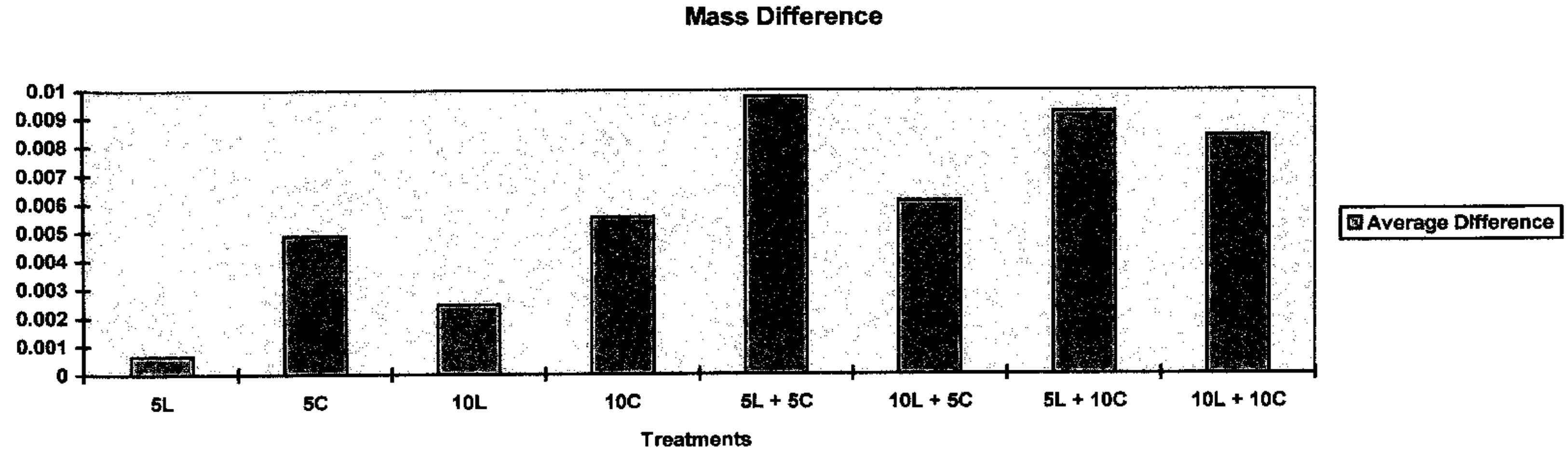


Table and Line Graph of Mass Difference

Table 1B

Densities	**0 larvae**	**5 larvae**	**10 larvae**	**15 larvae**	**20 larvae**
Mass Difference	0	0.0006578	0.002437	0.0060926	0.0083659
		0.0048697	0.0055244	0.0092234	
			0.0097301		
Avg. Mass Difference	0	0.0027638	0.0058972	0.007658	0.0083659

Figure 1B

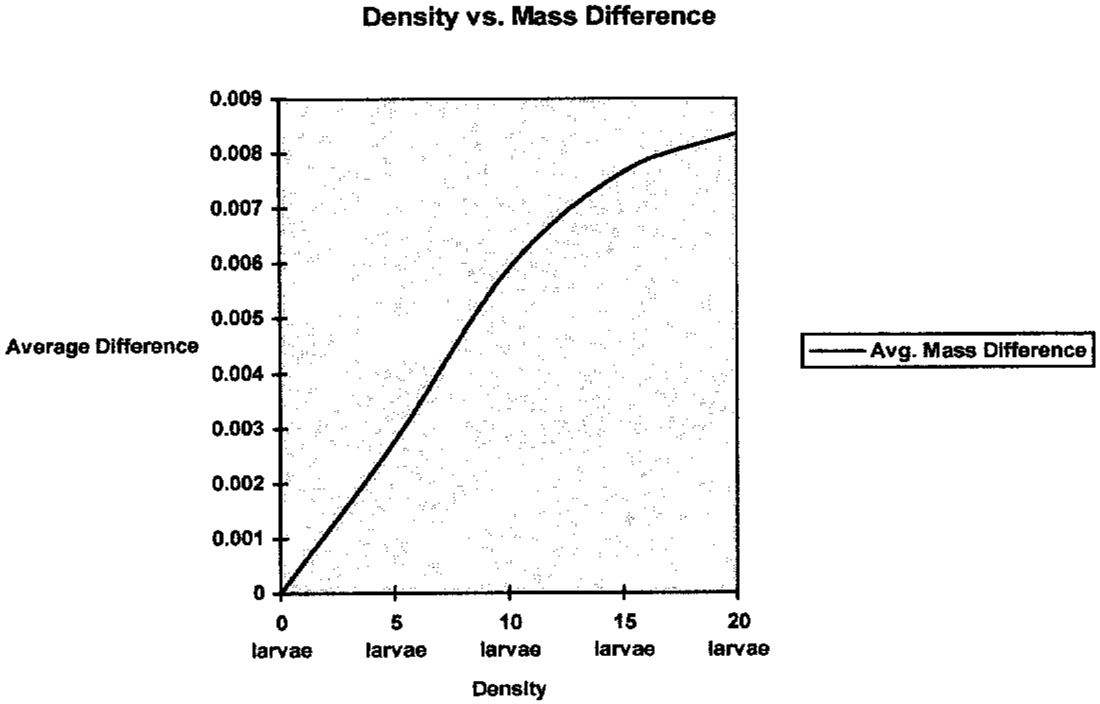


Table and Bar Graph of Proportion of Survivors [(Initial # of Larvae - Final # of Larvae) / Initial Number of Larvae]

Table 2A

Treatments	**5 Ladona**	**5 Cordulia**	**10 Ladona**	**10 Cordulia**	**5 Ladona + 5 Cordulia**	**10 Ladona + 5 Cordulia**	**5 Ladona + 10 Cordulia**	**10 Ladona + 10 Cordulia**
Rep. 1	1.00	0.20	0.60	0.20	0.30	0.73	0.67	0.60
Rep. 2	0.40	0.60	0.70	0.10	0.30	0.20	0.33	0.50
Rep. 3	0.40	0.40	0.40	0.30	0.20	0.60	0.47	0.20
Rep. 4	0.20	0.60	0.10	0.50	0.40	0.67	0.27	0.10
Avg. Proportion	0.50	0.45	0.45	0.28	0.30	0.55	0.44	0.35

Figure 2A

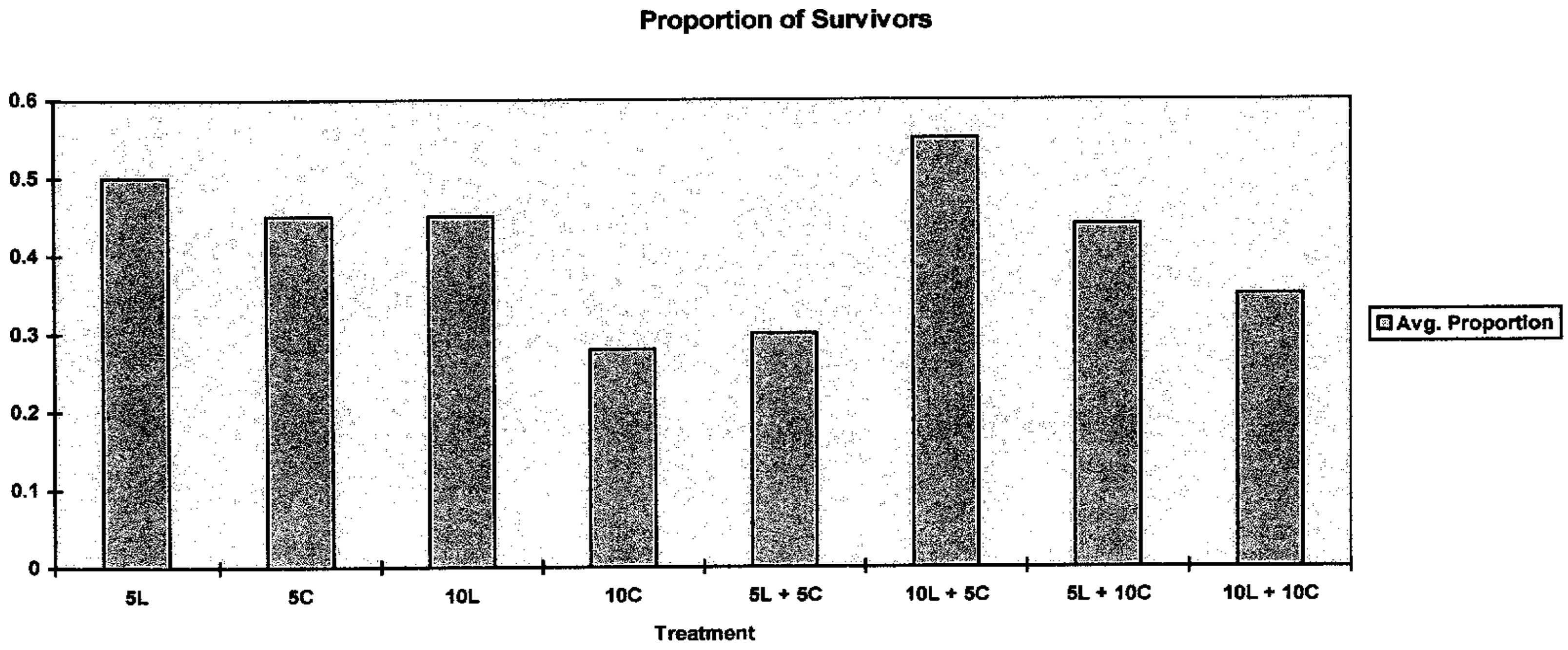


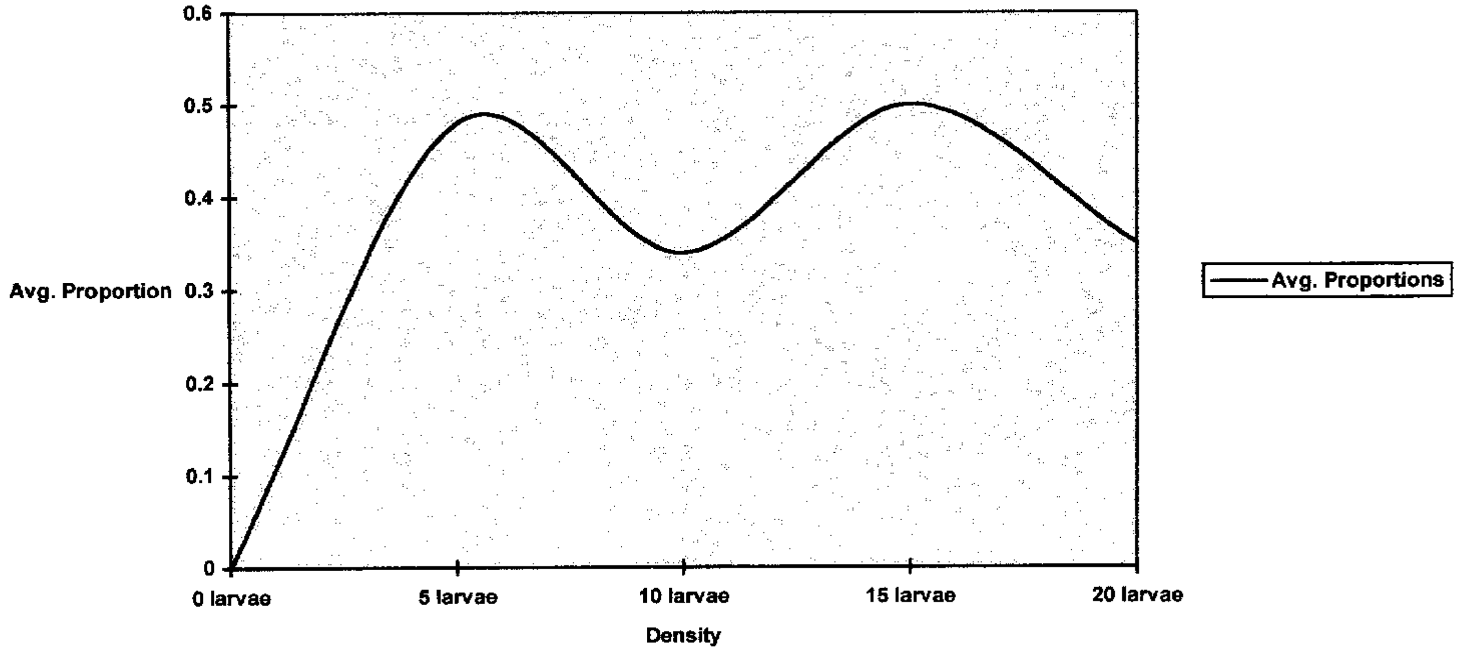
Table and Line Graph of Proportion of Survivors

Table 2B

Densities	**0 Larvae**	**5 Larvae**	**10 Larvae**	**15 Larvae**	**20 Larvae**
Proportions	0	0.50	0.45	0.55	0.35
		0.45	0.28	0.44	
			0.30		
Avg. Proportions	0	0.48	0.34	0.50	0.35

Figure 2B

Density vs. Proportion of Survivors



Discussion

The purpose of this experiment was to determine if the density of odonate larvae affected the degree of interference competition between the larvae. Based on previous studies done on similar research subjects, the hypothesis for this experiment stated that an increase in larvae density would cause an increase in interference competition. Results indicative of this proposal would illustrate that as the number of larvae (density) in a treatment increased, the average change in mass of the larvae decreased and the proportion of larvae that survived to the conclusion of the experiment also decreased.

The average change in mass of the larvae would show a decrease as the density was increased because as more larvae were constrained to a limited area, food availability would decrease and the failure of an individual to acquire this resource would lead to a lower growth rate or death.

The proportion of survivors would also decrease with an increased density because an increase in the number of larvae in a confined space would increase the physical proximity between individuals, thus increasing the probability that a hungry individual would encounter and cannibalize a vulnerable individual.

The results of this experiment showed neither a decrease in the average change in mass nor a decrease in the proportion of survivors as the density of the larvae was increased. As the number of larvae was increased, the average mass difference actually increased (Figure 1B). The proportion of survivors did not show any distinct relationship with an increase in density (Figure 2B).

Experimental error contributed, to a large extent, to the failure of this experiment to produce the expected data. The overall design of the experiment should have been both adequate and capable of determining if density does affect interference competition but several unforeseen factors came into play during the research that may have caused the results to be skewed.

The construction of the enclosures used in the experiment was, for the most part, sufficient. The planter bottoms provided a suitable "floor" for the cages and the wire and mesh cylindrical screening seemed to accomplish the task of keeping the experimental animals confined within the density-controlled microenvironment. The wire tops of the enclosures, however, were (most likely) the ineffective factor in the retention of the larvae. These lids were prepared by bending the four corners of a square piece of screening around the top of the cylinder and were secured with two pieces of wire opposite each other. If the water level rose up to or beyond the height of the enclosures, the larvae would not have a difficult time escaping through the top of the cages. Approximately four days after the cages were placed in Bay Lake, heavy rains were experienced and the water level did indeed rise and most of the enclosures were submerged. During this period some of the larvae may have entered and exited the enclosures, thus resulting in a failure to confine all of the experimental animals, leading to erroneous data.

The location of the enclosures along the shoreline of Bay Lake was ideal for this experiment. The only nuisance was the occasional deer that would step on or in the cages but no significant damage was done.

The preparation of the substrates within the enclosures was also suitable and sufficient for odonata habitation. The makeshift odonate micro-habitats consisted of mud and pre-soaked leaves. In hindsight, it is evident that these substrates were indeed appropriate because, while this experiment was in progress, a separate experiment was run to test odonata substrate preference.

The odonata substrate preference research involved an in-lab experiment in which plastic containers were divided in half, with the bottom of one side comprised of mud and the other side sand. The larvae were placed in the oxygenated containers and, after four days, the locality of the larvae (in the mud or sand) was noted. In each of the fifteen experimental containers, all of the larvae were found to be in the mud and none were in the sand. Thus, the conclusion can be drawn that Ladona and Cordulia larvae prefer mud substrate to sand.

The experimental enclosures were in Bay Lake for thirty-seven days. The growth rate of the odonate larvae is unknown so it is uncertain whether this time period was long enough to allow for significant growth of the larvae and, thus, an appreciable change in mass. Without a substantial change in mass over the experimental time period, the data cannot give an accurate measure of interference competition because any growth repression due to an elevated density would be infinitesimal and appear as negligible in the results.

The means of removal of the contents of the enclosures at the conclusion of the experiment seemed to be efficient. The retrieval of the odonates, however, may have left room for error. The contents of each cage were sorted through by hand and the odonates recaptured in this manner. This method could have allowed for some odonates to have been overlooked and, thus, not included in the final data. It is obvious that this would skew the results.

If the opportunity arose to repeat this experiment, there would be several changes that would be employed so as to collect more accurate data and, thus, conduct a more successful experiment.

(1) The tops of the enclosures would be constructed of clear, sturdy, flexible plastic that could be laid over the top of the cylinder and secured with a large rubber band. This would prevent any odonates from entering or exiting the cages, even if the enclosures became submerged due to heavy rains.

(2) Prior to the actual experiment, a growth rate-determining experiment would be conducted so as to measure a standard growth rate for the larvae and also be able to access the ideal time period for the enclosures to remain in the lake.

(3) At the end of the experiment, after the contents of the cages have been sorted through by hand, sugar floatation would be used in order to extract any larvae that were missed in the initial recovery.

Overall, this experiment was an excellent experience not only to show that science does not always run like clockwork (especially field experiments) but also to be able to appreciate all of the time and effort, in foresight and hindsight, that go into making an experiment a success.

Acknowledgments

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