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A Lotka-Volterra equation with cladocerans in multiple species competition

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**A LOTKA-VOLTERRA EQUATION WITH CLADOCERANS IN
MULTIPLE SPECIES COMPETITION**

A Thesis

Presented to

The Faculty of the Department of Biological sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science Degree

by

Susan Gilbreath

August 1998

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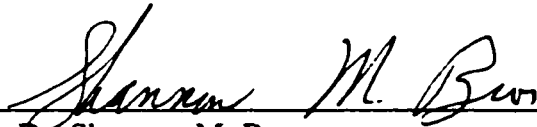
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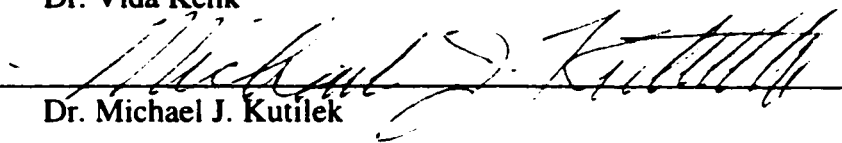
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ABSTRACT

A Lotka-Volterra Equation with Cladocerans in Multiple Species Competition

By Susan Gilbreath

I modified the Lotka-Volterra (LV) competition equations by summing components for multiple species interactions. The model was field tested with three genera of cladocerans. The competition experiments were validated by monitoring free-swimming cladoceran concentrations and comparing the concentrations to those inside the enclosures. During a 32 day period, 11 replicates of all possible combinations of *Alona*, *Bosmina*, and *Daphnia* were run with different initial conditions in enclosures at Jasper Ridge Biological Preserve, adjacent to Stanford University in California. In all cases, *Alona* and *Bosmina* were able to suppress or competitively exclude *Daphnia*. *Alona*'s numbers were significantly depressed when enclosed with *Bosmina* although there was no difference in *Alona*'s numbers when enclosed with both *Bosmina* and *Daphnia*. When the effects of *Alona* and *Bosmina* were summed against *Daphnia*, phase plane diagram analysis showed classic Gaussian competitive exclusion. This work demonstrated a new use of the LV equations.

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INTRODUCTION

Competition is an interaction that occurs between organisms of the same species (intraspecific) or different species (interspecific). Three general types of competition are recognized. Exploitive competition occurs when two or more species use a common resource that is in short supply. When competitors harm one another while seeking a resource the situation is referred to as interference competition. Apparent competition occurs when species have different levels of vulnerability to predators (Arthur, 1987). These categories are not discrete in that competitive interactions are usually a blend of the three types.

The symbolic representation of interactions define competition in terms of the type of impact (positive, negative, or neutral) that each species has on the other's population (Arthur 1987, Ginzburg and Golenberg 1985). For example, a (negative, neutral) representation indicates that the number of species A is depressed when with species B and that the number of species B remains the same with or without species A.

Roughgarden (1979) stated that the criterion for interspecific competition is that the fitness of individuals of each species must be a decreasing function of the abundance of the other species. The criterion for competition between n number of species is not necessarily an expansion of this idea. If species A, B, and C all utilize the same resource, the fitness of species A may be depressed by species B whose numbers are lowered by species C, and likewise, its population is reduced by species A. If we were to examine only the interactions of species A and B, we would miss a critical component of the system. Arthur (1987) suggested such complex situations are best avoided all together

because it is difficult to know what to call the overall interaction. However, if we are to use competitive interactions to help define what is happening at the community level we need to face these dilemmas. Therefore, we can describe competition between n number of species by using comparisons and evaluating the number of negative interactions to neutral and positive interactions. For example, we can first investigate the effects of species B on species A and, consequentially, the effects of species C on species A. Suppose there is a (negative, negative) interaction for both cases. We would explore this further by comparing the combined effects of species B and C on A. If this resulted in a different interaction we would need to evaluate the effects of species B versus species C.

The classic Lotka-Volterra (Volterra 1926, Lotka 1924) model is used to analyze competition and/or predator/prey relationships among two different species in a primarily theoretical manner. I hypothesized that by summarizing multiple components in the equation, the model would retain much of its simplicity, and, at the same time, have practical applications with competitive interactions involving more than two species. The LV equation works well as a specific model for some systems (Pascual and Kareiva 1996, Kerfoot and DeMott 1980, Park 1948, Gause 1934) and is a good general model (Roughgarden 1997, Stiling 1996). It is not possible at this time to develop a single model that will explain interactions for all species because they have evolved along several different phylogenetic paths, under different selection pressures.

Gause's classic laboratory work (Gause 1934) with *Paramecium* utilizing the LV equation has served as a stimulus to use mathematical models with experimental data to examine the behavior of interacting species (Pascual and Kareiva 1996). The LV

equation is a simple model that has some value in predicting whether or not two competing populations can stably coexist. The LV model is widely known and has been shown to work well in laboratory populations with two competing r- selected species (Pascual and Kareiva 1996, Connel 1983, Schoener 1983, Kerfoot and DeMott 1980, Roughgarden 1979, Park 1948, Gause 1934). While laboratory experiments are important in demonstrating principles of competition, the results are not always applicable to the natural world (Roughgarden 1997, Stiling 1996, Pascual and Kareiva 1996, Arthur 1987, Park 1948, Gause 1934). Additionally, competitive interactions are rarely limited to just two species; communities are based on interactions between many different species at several different trophic levels (Roughgarden 1997, Stiling 1996, Pascual and Kareiva 1996, Ives 1995, Arthur 1987, Salt 1983, Gilpin and Case 1981, Tilman 1981).

The logistic equation is a model of growth in a single population characterized by a sigmoid curve with an upper asymptote. The equation in differential form is

$$dN/dt = r*N*((K-N)/K)$$

where N is the population size, t is time, r is the intrinsic rate of natural increase and K is the carrying capacity of the system and equal to the maximum value of N.

The LV model utilizes logistic growth for two competing populations using two simultaneous differential equations

$$dN_1/dt = r_1 * N_1 * ((K_1 - N_1 - \alpha N_2) / K_1)$$

and

$$dN_2/dt = r_2 * N_2 * ((K_2 - N_2 - \beta N_1) / K_2)$$

where the subscripts denote parameters and variables for populations 1 and 2. α converts species 1 into units of species 2 and β converts species 2 into units of species 1 so that

1 species of $N_1 = \alpha N_2$ and 1 species of $N_2 = \beta N_1$.

This model has four possible solutions: Species 1 could always win, species 2 could always win, species 1 and 2 may permanently coexist or species 1 or 2 could win, depending on starting conditions. This model is usually analyzed graphically with the two populations superimposed on the same graphs. This has not been possible with a model of n species. The model I have developed is a variation of the LV equations. By prioritizing the interactions between the competing species, I used the competition coefficients to combine the interactions, allowing me to display the results in the graphical form usually reserved for two populations. In the two-population format, one can solve for competition coefficients with the equations

$$\alpha = (K_1 - N_1) / N_2 \text{ and } \beta = (K_2 - N_2) / N_1$$

We can think of the competition coefficients as a measure of the strength of interspecific competition relative to intraspecific competition (Roughgarden 1979).

Cladocerans are ideal organisms to test the validity of an LV model because they have rapid generation times and short life spans. This allows the investigator to run several replications and, unlike most competition experiments in the literature (Arthur 1987), maintain the experiments through to their conclusion (be it coexistence or competitive exclusion). For the most part, reproduction is parthenogenic and the eggs hatch from a brood pouch in a form very similar to adults. They maintain the same morphology throughout their life spans, thus aiding in identification. Cladocerans are (mostly) non-selective filter feeders (Pennak 1989). This is important because one of the assumptions of the model is that there is one common resource being shared. Because cladocerans are hardy creatures, they are less likely to become stressed from experimental manipulations. With the use of *in situ* enclosures, it is possible to test competition in the field instead of a laboratory environment.

The goals of this study were two-fold. First, I wanted to determine the importance of competition in the interactions between the three cladoceran genera, *Alona*, *Bosmina*, and *Daphnia*. I did not distinguish between interference and exploitive competition in my research because the common resource was not in short supply. Identifying the type of competition is not important when measuring changes of fitness. Apparent competition was not examined in my study, although susceptibility to predators is undoubtedly crucial in shaping the system I investigated. The second goal of this work was to demonstrate the practicality of using a well-recognized model in a complex

situation. A multiple species interaction was interpreted with a 2 species LV equation.

The utility of the model was graphically analyzed.

The importance of competition between the cladocerans was evaluated. With the exception of the exclusion of predators, every effort was made to minimize artificial conditions. Two experiments were used to evaluate the robustness of the competition study design. First, the free-swimming cladoceran density was compared at the initiation and termination of the study to determine the natural changes in composition over time. The cladoceran composition inside and outside the enclosures was compared to ensure that conditions were similar. If the composition inside the enclosures were different from the rest of the lake, any evidence of competition found during the study would have to be viewed as stemming from artificial conditions. Because different starting concentrations could lead to different competition results, cultures were started near equilibrium values (Arthur and Farrow 1987). Recommendations made by Pascual and Kareiva (1996) to use a variety of starting conditions for di- (and tri-) cultures were used to ascertain the individual effects of the cladoceran genera and determine the strength of each interaction. All possible comparisons between genera were examined to determine the outcome of interactions. For example, if the final numbers of a high density monoculture were compared to the final high density diculture of that genus with a low density of another a genus no change in numbers would indicate that the genus is not affected by low numbers of the other genus. If the numbers of the high density genus were significantly depressed when the low density genus were present, it can be ascertained that the high density genus is negatively affected by just a few individuals of the other species. Conversely, it

can be said that the low density genus is a strong competitor with the high density genus. To hypothesize possible reasons contributing to competition the sizes of the cladocerans were noted to examine if a correlation between size and fitness existed. There is evidence that different sized cladocerans have different competitive abilities (Xie and Takamura 1996, Boersma 1995, Pennak 1989). Finally, multiple species competition was evaluated with a 2 species LV competition equation by summing similar components to develop the model parameters α, β, K, N and r .

STUDY AREA AND FIELD METHODS

Because of its protected status, Jasper Ridge Biological Preserve (JRBP), adjacent to Stanford University, provided a unique opportunity for undisturbed field research. JRBP is home to two adjoining, freshwater, eutrophic lakes. Searsville Lake and Middle Lake are formed by the confluence of three streams and Searsville Dam (Fig. 1). Size and depth of the lakes vary with seasonal rainfall and temperature, as well as the height of the dam. Searsville Lake reaches a maximum volume of 1,534,800 cubic meters, covering 131,850 square meters of surface area and Middle Lake has a capacity of 289,750 cubic meters, covering 64,400 square meters of surface of area.

Zooplankton were trapped with a plankton tow net in substrates, open water, and littoral zones in both lakes. The three cladoceran genera, *Alona*, *Bosmina*, and *Daphnia*, found above the littoral zones, were identified and cultured in the lab. This study only looked at separate genera because hybridization between different species of

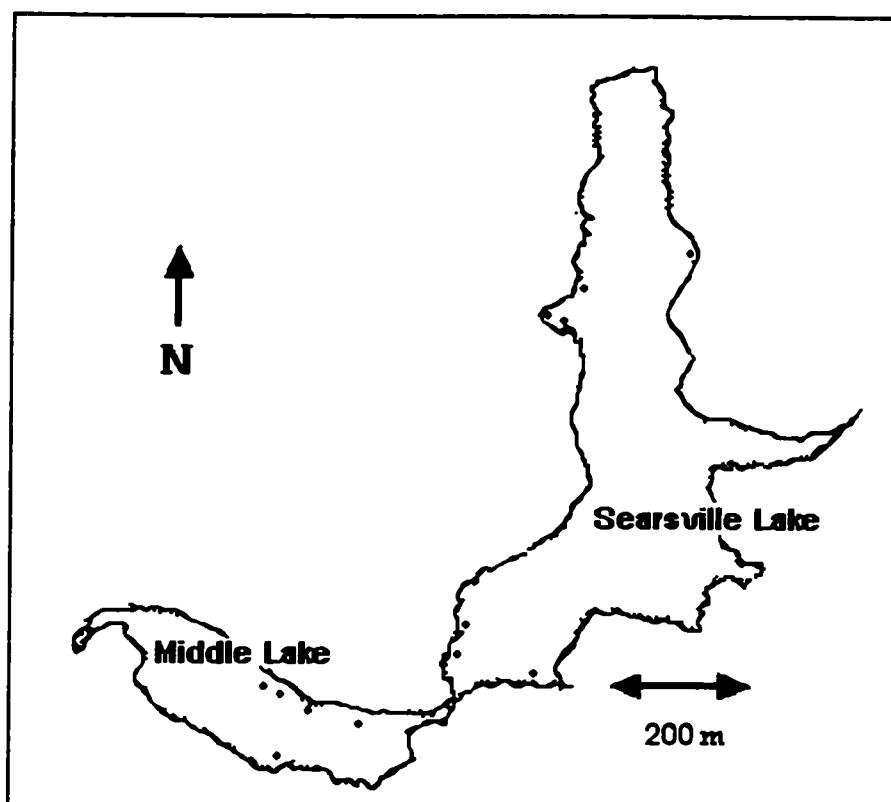


Figure 1. Searsville and Middle Lake at Jasper Ridge Biological Preserve. Sample sites are represented by *.

Table 1. Experimental design at each sampling area. The initial numbers of individuals include only parthenogenetic females without egg clutches. The numbers represent which combination of cladocerans were used.

Treatment Code	Initial Number of Individuals		
	<i>Alona</i>	<i>Bosmina</i>	<i>Daphnia</i>
<i>Alona</i> -high	20	0	0
<i>Alona</i> -low	5	0	0
<i>Bosmina</i> -high	0	20	0
<i>Bosmina</i> -low	0	5	0
<i>Daphnia</i> -high	0	0	20
<i>Daphnia</i> -low	0	0	5
<i>Alona</i> -high: <i>Bosmina</i> -low	20	5	0
<i>Alona</i> -low: <i>Bosmina</i> -high	5	20	0
<i>Bosmina</i> -high : <i>Daphnia</i> -low	0	20	5
<i>Bosmina</i> -low : <i>Daphnia</i> -high	0	5	20
<i>Daphnia</i> -high: <i>Alona</i> -low	20	0	5
<i>Daphnia</i> -low: <i>Alona</i> -high	5	0	20
<i>Alona</i> -high: <i>Bosmina</i> -low: <i>Daphnia</i> -low	20	5	5
<i>Alona</i> -low: <i>Bosmina</i> -high: <i>Daphnia</i> -low	5	20	5
<i>Alona</i> -low: <i>Bosmina</i> -low: <i>Daphnia</i> -high	5	5	20
<i>Alona</i> : <i>Bosmina</i> : <i>Daphnia</i> - equal	10	10	10

the same genus made identification to the species level difficult.

After sufficient stocks of each genus were obtained, they were divided into 16 combinations of monocultures, dicultures and tricultures with different initial concentrations (Table 1). Only parthenogenetic females without egg clutches were enclosed. The cladocerans were enclosed in 1 liter jars and sealed with 70um Nitex mesh. Sixteen jars containing all the treatment combinations were enclosed in a laundry basket to prevent breakage and loss, while still allowing water flow and light. I assumed that these steps insured conditions of food, light, temperature, nutrients and dissolved gasses similar to those experienced by natural populations (Smith and Cooper 1982). From June 20 to July 26 of 1997, 12 baskets, containing 16 treatments each, were randomly placed in accessible areas in Searsville and Middle Lakes (Fig. 1). Although 12 replicates of each treatment group were made, sample sizes for each group ranged from 9-11 due to loss or contamination. One liter water samples were taken outside the enclosures to determine natural cladoceran densities at the initiation and termination of the study. The experiment was staggered so that groups of 3 baskets were placed at a time in the lakes for 16 to 19 days, with an average of 17.9 days. Lake water was filtered through the 70um mesh into the jars and changed every 5 to 7 days. This prevented microcrustacean contamination (in most cases) and kept the jars clear of sediment, while allowing a natural food source of filamentous algae for the cladocerans. Handling was assumed to cause negligible stress and mortality (Smith and Cooper 1982). The mesh tops were cleaned every 2 to 3 days to remove the debris that collected on them. The cladocerans were kept at a constant depth 0.25 meters from the water surface; this

necessitated moving the enclosures as the water level receded. Water surface temperatures remained consistent throughout the study with initial and final water temperatures averaging 24°C ($\pm 1^{\circ}\text{C}$). At the termination of the experiment, the cladocerans were preserved with a 5% glycerin, 60% ethanol solution. The number of cladocerans in each group were counted with a hand counter and tabulated. Mean lengths of the cladocerans were calculated, based on 50 specimens (\geq the smallest specimen encountered with a brood pouch) for each genus.

Two experiments were performed to validate the competition study design. To assess the natural changes, cladoceran densities (numbers per liter) outside each basket were calculated at the initiation and termination of the experiment. A univariate F-test was used to compare changes outside the enclosures between *Alona*, *Bosmina*, and *Daphnia* concentrations during the study period. The Hotelling-Lawley F-test (Zar 1996) was used to compare overall changes in cladoceran densities throughout the study. To evaluate the effects of artificial enclosures on the experiment, the final cladoceran densities outside the baskets were compared to the final densities in the equal triculture treatments. A univariate F-test was used to compare differences in *Alona*, *Bosmina*, and *Daphnia* concentrations inside and outside the enclosures and the multivariate Hotelling-Lawley F-test was used to compare cladoceran densities inside and outside the enclosures.

To determine if the fitness of one genus was a decreasing function of another, a MANOVA (Zar 1996) was used to test for a general difference in final mean numbers of

Alona, *Bosmina*, and *Daphnia* in each treatment group. A series of 1-way ANOVAs (Zar 1996) were performed with a Tukey-Farver HSD post hoc test (Zar 1996) to compare all possible combinations of individual means in mono-, di-, and tricultures. The alpha level for significance was set at 0.025 for these tests.

THE LV MODEL AND METHODS

To examine the effects of *Alona* and *Bosmina* on *Daphnia*, I converted *Bosmina* into units of *Alona* and then summed the effects of *Alona* and *Bosmina* and called them population number 2, leaving *Daphnia* as population number 1. I determined the 6 possible intermediate competition coefficients from the tricultures; $\alpha_{1:2}$, $\alpha_{2:1}$, $\alpha_{1:3}$, $\alpha_{3:1}$, $\alpha_{2:3}$, and $\alpha_{3:2}$, where the subscript 1:2 represents a conversion factor for species 1 in terms of species 2 and the subscript 2:1 represents species 2 in terms of species 1, etc. I used these new coefficients to get the final α and β so that:

$$\alpha = (K_3 - N_3) / (N_1 + \alpha_{1:2} N_2) \quad \text{and} \quad \beta = ((K_1 + \alpha_{3:2} K_2) - (N_1 + \alpha_{3:2} N_2)) / N_3$$

The intrinsic rate of natural increase (r) was determined with the equation

$$r = \ln(N_t / N_i) / t_1$$

where N_t is the average number of organisms at time t , and N_i is the average initial number of organisms, and t is the average time in days. The carrying capacity (K) was determined for each genus by using the mean final numbers of the monocultures per jar. The population size (N) was determined for each genus by using the mean final numbers of the monocultures per jar. I used the data gathered in this study to proceed with the traditional phase plane graphical display used for 2 species competition. *Bosmina* was converted into *Alona* units and plotted against *Daphnia*.

RESULTS

Changes in free-swimming cladocerans composition during the study period indicated the populations were experiencing a natural flux. One liter water samples taken near each site showed significant differences (Hotelling-Lawley p value ≤ 0.001) in free-swimming cladoceran densities at the initiation and termination of the study (Fig. 2). *Alona* concentrations decreased insignificantly (p value = 0.054) from a mean 97 individuals per liter to 82 individuals per liter. *Bosmina* numbers decreased significantly (p value ≤ 0.001) from a mean 126 individuals per liter to 64 individuals per liter. *Daphnia* disappeared from the lakes (p value ≤ 0.001) with an initial mean of 8 individuals per liter to 0 individuals per liter.

The results of the comparison between the inside and outside of the enclosures showed that artificial conditions were not likely to have a large influence on the outcome of the competition experiments. One liter water samples taken near each site at the end

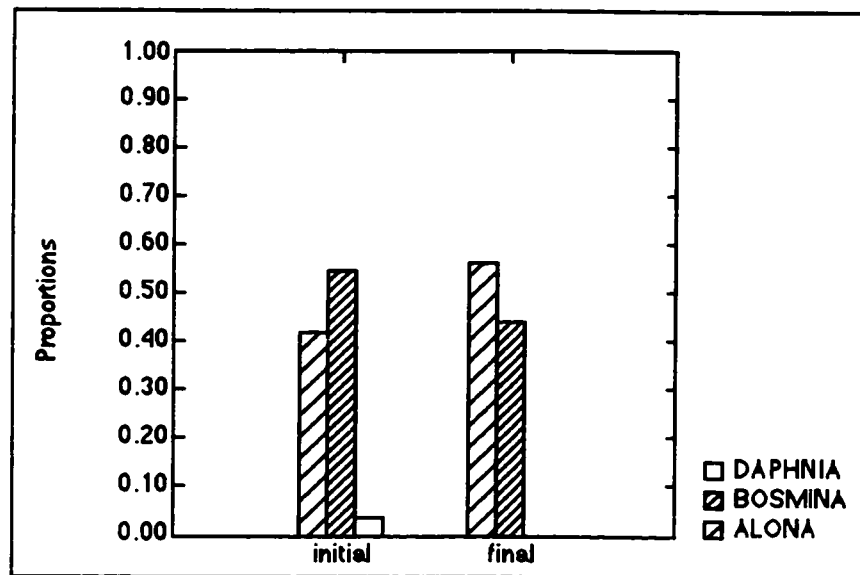


Figure 2. A comparison of the proportions of *Alona*, *Bosmina*, and *Daphnia* outside the enclosures at the beginning (initial) and the termination (final) of the study.

of the study were compared to the *Alona* –*Bosmina*- *Daphnia*- equal treatment group revealed no significant differences in overall composition (Hotelling-Lawley p value = 0.081). The differences between *Alona*, *Bosmina*, and *Daphnia* inside and outside the enclosures were insignificant (p values = 0.059, 0.547, and 0.305 respectively).

The competition experiments indicate that species belonging to the *Alona* genus experience a negative effect on population growth and survival when cultured with other species of cladocerans (Table 2). This effect was only significant when comparing the *Alona* -high and *Alona* -low cultures to the *Bosmina* -high- *Alona* -low cultures. There were no significant differences in any of the comparisons between dicultures and tricultures, and monocultures and tricultures. There was a significant overall effect when using a multivariate comparison with *Bosmina* and *Daphnia*.

The competition experiments indicate that species belonging to the *Bosmina* genus experience no effect on population growth and survival when cultured with other species of cladocerans (Table 3). Multivariate analysis revealed no significant effects between *Bosmina* and *Alona* or *Bosmina* and *Daphnia* . There were no significant differences in *Bosmina* mono-, di- or triculture pairwise mean comparisons.

The competition experiments indicate that species belonging to the *Daphnia* genus experience significant negative effect on population growth and survival when cultured with other species of cladocerans (Table 4). Mean *Daphnia* numbers were significantly lower in all di- and tricultures, when compared to *Daphnia* –high and low monocultures with an overall multivariate effect. There were no significant differences

Table 2. The final means for *Alona* in each treatment group and the p values for the number of individuals of *Alona* in *Alona* -high and *Alona* -low versus the number of individuals of *Alona* in each other treatment group. Values marked with an asterisk (*) are \leq the significance level of 0.025.

Comparison	Final Means <i>Alona</i>	p value	
		<i>Alona</i> -high	<i>Alona</i> -low
<i>Alona</i> -high	107.3	1.000	1.000
<i>Alona</i> -low	111.6	1.000	1.000
<i>Alona</i> -high: <i>Bosmina</i> -low	78.8	0.017*	0.002*
<i>Alona</i> -low: <i>Bosmina</i> -high	96.5	0.921	0.586
<i>Daphnia</i> -high: <i>Alona</i> -low	87.2	0.231	0.049
<i>Daphnia</i> -low: <i>Alona</i> -high	92.1	0.648	0.262
<i>Alona</i> -high: <i>Bosmina</i> -low: <i>Daphnia</i> -low	95.0	0.862	0.489
<i>Alona</i> -low: <i>Bosmina</i> -high: <i>Daphnia</i> -low	90.4	0.463	0.140
<i>Alona</i> -low: <i>Bosmina</i> -low: <i>Daphnia</i> -high	98.4	0.980	0.781
<i>Alona</i> : <i>Bosmina</i> : <i>Daphnia</i> - equal	95.7	0.912	0.589
Multivariate effect	p value	0.004*	

Table 3. The final means for *Bosmina* in each treatment group and the p values for the number of individuals of *Bosmina* in *Bosmina* -high and *Bosmina* -low versus the number of individuals of *Bosmina* in each other treatment group.

Comparison	Final Means		p value
	<i>Bosmina</i>	<i>Bosmina</i> -high	<i>Bosmina</i> -low
<i>Bosmina</i> -high	94.0	1.000	1.000
<i>Bosmina</i> -low	88.7	1.000	1.000
<i>Alona</i> -high: <i>Bosmina</i> -low	76.7	0.690	0.944
<i>Alona</i> -low: <i>Bosmina</i> -high	66.4	0.082	0.265
<i>Bosmina</i> -high : <i>Daphnia</i> -low	78.5	0.731	0.649
<i>Bosmina</i> -low : <i>Daphnia</i> -high	89.5	0.638	0.862
<i>Alona</i> -high: <i>Bosmina</i> -low: <i>Daphnia</i> -low	78.3	0.979	0.897
<i>Alona</i> -low: <i>Bosmina</i> -high: <i>Daphnia</i> -low	80.0	0.763	0.876
<i>Alona</i> -low: <i>Bosmina</i> -low: <i>Daphnia</i> -high	84.4	0.989	0.701
<i>Alona</i> : <i>Bosmina</i> : <i>Daphnia</i> - equal	69.8	0.900	0.789
Multivariate effect	p value		0.072

Table 4. The final means for *Daphnia* in each treatment group and the p values for the number of individuals of *Daphnia* in *Daphnia* -high and *Daphnia* -low versus the number of individuals of *Daphnia* in each other treatment group. Values marked with an asterisk (*) are \leq the significance level of 0.025.

Comparison	Final Means		p value
	<i>Daphnia</i>	<i>Daphnia</i> -high	<i>Daphnia</i> -low
<i>Daphnia</i> -high	22.6	<0.001*	<0.001*
<i>Daphnia</i> -low	22.6	<0.001*	<0.001*
<i>Daphnia</i> -high: <i>Alona</i> -low	7.5	<0.001*	<0.001*
<i>Daphnia</i> -low: <i>Alona</i> -high	1.6	<0.001*	<0.001*
<i>Bosmina</i> -high: <i>Daphnia</i> -low	5.0	<0.001*	<0.001*
<i>Bosmina</i> -low : <i>Daphnia</i> -high	1.9	<0.001*	<0.001*
<i>Alona</i> -high: <i>Bosmina</i> -low: <i>Daphnia</i> -low	0	<0.001*	<0.001*
<i>Alona</i> -low: <i>Bosmina</i> -high: <i>Daphnia</i> -low	2.4	<0.001*	<0.001*
<i>Alona</i> -low: <i>Bosmina</i> -low: <i>Daphnia</i> -high	0.5	<0.001*	<0.001*
<i>Alona</i> : <i>Bosmina</i> : <i>Daphnia</i> - equal	0	<0.001*	<0.001*
Multivariate effect	p value		<0.001*

Table 5. Intermediate and final α and β values.

Organism	Symbol	Value
<i>Alona : Bosmina</i>	$\alpha_{1:2}$	0.187
<i>Bosmina : Alona</i>	$\alpha_{2:1}$	0.140
<i>Alona : Daphnia</i>	$\alpha_{1:3}$	20.410
<i>Daphnia : Alona</i>	$\alpha_{3:1}$	0.231
<i>Bosmina : Daphnia</i>	$\alpha_{2:3}$	18.500
<i>Daphnia : Bosmina</i>	$\alpha_{3:1}$	0.280
<i>Alona + Bosmina : Daphnia</i>	α	0.200
<i>Daphnia : Alona + Bosmina</i>	β	23.865

Table 6. Mean K, N, and r values for the three genera and the combination of *Alona* and *Bosmina*.

Organism	Monoculture final (Kx)	Triculture final (Nx)	r
<i>Alona</i>	109.468	94.858	0.095
<i>Bosmina</i>	91.364	78.120	0.085
<i>Daphnia</i>	22.636	0.716	0.007
<i>Alona + Bosmina</i>	126.553	109.455	0.090

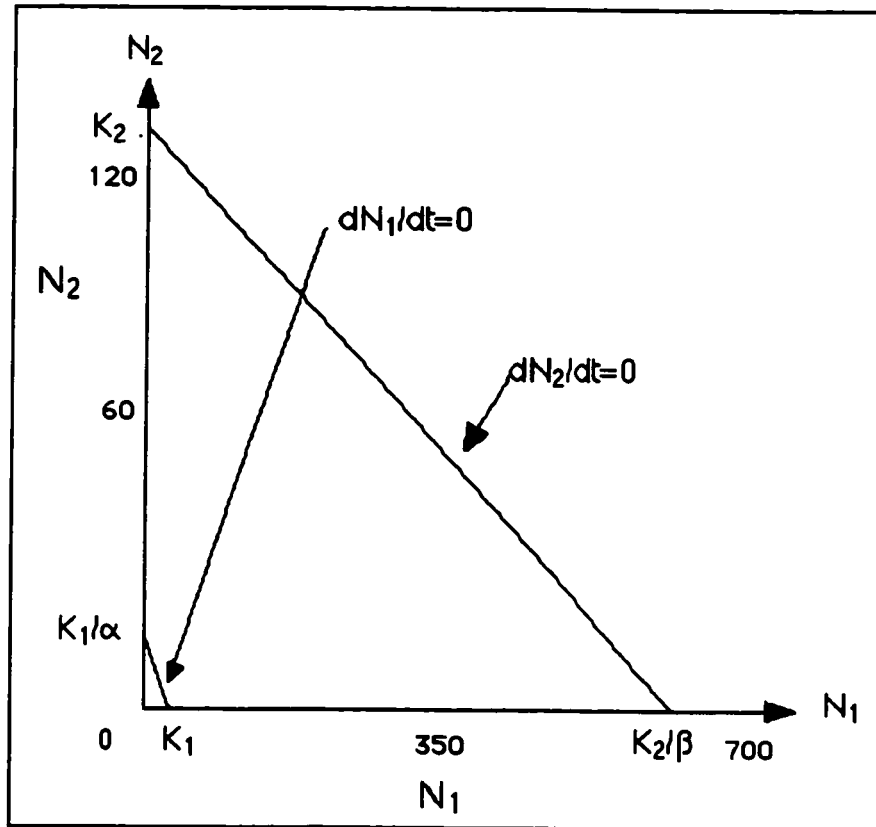


Figure 3. Phase plane diagram of shows that *Alona* + *Bosmina* will exclude *Daphnia* in levels above $dN_2/dt = 0$.

between the final mean numbers in di- and tricultures.

Based on 50 random samples from each genus, *Daphnia* was approximately twice the length of *Alona* and *Bosmina*. The range in lengths for adult *Alona* females was 0.35-0.6 mm. The range in lengths for adult *Bosmina* females was 0.3-0.5 mm. The range in lengths for adult *Daphnia* females was 0.8-1.1 mm. Males and sexual females were not encountered during the study period.

The two species LV equation was successfully used to model the multiple genera competition. The final α for *Alona* and *Bosmina* (summed in *Alona* units) versus *Daphnia* was 0.200. The final β for *Daphnia* versus *Alona* and *Bosmina* (summed in *Alona* units) was 23.865. Intermediate values were used to get the final values (Table 5). *Alona* and *Bosmina* had similarly large carrying capacities (K), population sizes (N), and r values and were summed in *Alona* units (Table 6). *Alona* and *Bosmina* summed in *Alona* units had the largest carrying capacity (K), population size (N), and r value. *Daphnia's* carrying capacity (K), a population size (N), r value for were the lower than the others and left as they were. The traditional LV graph (Fig. 3) shows *Alona* + *Bosmina* against *Daphnia*. It predicts that *Alona* and *Bosmina* (summed in *Alona* units) will outcompete *Daphnia* in levels above $dN_2/dt = 0$.

DISCUSSION

The cladoceran experiment assumed a common resource for the three genera. At first glance, it appears that *Alona* and *Bosmina* were able to utilize the available resources more readily than *Daphnia*. Although aquatic environments are relatively

homogeneous, resource partitioning still occurs (Ives 1995). There is conflicting evidence for size selectivity, that is, small cladocerans are able to filter small particles while larger cladocerans filter bigger particles (Xie and Takamura 1996, Smith and Cooper 1982, Frost 1980). *Alona* and *Bosmina* were approximately half the size of *Daphnia*, and perhaps able to filter the small nutrient particles more effectively. However, *Daphnia* died out in the enclosures where the smaller nutrients were likely to be, and disappeared from the lakes. Presumably, particles of any size would be available to the cladocerans that were not enclosed. The free cladocerans were subject to predation, and larger zooplankton are more susceptible to predators (Xie and Takamura 1996, Pennak 1989). The enclosed cladocerans were not exposed to predation, so this could not be reason for the demise of *Daphnia*. Marked population shifts in zooplankton communities are often observed and attributed to seasonal changes, predation, competition, nutrient availability, and habitat change (Xie and Takamura 1996, Boersma 1995, Dohet and Hoffman 1995, Pennak 1989).

Outside of the enclosures, *Alona* and *Bosmina* reversed dominance during the study period. Initially, there was a greater proportion of *Bosmina*, but at the termination of the study there was a greater proportion of *Alona*. The numbers of *Bosmina* outside the enclosures decreased significantly, while *Alona*'s numbers did not. However, *Bosmina* was not affected by the presence of *Alona* and *Daphnia* inside the enclosures, indicating there was something protective about the enclosures. This is interesting because *Alona* experienced a decrease of numbers when enclosed with *Bosmina*, while the *Bosmina* population demonstrated no differences in its numbers. *Alona* could be a

stronger competitor when the only factor is sharing a common resource (inside the enclosures) while *Bosmina* could be better at avoiding predators (e.g., outside the enclosures).

The fact that *Daphnia* disappeared from the lakes while there were still a few individuals of *Daphnia* alive in the jars is another example of the effect of the artificial environment on population abundance in the enclosures. However, there were no significant differences in cladoceran composition inside and outside of the enclosures at the termination of the experiment. Therefore, it is not likely that predation played a major role in the population dynamics of this zooplankton community.

Following Ginzburg and Golenberg's (1985) definitions of population interactions, the *Alona* : *Bosmina* , *Alona* : *Daphnia*, and the *Bosmina* : *Daphnia* interactions could be described as amensalism (negative, neutral). I can also describe the *Alona* + *Bosmina* : *Daphnia* interaction as amensalism (neutral, negative). The other interactions all show no effect (neutral, neutral). Because of the similarities between *Alona* and *Bosmina*, it is more efficient to look at their effects on *Daphnia*. It should be noted that if the effects of *Alona* and *Bosmina* were multiplicative instead of additive, it would be inappropriate to merely sum them. In other words, if *Alona* by itself had excluded *Daphnia* in 17 days and *Bosmina* alone excluded *Daphnia* in 16 days but the combination of *Alona* and *Bosmina* excluded *Daphnia* in 2 days, a more complex equation would have been needed.

There are other, more accurate models that examine competition between more than two species, but they are complex and generally used in theoretical work (Strobeck

1973, Nisbet and Gurney 1982, Gilpin and Case 1981, but see Ives 1995). Integrating comparisons into the LV equation allows it to be used to examine competition between an infinite number of species in an experimental setting. The resulting equations retain the simplicity of the original LV equations while at the same time providing practical applications to field experiments. These comparisons could be particularly useful in situations where species are vertically or horizontally partitioning resources. To illustrate this point, let us say that species A, B and C are all using similar patches, and species A is found in the middle patch. It stands to reason that species A will interact with both species B and C due to habitat overlap, while B and C will interact only with species A (Arthur 1987). Therefore, it makes sense to use an equation that can examine the effects of B and C on species A.

Using this model, multiple species competition can be introduced in beginning ecology courses. Although I applied these ideas to the LV competition model, they could just as easily be used in the LV predator/prey model. The value in studying competition is not limited to the interacting species, but to the community to which they belong as well. For example, competition models can be used by conservationists to evaluate if decreasing a resource can lead to competitive exclusion of some species by lowering the carrying capacity of the system.

Field studies of competition seldom include models in their analyses. This could be because of the dichotomy between field ecologists and biomathematicians. Ever since Gause's (1934) work with *Paramecium*, theoreticians have wanted to design the perfect model that would ignore the imperfections of the natural world, while ecologists want a

model that could explain every nuance of the system in question (Salt 1983). Neither of these goals can be realized, but integrating the two methods has led to promising results. Although the LV model cannot describe many systems, it has stimulated research in the areas of predator/prey and competitive interactions as well as describing the dynamics of simple systems (Connell 1983, Kerfoot and DeMott 1980, Roughgarden 1979, Schoener 1983). I hope that my work can stimulate further research with multiple species interactions.

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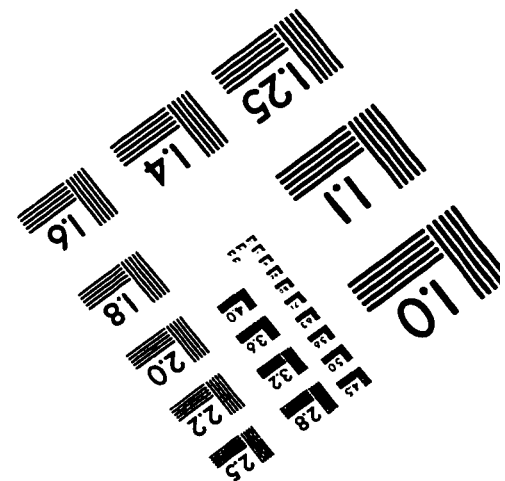
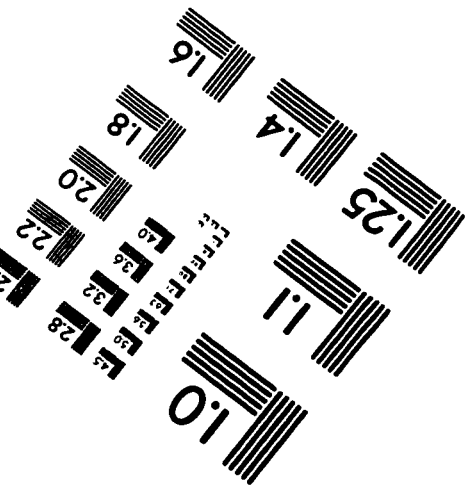
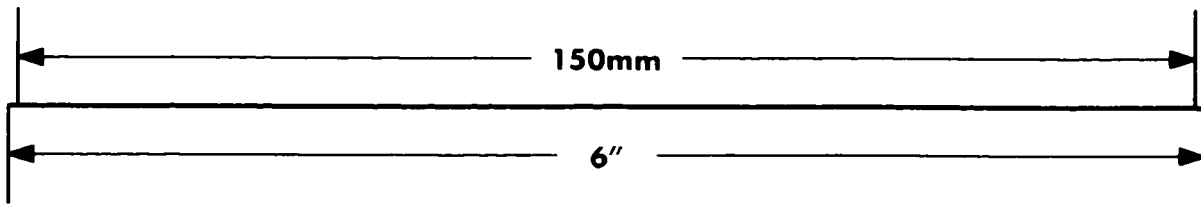
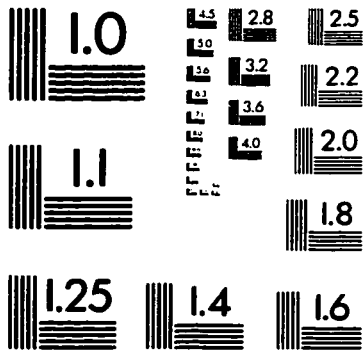
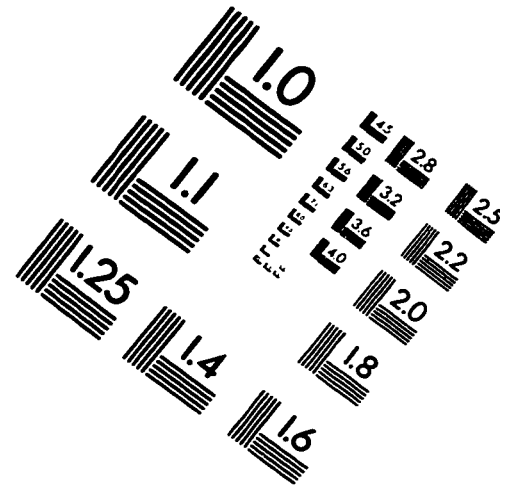
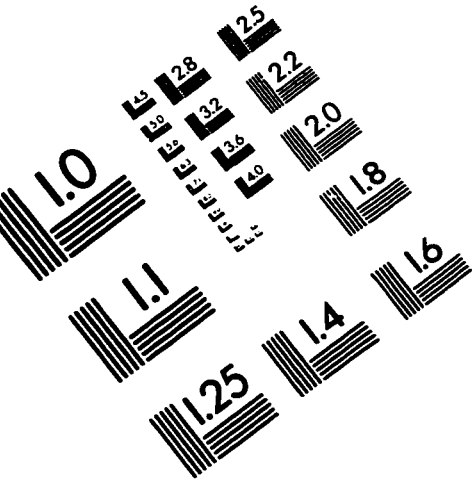
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