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SEASONAL VARIATION IN THE INTENSITY OF COMPETITION AND PREDATION AMONG DRAGONFLY LARVAE[1]

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Abstract. In nature, both similar and disparate sizes of *Libellula lydia* and *L. luctuosa* larvae frequently co-occur in time and space. To determine if these larvae interact as competitors, and/or as predators and prey, I used artificial ponds to manipulate density, species composition, and size range of co-occurring larvae. Detailed life history data were used to design separate fall and spring experiments. In both experiments, "competition treatments" contained only larvae similar in size, whereas "predation treatments" contained larvae disparate in size.

In fall competition treatments there were no density-dependent growth responses. However, in the spring experiment, larvae of both species grew significantly faster in low density than in high density treatments. This seasonal difference in competition was attributed to fluctuations in resource abundance. Competition did not directly affect survivorship.

In spring and fall predation treatments, mortality was significantly higher than it was in competition treatments. Inter-odonate predation accounted for 25–45% of total larval mortality in fall, but only 10–15% in spring. In the absence of inter-odonate predation, total mortality was lower for larger larvae than smaller larvae, suggesting the latter are more susceptible to predation by other invertebrate predators. Thus, competition, by decreasing growth rates, should indirectly affect larval survivorship.

These data provide evidence that competition and predation will simultaneously affect coexistence between these two dragonfly species. Predation early in larval development should ameliorate the intensity of subsequent competitive interactions at a time when resources are most likely to be limiting. This type of mixed competition/predation interaction is analogous to predator-mediated coexistence, and might explain how such ecologically similar species can coexist at such high densities.

Key words: benthos; cannibalism; competition; dragonflies; field experiments; Libellula; *ponds; predation; size-structured populations.*

INTRODUCTION

Most evidence for community-level effects of population interactions (e.g., Connell 1983, Schoener 1983, Sih et al. 1985) is based on studies involving species that interact *either* as competitors *or* as predators and prey (Werner 1986). But in many invertebrates, fish, and amphibians, dramatic size increases during development are accompanied by changes in the type and intensity of population interactions (Wilbur 1980, Werner and Gilliam 1984). Individuals similar in size are potential competitors, whereas combinations of larger and smaller individuals are, respectively, potential predators and prey (e.g., Paine 1965, Wilbur 1972, Benke 1978, Werner et al. 1983, Polis and McCormick 1986). Although recent reviews suggest that mixed competition/predation interactions are probably ubiquitous in nature, the ecological consequences have been explored in only a few groups of taxa (Polis 1984, Werner 1984, 1986, Werner and Gilliam 1984, Wilbur 1984).

Dragonfly larvae are often the most abundant ($>1000/m^2$) and diverse (10–20 coexisting species) invertebrate predators in the littoral zone of lentic habitats (Benke and Benke 1975, Johnson et al. 1980, Morin 1984*a*, Wissinger 1988*b*). Two characteristics of their biology suggest that competition and predation should simultaneously affect the relative abundance of species. First, larvae grow through 8–16 stages, or instars, and increase in size by three to four orders of magnitude (Benke 1972, Wissinger 1986). Second, all instars are extremely opportunistic predators that will eat almost any type of prey they can detect and subdue (Pritchard 1964, Thompson 1978*b*, Merrill and Johnson 1984 and references therein). The first consequence of this polyphagy is that resource partitioning by prey type per se is unlikely; larvae that are similar in size at the same time and place should concentrate on the same prey (Crowley and Johnson 1982*a*). A second consequence is that large larvae will eat smaller larvae, including conspecifics (Merrill and Johnson 1984, Wissinger 1988*a*). The simultaneous potential for competition and predation makes it difficult to mea-

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sure accurately the intensity of either type of interaction because both can affect conventional response variables such as growth and survival (Benke 1978, Benke et al. 1982, Morin 1984*a*, Johnson et al. 1985). For example, reduced survivorship at increased densities or in the presence of a second species can be due to increased competition, predation, or some combination of the two (Reichert and Cady 1983).

Here I report the results of field experiments that separate the effects of competition and predation among larvae of two species of pond-dwelling dragonflies, *Libellula lydia* (Drury) and *Libellula luctuosa* Burmeister (Anisoptera: Libellulidae). These species co-occur over a broad geographic area of eastern and central North America where they are frequently microsympatric in shallow littoral habitats (Walker and Corbet 1975, Crowley and Johnson 1982*b*, Wissinger 1986). I was especially interested in quantifying their population interactions because they frequently coexist at high densities, even in the absence of fish, their major vertebrate predators, and with little evidence for resource partitioning (Wissinger 1989).

To separate the effects of competition and predation I manipulated the density, species composition, and instar structure of experimental populations. The artificial ponds (galvanized steel tanks) used for these experiments minimized the confounding effects of other predators including fish, amphibians, and other dragonflies (see also Wilbur 1984). At the same time these tanks provided natural temperatures and photoperiods—the two most important abiotic factors that regulate dragonfly growth and development (Corbet 1980). The tanks also provided seminatural conditions of habitat complexity and resource renewal, two factors known to have important effects on dragonfly population dynamics (Benke 1976, 1978, Thorp and Bergey 1981). While it is known that dragonfly larvae will prey on each other in simple laboratory habitats (Wissinger 1988*a*), it is not known whether this potential for predation is realized in the spatially complex weedbeds of littoral zones, and in the presence of natural densities of alternative prey. Because odonate population dynamics depend on high rates of resource renewal (Benke 1976), natural conditions of prey recruitment are requisite for measuring ecologically relevant (cf. Connell 1983) intensities of competition and predation.

Experimental Ponds

Field experiments were conducted in galvanized steel cattle tanks (2.7 m diameter, 0.76 m depth, 5.5 m^2 bottom area, 4500 L volume) on the Ross Biological Research Reserve of Purdue University (Tippecanoe County, Indiana). Seven tanks were sunk flush with the ground in fall 1982, and an additional five tanks in spring 1983. The tanks were situated in an open field with no obvious environmental gradients. Water temperature, dissolved oxygen, pH, and alkalinity were similar among tanks and to the pond where I was studying natural populations of these species (Wissinger 1988*b*).

I placed 5 cm of soil in the bottom of each tank before filling it with well water. In spring 1983, I "seeded" the ponds with approximately equal amounts of coarse detritus and vegetation (*Potamogeton foliosus*, *Myriophyllum spicatum*) that contained benthic invertebrates and littoral zooplankton. Most anisopteran species were near the end of larval development, and were easily removed as part of an ongoing life history study (Wissinger 1988*b*). A few newly hatched *Sympetrum vicinum* were inadvertently added to the ponds, but emerged during summer, before initiation of the experiments. To increase the number of experimental units, I partitioned the ponds into four 1.25-m^2 sections using wooden frames with fiberglass screening (0.9-mm mesh).

I quantitatively monitored emergence and recruitment of benthic fauna in the ponds. Numerous aquatic insects with a terrestrial adult stage emerged and recolonized the ponds including mayflies (*Caenis*, *Callibaetis*), a variety of tanypodinid and chironomid midges, other aquatic Diptera (*Chaoborus*, Ceratopogonidae, Tabanidae), and Zygoptera (mainly *Ischnura verticalis*, *Enallagma civile*, *E. basidens*). In addition, Hemiptera (Corixidae, Notonectidae, Geridae, Nepidae) and numerous Coleoptera (Hydrophilidae, Gyrinidae, Dytiscidae, and Pleiidae) were abundant as larvae (mainly spring) and adults (summer and fall). Cladocera were seasonally abundant in spring. The phenologies of prey life cycles were similar to those in the natural ponds I was studying. The lush growth of macrophytes and algae in the tanks provided natural conditions of habitat complexity.

The tanks were covered with wire mesh cages (3 × 3 × 1 m) to exclude adult Anisoptera. The two overlapping layers of 5-cm mesh chicken wire prevented all but a few adults of a small dragonfly species (*Sympetrum vicinum*) from ovipositing in the tanks, but were large enough to allow other taxa, including Zygoptera, access to the ponds. The entire area was surrounded by a drift fence to intercept the numerous amphibians that were attracted to the ponds.

Experimental Design

In the fall and spring experiments described below, "competition treatments" contained only larvae similar in size. To assay competition I compared growth rates of larvae among low intraspecific, high intraspecific, and high interspecific density treatments (Connell 1983; Tables 1 and 2). In contrast, "predation treatments" contained larvae that differed considerably in size, and mortality of the smaller larvae in these treatments was compared to that observed in the competition treatments (Tables 1 and 2). Predation treatments in each season contained the same initial larval densities as in the high density competition treatments.

TABLE 1. Design of the spring competition and predation experiments (November 1983–June 1984). All larvae were field collected and stocked in the experimental ponds during late November. F = final instar, F − 1 = penultimate instar, etc.

Treatment		Initial density (No./m²)	Larval instars		Replicates
A. Competition treatments					
Low *Libellula lydia*		50	F − 4, F − 3		4
High *L. lydia*		100	F − 4, F − 3		4
Mixed *L. lydia* + *L. luctuosa*		50 + 50	F − 4, F − 3		4
High *L. luctuosa*		100	F − 4, F − 3		4
Low *L. luctuosa*		50	F − 4, F − 3		4
B. Predation treatments					
Pred.	Prey		Pred.	Prey	
L. lydia	*L. luctosa*	50 + 50	F	F − 4, F − 3	4
L. luctuosa	*L. lydia*	50 + 50	F − 1	F − 4, F − 3	4
					Σ = 28

This general approach relied on the following assumptions:

1) Predation was rare between larvae that were similar in size.
2) Competition did not increase mortality due to starvation.
3) Competition affected larval growth by changing the rate of instar development, but not the number or size of larval instars.

Laboratory experiments involving the effects of prey availability on growth rates show that the duration of time spent in each instar is inversely proportional to food availability (Wissinger 1988*a*). However, the number and size of instars vary little with growth rate in these experiments; thus for these species, mean instar number can be used as an assay for growth rate (see also Benke 1970). Mortality is unaffected by food availability across a wide range of growth rates (Wissinger 1988*a*); thus, asymmetric competition between large and small larvae in the predation treatments should not confound the effects of inter-odonate predation.

I also knew from laboratory experiments that predation rates are size-specific. While larger larvae readily attack smaller larvae, similarly sized larvae rarely prey on each other (Wissinger 1988*a*). Thus, mortality in the competition treatments should be due to factors other than inter-odonate predation.

The efficacy with which this experimental design decoupled competition and predation depended on maintaining a narrow range of instars in the competition treatments. Because growth rates were likely to vary among individuals, faster growing larvae could become predators on slower growing larvae during the course of the experiments. To minimize this potential problem I conducted two experiments that corresponded to the two periods of rapid growth and high mortality observed in natural populations (Wissinger 1989). The first experiment ("Spring Experiment," November 1983 to June 1984) addressed larval interactions dur-

TABLE 2. Design of the fall competition and predation experiments (August 1984–December 1984). F − 7 and F − 6 larvae were reared from eggs in the laboratory and stocked in the experimental ponds on 25 August. Large instars were field collected and stocked during the following 2 wk.

Treatment		Initial density (No./m²)	Larval instars		Replicates
A. Competition treatments					
Low *Libellula lydia*		100	F − 7, F − 6		3
High *L. lydia*		200	F − 7, F − 6		3
Mixed *L. lydia* + *L. luctuosa*		100 + 100	F − 7, F − 6		3
High *L. luctuosa*		200	F − 7, F − 6		3
Low *L. luctuosa*		100	F − 7, F − 6		3
B. Predation treatments					
Pred.	Prey		Pred.	Prey	
L. lydia	*L. lydia*	100 + 100	F − 3	F − 7, F − 6	3
L. lydia	*L. lydia*	100 + 100	F − 1	F − 7, F − 6	3
L. lydia	*L. luctuosa*	100 + 100	F − 3	F − 7, F − 6	3
L. lydia	*L. luctuosa*	100 + 100	F − 1	F − 7, F − 6	3
L. luctuosa	*L. lydia*	100 + 100	F − 3	F − 7, F − 6	3
L. luctuosa	*L. luctuosa*	100 + 100	F − 3	F − 7, F − 6	3
C. Open control (no dragonflies)					12 (1 per tank)
					Σ = 48

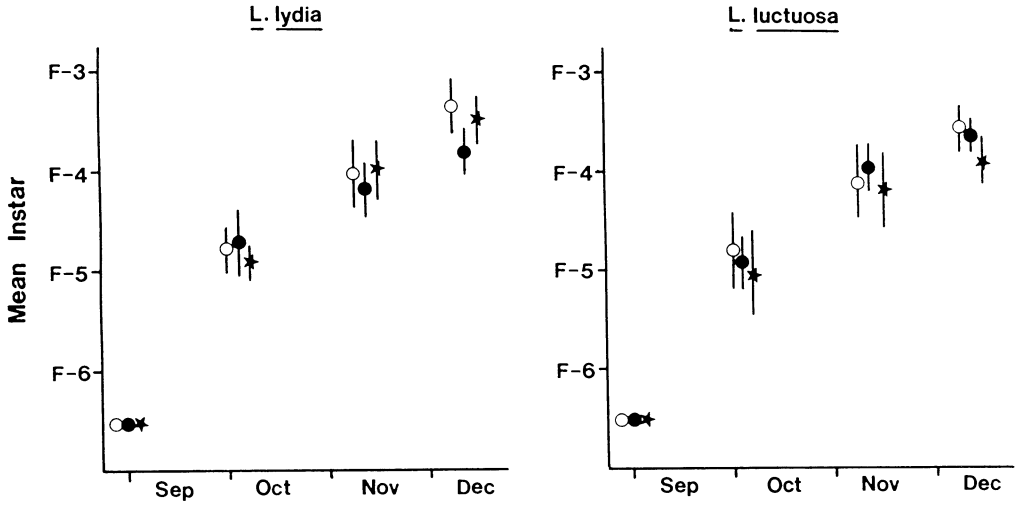


FIG. 1. Temporal paterns of growth for *Libellula lydia* and *L. luctuosa* in the fall competition treatments. ○ low intraspecific density, ● high intraspecific density, ★ interspecific treatment. Values are treatment means ± SD. December values are based on total populations at the end of the experiment.

ing winter and spring (Table 1), while the second ("Fall Experiment," August 1984 to December 1984) addressed those in late summer and fall (Table 2). Densities in both experiments bracketed those observed in natural populations (Wissinger 1989). Instars used in competition treatments were common to both populations and provided the best opportunity to observe the effects of density on development rates. Predation treatments contained the same instars as were used in competition treatments, but in combination with larger instars with which they frequently co-occur in nature (Wissinger 1989).

All larvae in the spring experiment were field collected and stocked in the tanks in late November (Table 1). In the fall experiment, larvae used as competitors and prey were reared from eggs in the laboratory and stocked in the tanks during the 3rd wk of August (Table 2). The large instars in the fall predation treatments were collected from natural populations and added during the last week of August. In total, >5000 laboratory-reared and 6000 field-caught larvae of the appropriate species and instar were used in the experiments.

The following additional treatments were added to the experimental design in fall (Table 2): (1) two different sizes of *L. lydia* predators to mimic the slight phenologic head start *L. lydia* has on *L. luctuosa* in nature (Wissinger 1989), (2) cannibalism treatments for comparison to interspecific predation treatments, and (3) an open control in each tank to determine baseline densities of prey in the absence of Anisoptera. Treatments were randomly assigned to the experimental units with the stipulation that no more than one replicate of a treatment occurred in a particular tank, thus avoiding pseudoreplication.

During the experiments I sampled larvae once a month (except during winter) using a 0.125-m^2 drop box (Wissinger 1986). Larvae were identified to species and instar before being returned to the sample site. At the end of the experiments, tanks were drained and all larvae were removed and preserved in 90% ethanol. Statistical analyses focus on population parameters at the end of the experiment. Treatment effects on mean instar number and percent survivorship were analyzed using ANOVA (SPSS, Nie et al. 1975). There were no serious deviations from normality or homoscedasticity. Tukey's hsd multiple comparison test was used to compare treatment means.

To minimize handling time of the experimental organisms, I did not estimate prey densities during monthly samples. I did estimate prey densities at the beginning and end of each experiment based on drop box samples taken from each experimental unit.

RESULTS

Fall experiment

Growth responses.—Growth was rapid in the competition treatments during September and October but slowed during November (Fig. 1). Although some larvae molted only twice during the 3 mo, most molted three or four times, and the degree of intraspecific variation in growth rates was similar for both species. Mean instar number did not differ among treatments at any of the sampling dates during the course of the experiment, nor at the end of the experiment when all larvae were removed from the tanks (*L. lydia*, $F = 3.32$, $P = .11$; *L. luctuosa*, $F = 1.97$, $P = .22$). Thus, I could find no evidence for intra- or interspecific competition

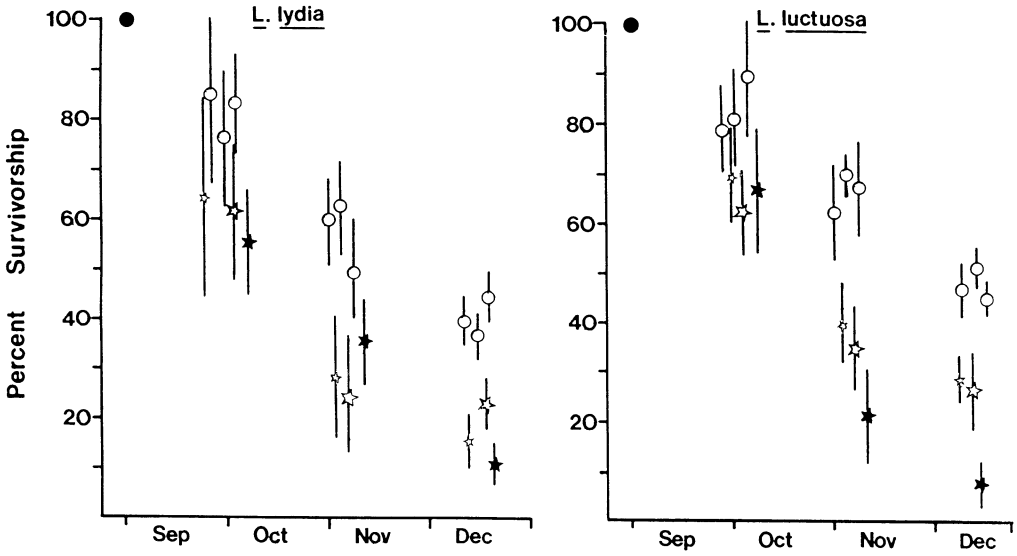


FIG. 2. Temporal patterns of survival for *Libellula lydia* and *L. luctuosa* during the fall experiment. Open circles denote survival in the three competition treatments, stars denote survival of small larvae in the predation treatments, where ☆ = F − 3 *L. lydia* predators, ★ = F − 1 *L. lydia* predators, and ☆ = F − 3 *L. luctuosa* predators. (F = final instar, F − 1 = penultimate instar, etc.) Values are percentages of the initial population ± SE.

among *L. lydia* and *L. luctuosa* larvae in the fall experiment.

Survivorship responses.—Differences in survivorship between larvae in the competition treatments and small larvae in the predation treatments became evident in early October (Fig. 2). At the end of the experiment, survivorship was significantly higher in the competition treatments than in any of the predation treatments (*L. lydia*, $F = 15.3$, $P < .001$; *L. luctuosa*, $F = 13.7$, $P = <.001$). Survivorship did not differ among competition treatments, and medium-sized *L. lydia* and *L. luctuosa* had similar effects on the survivorship of smaller larvae (Tukey's hsd >0.05). However, survivorship of both species was significantly lower in the presence of very large (F, F − 1) as compared to medium-sized (F − 2, F − 3) instars of *L. lydia* (Tukey's hsd <0.05, Fig. 2).

Spring experiments

Growth responses.—Growth was negligible during winter in all treatments (Fig. 3). Mean instar values first increased in April, after which larval growth continued through the end of the experiment. Mean instar values began to diverge among treatments in May, and at the end of the experiment I found that density significantly affected growth (*L. lydia*, $F = 45.9$, $P < .001$; *L. luctuosa*, $A = 54.0$, $P < .001$). Mean instar numbers were significantly higher in low density treatments than in both high intra- and interspecific density treatments (Tukey's hsd <0.05; Fig. 3). Mean instar numbers did not differ between the high density intra- and interspecific treatments, and the effects of increased interspecific densities were symmetrical for the two species (Tukey's hsd >0.05).

Survivorship responses.—Survivorship was high during winter with >80% of the larvae in all treatments surviving to early April (Fig. 4). Although mortality increased dramatically in spring, there were no treatment differences in April or May. However, by the end of the experiment, *L. lydia* survivorship was significantly lower in the presence of larger *L. luctuosa* than it was in any of the competition treatments ($F = 4.9$, $P = .018$). A similar but marginally significant difference was observed for the effect of *L. lydia* predation on *L. luctuosa* survivorship ($F = 3.7$, $P = .056$). As in fall, survivorship did not differ among the competition treatments.

Seasonal intensity of inter-odonate predation

To compare the intensity of predation betwen experiments, I needed to consider seasonal differences in mortality (e.g., winter mortality, non-odonate invertebrate predators) other than those related to the dragonfly manipulations. Because survivorship did not vary among competition treatments in either spring or fall, I used the average values in these treatments to estimate the baseline level of mortality in the absence of inter-odonate predation. By assuming similar baseline levels of mortality in predation and competition treatments, I estimated that inter-odonate predation accounted for 25–45% of the total mortality in fall as compared to 11–15% in spring predation treatments (Table 3).

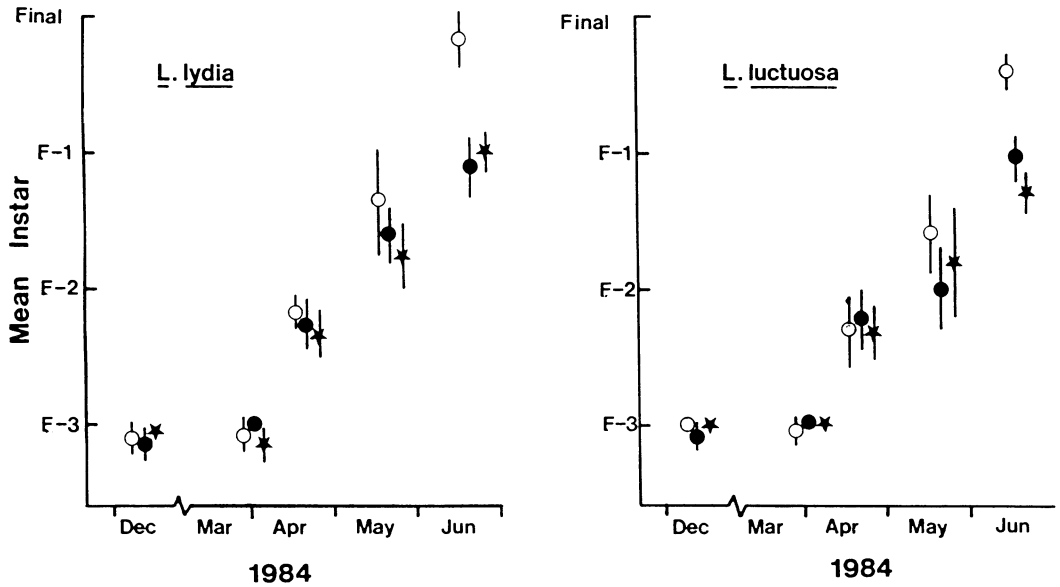


FIG. 3. Temporal patterns of growth for *Libellula lydia* and *L. luctuosa* in the spring competition treatments. ○ low intraspecific density, ● high intraspecific density, and ★ interspecific treatments. Values are treatment means ± SE. June data are based on total populations at the end of the experiment.

Non-odonate sources of mortality

There was little opportunity for inter-odonate predation among larvae in the competition treatments or among the large larvae used in the predation treatments. On average, ≈80% of the latter survived to the end of the two experiments. This was about twice the survivorship observed for the smaller larvae in the competition treatments (Figs. 2 and 4). This result suggests that predation by other invertebrate predators is more intense on small larvae. Potential predators in the fall included tanypodinid midges, tabanid fly larvae, adult Hemiptera (Nepidae, Notonectidae), and Zygoptera larvae. In spring, the most abundant predators were Zygoptera and a variety of Coleoptera larvae (Hydrophilidae, Gyrinidae, Dytiscidae).

Seasonal abundance of prey

During the fall experiment, total prey density increased from about 7000 individuals/m^2 to more than 10 000 individuals/m^2 (Fig. 5). Observations from emergence traps and from benthos samples indicated that this was a period of intense prey recruitment marked by the appearance of new cohorts and taxa. In contrast, prey decreased during winter and spring to only 4000 individuals/m^2 by the end of the spring experiment in May (Fig. 5). Although some prey taxa (e.g., chironomids, *Caenis* mayflies) emerged near the end of the spring experiment, recruitment of new generations was not observed until later in spring, after the experiment was terminated.

DISCUSSION

Experimental manipulation of the density and size structure of *L. lydia* and *L. luctuosa* populations affected both growth rate and survivorship. In treatments containing larvae similar in size, growth rate was density-dependent in spring, but not in fall. Mortality was unaffected by density in all of these treatments. However, mortality was sigificantly higher in treatments with disparate sizes of larvae than it was when all larvae were similar in size. Together these results provide evidence that both competition and predation can occur simultaneously between two species depending on the relative sizes of individuals that encounter each other.

Below, I first discuss these results in light of previous field and laboratory experiments involving dragonfly larvae. I then consider why the relative intensities of competition and predation varied seasonally between experiments, and suggest that similar seasonal fluctuations are expected in nature. Finally, I argue that the type of interplay between competition and predation in natural populations will depend on when during ontogeny each interaction is most intense.

Effects of competition on growth and survivorship

In the spring competition experiment, increasing inter- and intraspecific densities resulted in the same negative growth response for both species. The symmetrical competitive interactions that I observe may not be surprising given the morphological and behav-

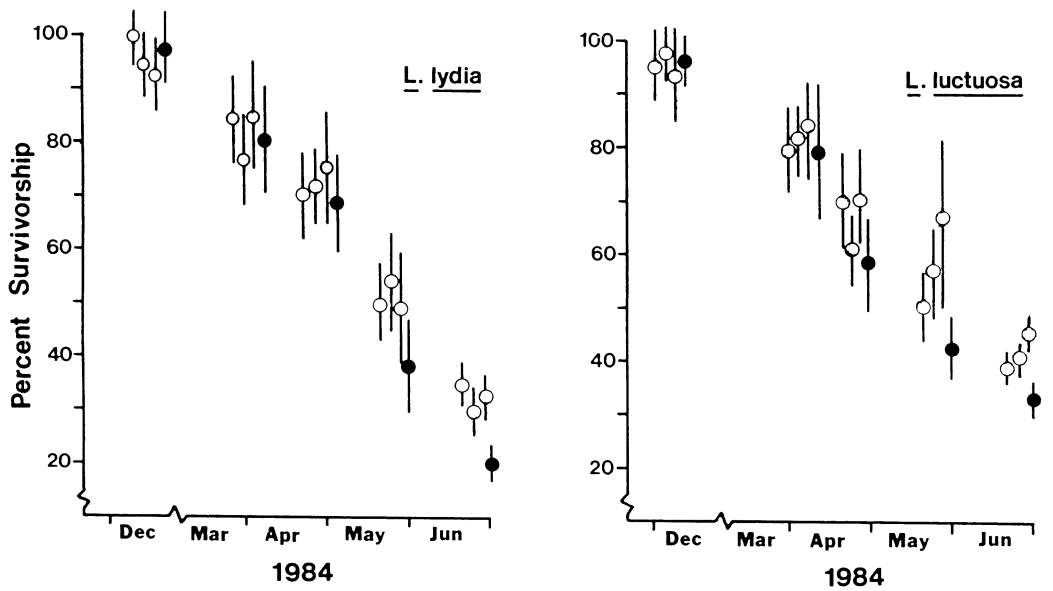


FIG. 4. Temporal patterns of survival for *Libellula lydia* and *L. luctuosa* in the spring experiment. ○ competition treatments, ● predation treatments. Values are percent of the initial population ± SE. June data are based on the final population census.

ioral similarities between *L. lydia* and *L. luctuosa*, and the extremely generalized predatory habits of dragonfly larvae (see reviews by Pritchard 1964, Merrill and Johnson 1984). At a given instar, these two species probably converge on the same abundant prey.

In this study, I could not detect any density-dependent growth response until after 3 mo of experimentation in spring. The absence of evidence for competition in a previous study conducted in spring might be due to the 1-mo duration of that experiment (Johnson et al. 1985). Furthermore, in Johnson et al. and in other experimental studies, instar structure is not controlled (Benke 1978, Benke et al. 1982). Inter-odonate predation in these experiments could reduce densities so that competitive effects are difficult to detect. This confounding effect would be exaggerated if alternative prey are depleted (Benke et al. 1982, Crowley et al. 1983).

Laboratory data suggest that competition should have little direct effect on dragonfly survivorship (Lawton et al. 1980). In the laboratory, survivorship does not vary across a wide range of food availabilities, even when growth is severely retarded (Hassan 1976, Lawton et al. 1980, Wissinger 1988*a*). In this study, survivorship in the competition treatments was not density dependent even when growth was. This result is consistent with the prediction that the low feeding regimes required to starve odonate larvae are unlikely to occur in nature (Benke 1978, Lawton et al. 1980). These data also show that the low predation rates expected between larvae similar in size (Wissinger 1988*a*) do not increase with density (as in Fischer 1961, Duelli 1981, Van Buskirk 1987), even though growth rates are reduced, and hunger levels are presumably higher. Unlike a number of studies involving zygopteran dragonflies (e.g., Baker and Dixon 1986, McPeek and

TABLE 3. Proportion of prey mortality due to inter-odonate predation.

Predator treatment		
Prey	Predator	% inter-odonate mortality*
A. Fall		
Libellula lydia	F − 3 *L. lydia*, cannibalism	25
	F − 3 *L. luctuosa*, predation	34
	F − 1 *L. lydia*, cannibalism	35
Libellula luctuosa	F − 3 *L. lydia*, predation	32
	F − 3 *L. luctuosa*, cannibalism	33
	F − 1 *L. luctuosa*, predation	45
B. Spring		
Libellula lydia	F − 1 *L. luctuosa*	15
Libellula luctuosa	F *L. lydia*	11

* % mortality that was due to inter-odonate predation = 100 × [1 − (mean mortality in competition treatment) ÷ (total mortality in predation treatment)].

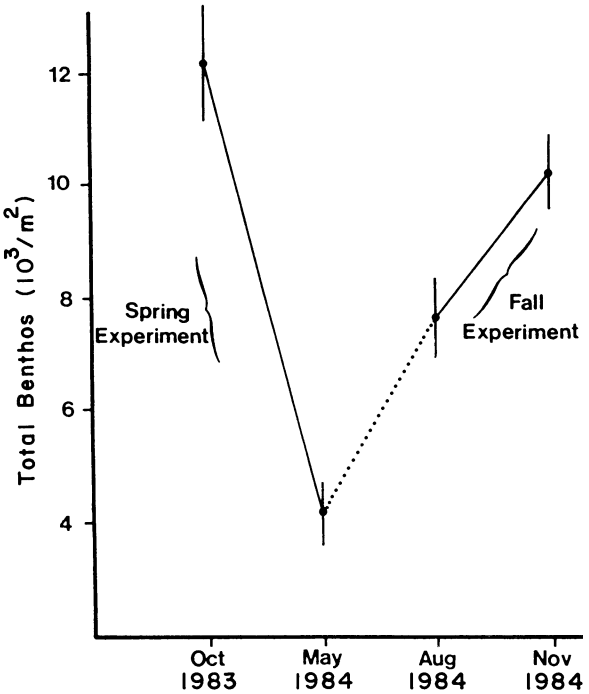


FIG. 5. Seasonal patterns of resource abundance in the experimental ponds. Values are densities for all macrobenthos combined ± SE. August and November data are based on a random sample from one experimental unit in each artificial pond, whereas October and May data are based on samples taken in each of the experimental units (N = 28 and 48, respectively).

Crowley 1987), I could find no evidence of appendage loss or other physical damage that might indicate increased interference competition at higher densities. While it is likely that large larvae act as interference competitors with smaller larvae by suppressing foraging activity (as in Crowley et al. 1987), my results (see also Wissinger 1988*a*) do not suggest that aggressive interference between similarly sized anisopterans is as important as it is between zygopterans (Baker 1981, Baker and Dixon 1986). In summary, the combined results of laboratory and field experiments with these species imply that competition is the main biotic interaction between larvae similar in size, and that the only direct effect of this competition is to reduce larval growth rates.

Temporal constancy of competition

Although competition is documented between many kinds of organisms in a broad array of communities, few studies assess temporal variation in its intensity (see reviews by Wiens 1977, Connell 1983, Schoener 1983). In Schoener's and Connell's reviews, such studies document how temporal variability in the intensity of competition can depend on year-to-year fluctuations in resource abundance (e.g., Dunham 1980, Smith 1981). More recently, a few studies demonstrate seasonal variation in competitive intensities (Spiller 1984, Schmitt and Holbrook 1986; see also Lynch 1978).

The results of this study suggest competition within and between *L. lydia* and *L. luctuosa* populations will be more intense in spring than in fall. I attribute this result to seasonal differences in the degree to which resources are limiting, rather than to changes in competitive ability (Chesson and Warner 1981, Spiller 1984) or to seasonal differences in resource partitioning (Rice and Menke 1985, Schmitt and Holbrook 1986) because:

1) If the absence of competitive effects in fall was only due to interspecific resource partitioning, I would expect to find decreased growth rates in high density intraspecific treatments. Instead, density did not affect growth in either intra- or interspecific treatments in fall, but affected both in spring.

2) Odonate larvae are polyphagous predators that choose prey based mainly on size (see reviews by Pritchard 1964, Thompson 1978*a*, *b*, Merrill and Johnson 1984). Analysis of *L. lydia* and *L. luctuosa* fecal pellets suggest that same-sized larvae of the two species converge on, rather than partition, prey (S. A. Wissinger, *personal observation*).

3) Prey abundance at the end of the fall experiment, when competition was not detected, was about three times higher than at the end of the spring experiment, when competition was detected (Fig. 5).

The seasonal fluctuations in prey abundance observed in the experimental ponds are similar to those in the littoral zone of natural ponds (Benke 1972, Hubert and Krull 1973, Thorp and Bergey 1981, Gilinsky 1984). Summer and fall are periods of rapid prey renewal in ponds, and resources may be rarely limiting for dragonflies during these seasons (see also Benke 1976, 1978). However, in winter and early spring, prey mortality is unaccompanied by recruitment, and dragonfly larvae probably experience a seasonal resource crunch (sensu Wiens 1977) before new cohorts of prey hatch in late spring.

Predation among L. lydia *and* L. luctuosa *larvae*

Larvae of *L. lydia* and *L. luctuosa* interact not only as competitors, but also as predators and prey. Survivorship of small instars in both spring and fall was significantly lower in the presence of large odonates than it was in the competition experiments. Inter-odonate predation accounted for a larger proportion of the total mortality in fall (25–45%) than in spring (11–15%).

Inter-odonate predation in nature should also be most intense in late summer and fall when intra- and interspecific size differences are greatest (Wissinger 1988*b*, 1989). Because the opportunity for cannibalism is greatest early in larval development, it should play an important role in population regulation (Fox 1975, Polis 1981). In these and many other species of North American Anisoptera, size differences decrease in spring, as

do the opportunities for inter-odonate predation (Benke and Benke 1975, Wissinger 1988*b*). Species with different life histories will exhibit different seasonal changes in the intensity of inter-odonate predation (e.g., Merrill and Johnson 1984, Crowley et al. 1987).

Interplays between competition and predation

A characteristic feature of larval dragonfly assemblages is the extraordinary size range of larvae present at any time (Benke and Benke 1975, Johnson and Crowley 1980, Wissinger 1988*b*). The results of this study suggest that coexistence in these highly size-structured assemblages will depend on one or a number of different types of complex interplays between competition and predation. Competition could affect the intensity of predation and/or the converse depending on when the two interactions are most intense during ontogeny. For example, in larval amphibian assemblages, competition, by slowing growth rates, increases the time that individuals are vulnerable to predation by larger individuals of the competing species (Wilbur 1972, Morin 1983*a*, *b*, Morin et al. 1983, Wilbur et al. 1983). This type of interplay should be most important when competition is intense early in ontogeny, as is the case in those freshwater fishes (Centrarchidae, Percidae, Esocidae) in which competition among juvenile age classes is known to affect vulnerability to predation by larger age classes (reviewed by Werner and Gilliam 1984, Werner 1986).

The above interplay between competition and predation should be of only minor importance within generations of *L. lydia* and *L. luctuosa* because competition appears to be more intense near the end, rather than at the beginning, of larval development. However, an analogous interaction could operate between generations because competition at any time during development should result in later emergence and breeding. Offspring of later breeding individuals will be at a size disadvantage in the subsequent generation both as competitors and as inter-odonate prey (Benke 1978, Benke et al. 1982, Morin 1984*a*, *b*, Johnson et al. 1985). The size-specific increases in mortality observed among predator treatments in the fall experiment (Fig. 2) emphasize that the importance of this disadvantage will depend on the degree to which phenologies differ.

The within-generation interplay between dragonfly competition and predation might be opposite to that described above for fish and amphibians. Mortality in most odonate species is highest in summer and fall, when the most disparate size combinations of larvae co-occur (Wissinger 1988*c*). This study provides direct evidence that a significant proportion of this mortality is attributable to inter-odonate predation. Predation early in larval development will ameliorate the intensity of competition among older larvae. Wilbur (1984) describes how individual tadpoles that escape predation early in life benefit from this type of interaction because they have little competition later in development (see also Morin 1983*b*, Wilbur et al. 1983, Wilbur and Alford 1985). In summary, the potential for different types of complex interplays between competition and predation emphasizes the need for identifying when during ontogeny each interaction is most intense.

I have suggested that mixed competition–predation effects between *L. lydia* and *L. luctuosa* will depend on the seasonal intensities of these interactions. Competition at any time during larval development will also affect the vulnerability of these species to other size-limited predators (e.g., small fish, salamander larvae, other invertebrates including larger dragonfly species [Lawton et al. 1980, Travis and Trexler 1986]). Predation by size-limited invertebrate predators would explain why large larvae in predation treatments survived better than smaller conspecifics in competition treatments. The largest instars of *L. lydia* and *L. luctuosa* should have a size refuge (sensu Paine 1965) from almost all other invertebrate predators. Detecting this type of size-specific mortality in natural populations would be difficult because changes in instar distributions reflect both mortality and molting.

Complex population interactions and coexistence

The presence of mixed competition/predation interactions could explain why these morphologically and ecologically similar odonate species can coexist at high densities without partitioning resources, and without the mediating effects of other predators such as fish (Wissinger 1989). Resources may rarely be limiting for odonate larvae in summer and fall because of high rates of prey recruitment (see also Benke 1978). Although rates of resource renewal are lower in spring, competition may be of only moderate intensity in spring (as in this study) because of the dramatic reduction in dragonfly densities, due in part to intense inter-odonate predation earlier in larval development.

This type of interplay between predation and competition could result in conditions of coexistence that differ from those expected when only competition is occurring, much in the same way that predators can influence the outcome of competition at lower trophic levels (cf. Paine 1966). Whether predators enhance or destabilize coexistence at lower trophic levels depends on whether superior or inferior competitors are preyed on more heavily (Sih et al. 1986). Similarly, coexistence of species with mixed competition–predation interactions should depend on whether the species with a predatory advantage is the superior or inferior competitor. The results of this and previous studies (reviewed by Wilbur 1984, Werner 1986) suggest that the temporal sequence of these interactions will be an important variable to incorporate into theoretical models that predict the conditions for coexistence between competitors that also interact as predators and prey.

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