

Comparative population ecology of the dragonflies *Libellula lydia* and *Libellula luctuosa* (Odonata: Libellulidae)

SCOTT A. WISSINGER¹

Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, U.S.A.

Received May 10, 1988

WISSINGER, S. A. 1989. Comparative population ecology of the dragonflies *Libellula lydia* and *Libellula luctuosa* (Odonata: Libellulidae). *Can. J. Zool.* **67**: 931–936.

Temporal and spatial patterns of habitat use, population size structure, and survivorship were compared over three generations of *Libellula lydia* and *Libellula luctuosa* in a small pond in Indiana. The two species were univoltine, had similar phenologies, and converged on the same within-pond habitats. There was little evidence for any spatial and (or) temporal habitat partitioning that might be expected between such morphologically and ecologically similar species. Larval populations of each species were highly size structured because oviposition and hatching were extended over 3 months in summer. Intraspecific size differences were greater than those frequently reported to accommodate interspecific coexistence. Thus, intraspecific resource partitioning and cannibalism should have an important effect on population dynamics. Both similar and disparate interspecific size combinations frequently co-occurred in time and space so that competition and predation should simultaneously affect coexistence. Larval mortality was high in late summer and fall, negligible in winter, and high again in spring. Fewer than 10% of either species survived to emerge from the pond. Interodonate predation is a likely source of much of this larval mortality, given that other odonates are among the most abundant large predators in fishless ponds.

WISSINGER, S. A. 1989. Comparative population ecology of the dragonflies *Libellula lydia* and *Libellula luctuosa* (Odonata: Libellulidae). *Can. J. Zool.* **67**: 931–936.

Les aspects temporel et spatial de l'utilisation de l'habitat, de la structure de la population quant à la taille des individus et de la survie ont été comparés durant trois générations chez *Libellula lydia* et *Libellula luctuosa* dans un petit étang d'Indiana. Les deux espèces sont univoltines, ont des phénologies semblables et utilisent les mêmes habitats dans l'étang. Il ne semble pas y avoir de partitionnement spatial ou temporel de l'habitat comme on aurait pu le croire chez des espèces aussi semblables morphologiquement et écologiquement. Les populations larvaires des deux espèces sont très structurées du point de vue de la taille, car la ponte et l'éclosion s'étalent sur 3 mois au cours de l'été. Les variations de taille intraspécifiques sont plus importantes que celles qui ont été observées souvent dans les cas de coexistence interspécifique. Le partitionnement des ressources entre individus de la même espèce et le cannibalisme devraient donc avoir un effet important sur la dynamique des populations. Deux types de combinaisons interspécifiques de tailles, tailles semblables et tailles disparates, prévalent souvent ensemble, en même temps et au même endroit; la compétition et la prédation devraient donc affecter simultanément la coexistence. La mortalité larvaire est élevée à la fin de l'été et à l'automne, négligeable en hiver et élevée de nouveau au printemps. Moins de 10% des individus survivent jusqu'à l'émergence chez les deux espèces. La prédation inter-odonates est probablement responsable d'une grande partie de cette mortalité, étant donné que les autres odonates représentent la majorité des gros prédateurs dans les étangs sans poissons.

[Traduit par la revue]

Introduction

Libellula lydia (Drury) and *Libellula luctuosa* Burmeister (Anisoptera: Libellulidae) are closely related dragonflies that co-occur across a broad area of central and eastern North America (Walker and Corbet 1975; Crowley and Johnson 1982). They are ubiquitous within this range and frequently co-occur in small ponds. In this paper I compare their temporal and spatial patterns of habitat use, population size structure, and patterns of mortality in a small pond in Indiana where they were among the numerical dominants of an 18-species odonate assemblage (Wissinger 1988b). The results provide the base-line information used to design ecologically relevant (Connell 1983) field experiments to quantify population interactions between these species (Wissinger 1989).

Libellula lydia and *L. luctuosa* spend most of their life cycles as aquatic larvae that molt through 13 instars and increase in size by four orders of magnitude (Wissinger 1986). Larvae will eat almost any prey (including other dragonflies) of a size that can be detected and subdued (reviews by Pritchard 1964; Thompson 1978a; Merrill and Johnson 1984). Thus, depending on the size combinations that overlap in time

and space, competition and (or) predation are possible inter-specific interactions (Benke 1978; Merrill and Johnson 1984).

Because *L. lydia* and *L. luctuosa* are similar in size at a given instar, the size combinations of larvae that co-occur most frequently will depend mainly on voltinism, phenology, and synchrony (Butler 1984; Wissinger 1988b). Here I provide data on (i) duration and phenology of emergence, oviposition, and hatching, (ii) timing and rate of larval development, and (iii) seasonal and spatial trends in larval abundance. These data suggest convergence, rather than segregation, in life history and habitat use, and imply the potential for mixed competition–predation interactions (cf. Werner and Gilliam 1984).

Study site

Data were collected in a small (0.12 ha) pond located on the Horticulture Research Farm of Purdue University in Indiana. The results reported for this site were representative of those observed in other ponds at a similar latitude (all about 40°N) in Indiana, Ohio, and Pennsylvania (unpublished data).

The pond was shallow (maximum depth 2 m, average depth 1 m), moderately vegetated (mainly *Potamogeton crispus* and *Chara* sp.), and without fish. Emergent vegetation (mainly *Scirpus atrovirens* and *Scirpus cyperinus*) covered less than 10% of the pond. The remainder of the pond perimeter was bordered by sedges (*Carex hystricinus* and *Juncus tenuis*) and a few willows (*Salix* sp.). The clay substrate

¹Present address: Departments of Biology and Environmental Science, Allegheny College, Meadville, PA 16335, U.S.A.

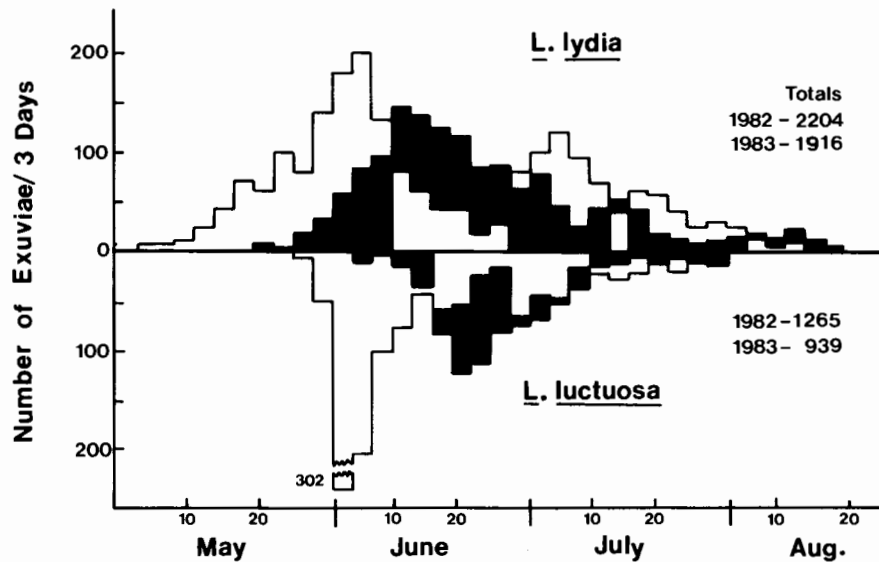


FIG. 1. Emergence phenology for *L. lydia* and *L. luctuosa*. Histograms for 1982 (open) are 3-day totals of daily collections of exuviae, whereas 1983 (solid) data are from exuviae collected every 3rd day.

was covered by approximately 4–8 cm of plant debris and other organic detritus.

Libellula lydia and *L. luctuosa* were among the most abundant of the 18 species of Anisoptera (mainly Libellulidae) that completed their life cycles in the pond (Wissinger 1988b). Other abundant benthic taxa included 12 species of zygopteran odonates (mainly Coenagrionidae), numerous herbivorous and predatory chironomids, Ephemeroptera (*Caenis* sp. and *Callibaetis* sp.), and a variety of Hemiptera and Coleoptera. The density and diversity of macroinvertebrates decreased with depth. Diptera (Ceratopogonidae, Chaoboridae, and Chironomidae) dominated the sparser fauna at depths > 1 m.

Methods

To assess the spatial distribution of larvae, the pond was divided into the following habitat categories based on depth and incline: shallow nearshore shelf (<0.5 m depth), steep slope (0.5–1.0 m depth), central basin (1.0–1.5 m depth), and deep trough (>1.5 m depth). Larval densities on the shallow nearshore shelf were sampled at least monthly from September 1981 to September 1984. Six replicate samples were taken at each date using a 0.25-m² drop box (after Benke 1969). Larvae were removed from the box using a 1-mm mesh D-shaped net. From May 1982 to August 1983, I also sampled each of the three deeper habitat categories using a 0.125-m² Ekman grab lowered from a small boat. Ice cover prevented the collection of winter samples (December to February) in 1981–1982 and 1983–1984. An unusually mild winter in 1982–1983 allowed year-round sampling.

Samples were passed through a 1-mm mesh net and repeatedly rinsed until most of the sediment was removed. Larvae were sorted live in the field. In 1981 and 1982 I retained and preserved all larvae in 90% EtOH to establish instar categories based on head width (after Benke 1970). Later, to reduce sampling effects, I returned most larvae to the sample site after identifying them to species and instar. Small instars were always retained for more detailed study. I reared both species from eggs to confirm the instar categories inferred from field data. Nomenclature follows Walker and Corbet (1975).

Field densities of the first five instars (including the prolarva) were probably underestimated because many probably passed through the 1-mm mesh of the collecting net. To better estimate the timing of hatching and larval recruitment, I sampled qualitatively with a finer meshed (0.5 mm) net from May to September. The additional size classes retained in these samples were not included in mean instar

values, but were used to calculate ratios of the largest to smallest instar present at any time.

Emergence was monitored from April to October by collecting exuviae daily (1982) or every 3rd day (1983) from the entire pond perimeter. A 2-week comparative study suggested that the 3-day sampling scheme underestimated emergence by 15%. The 1983 data were adjusted accordingly. The abundance and breeding activity of adults was visually censused at least once a week from April to October.

The effects of date and depth on larval density were analyzed with ANOVA. There were no serious deviations from normality, and variances were homoscedastic. Covariance between *L. luctuosa* and *L. lydia* density was analyzed with partial correlation analysis. Statistics were computed using SPSS (Nie *et al.* 1975).

Survivorship was based on temporal changes in total population size, calculated by summing the product of density and area for all habitats on a given date. I used population sizes, rather than densities, because (i) larvae were distributed across habitats that differed in area and thus densities represented different total number of individuals, depending on the habitat, and (ii) larvae migrated between spatial habitats (see Results), so that temporal changes in density in a particular habitat could have been due to interhabitat movement and (or) mortality.

Results

Developmental phenologies

Emergence of *L. lydia* and *L. luctuosa* was protracted over much of the summer in 1982 and 1983 (Fig. 1). Although the onset of emergence varied between years, relative phenology and duration of emergence remained similar across years. In both years, *L. lydia* emerged about 3 weeks earlier and continued to emerge about 2 weeks longer than *L. luctuosa*. Peak emergence for the two species occurred at the same time in 1982 (June 1), but in 1983, the mode in *L. lydia* emergence occurred about 10 days before that of *L. luctuosa* (Fig. 1). Adult males first returned to the pond about 2 weeks after the first individuals emerged. Males were present from May to September, but most matings occurred from mid-June to mid-August. Mating and (or) ovipositing females were seen almost daily during this 3-month period (Fig. 2).

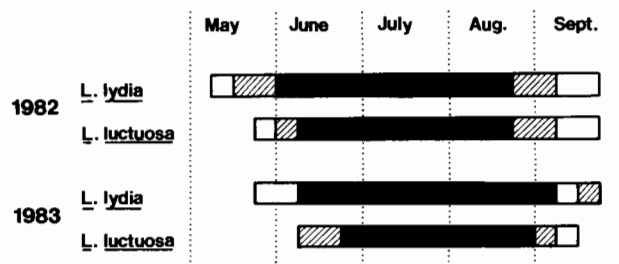


FIG. 2. Adult activity and breeding of *L. lydia* and *L. luctuosa* in 1982 and 1983. Open bars, presence of mature adults; hatched bars, 1–3 matings and (or) ovipositing females per week; solid bars, >3 matings and (or) ovipositing females per week.

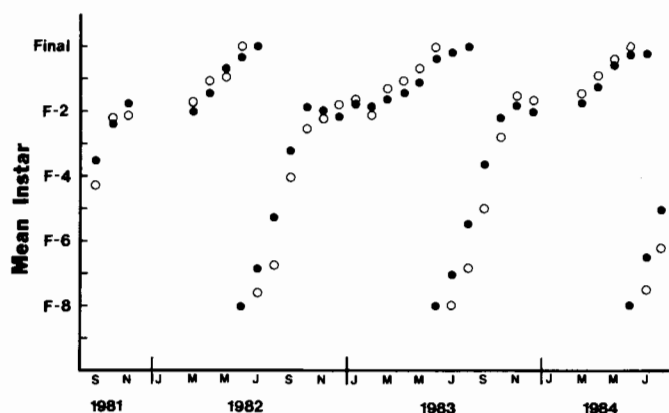


FIG. 3. Mean instar number versus time for *L. lydia* (solid circles) and *L. luctuosa* (open circles). Values for the 1982–1983 generation are based on data from all spatial habitat categories. All other values are from the nearshore habitat.

The phenology of larval development was also similar among years (Fig. 3). Early instars of *L. lydia* and *L. luctuosa* first appeared in mid-June and early July, respectively, and eggs continued to hatch through early September. Larval development was rapid during late summer and early fall but was negligible in winter. Growth resumed again in spring when many individuals completed development. Initially, mean instar values of *L. lydia* were slightly larger than those of *L. luctuosa* because of the head start in hatching (Fig. 3). However, the mean instar values of the two populations converged by October and remained similar through emergence. Although both species were univoltine, larvae from different year classes overlapped in June and July (Fig. 3).

Asynchrony in larval development

There was considerable intraspecific variability in the phenology of larval development. As a result, mean instar plots do not accurately describe the seasonal pattern of development for many individuals (see Benke and Benke 1975). For example, early hatching *L. lydia* larvae completed development during summer and fall, overwintered as final instars, and presumably emerged the following May (Fig. 4). In contrast, later hatching *L. lydia* overwintered in a variety of smaller instars (F-1 to F-6), completed much of instar development in spring, and emerged later the following summer.

This intraspecific asynchrony meant that at any time both populations included a broad size range of instars (Table 1).

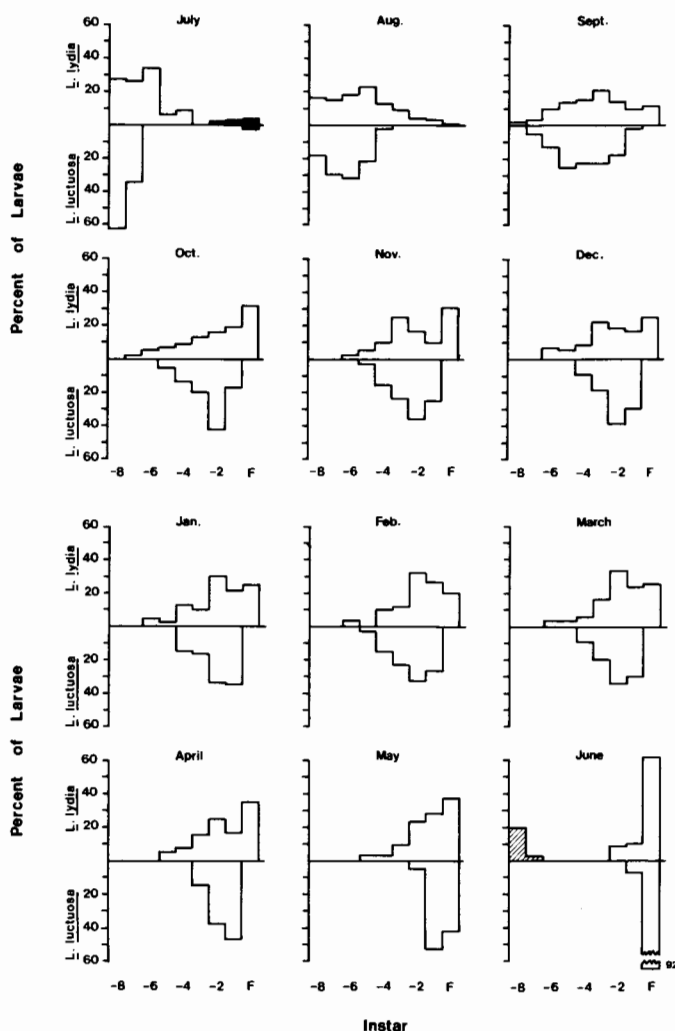


FIG. 4. Instar histograms for the 1982–1983 generation of *L. lydia* and *L. luctuosa*. Values are percentages of all larvae collected on a given date in each instar. Solid bars, larvae from the previous (1981–1982) generation; hatched bars, newly hatched larvae of the subsequent (1983–1984) generation.

The largest within-generation size differences were observed in late summer and early fall when large instars were 7–10 times as large as smaller larvae. Although the range in larval sizes decreased during spring, many individuals were still 2 to 3 times larger than other conspecific and interspecific larvae. Average intraspecific size differences were 1.5 times greater among *L. lydia* than *L. luctuosa*. Average interspecific size differences were slightly asymmetric, favoring *L. lydia* (Table 1).

During larval development, the range of instars of *L. luctuosa* decreased more rapidly than for *L. lydia*. This decrease was due, in part, to the arrested development of F-1 (and probably F-2) instars in fall. Although F-1 instars of *L. luctuosa* first appeared in early September, they never molted to the final instar before April of the following year. In contrast, *L. lydia* continued to molt in fall without an accumulation of larvae in the F-1 and F-2 stages (Fig. 4). The size range of *L. luctuosa* larvae also decreased rapidly in spring because smaller instars (F-3 and F-4) resumed development earlier than larger conspecifics (F-2 and F-1).

TABLE 1. Size ratios of co-occurring (largest/smallest) *L. lydia* (LLY) and *L. luctuosa* (LLU) larvae (1982–1983)

	Size ratios of maximum labial width (largest/smallest larva)			
	Intraspecific		Interspecific	
	LLY/LLY	LLU/LLU	LLY/LLU	LLU/LLY
July	4.5 (10.4)	3.2 (11.2)	3.0 (4.9)	1.9 (12.9)
Aug.	8.2	5.8	10.0	5.4
Sept.	11.8	6.9	9.9	8.6
Oct.	6.7	5.1	4.6	5.2
Nov.	5.6	3.1	3.2	3.5
Dec.	5.6	2.0	2.2	3.5
Jan.	3.8	2.0	2.2	2.8
Feb.	3.8	2.0	2.2	2.8
March	3.8	2.0	2.2	2.8
April	3.8	2.0	1.7	2.8
May	3.0	1.6	1.4	3.6
June	2.3 (10.4)	1.6	1.4	2.0 (12.9)
Mean	4.9	3.1	3.8	3.7

NOTE: Values in parentheses include larvae from different year classes. Means do not include between year class data.

Spatiotemporal abundance of larvae

The density of larvae varied significantly with date and depth (Table 2). On any given date, densities were highest in the nearshore shelf habitat. Across all habitats, densities decreased rapidly during fall, changed little in winter, and decreased again in spring. The date \times depth interaction was due to the proportional increase in abundance in deeper habitats in late fall and winter compared with spring and summer.

Libellula lydia and *L. luctuosa* densities were highly correlated across all samples ($r = 0.95$, $p = 0.001$). First-order partials indicate that the two species were similarly distributed in time (controlling for depth, $r = 0.93$, $p = 0.001$) and in space (controlling for date, $r = 0.94$, $p = 0.001$). The second-order partial (controlling for date and depth, $r = 0.93$, $p = 0.001$) revealed that the densities of the two species were also positively associated among samples within date and depth categories. This result is consistent with my qualitative impression that the two species were frequently most abundant at the same sampling locations around the pond.

Larval survivorship

Because hatching and early larval mortality occurred simultaneously during July and August initial population size and early larval survivorship could not be estimated. Peak abundance in late summer was followed by high mortality in late summer and fall (September to November > 70%). There was little mortality in winter (December to March, < 15%), but mortality was high again in spring (March to emergence, > 50%) (Fig. 5).

Fewer than 5% of the larvae survived from peak abundance to the teneral adult stage. By assuming negligible mortality in May for the final two instars of *L. luctuosa*, I estimated that at least 92% of all individuals died during larval development. This value is undoubtedly an underestimate because it does not include early instar mortality. Total larval mortality for *L. lydia* was difficult to estimate because late instar development was so asynchronous.

TABLE 2. Mean density (larvae/m²) of *L. lydia* and *L. luctuosa* larvae in the 36 (4 depths and 9 dates) spatiotemporal habitat categories

	Depth category (m)			
	<0.5	0.5–1.0	1.0–1.5	>1.5
July	289	17	0	0
Aug.	389	47	0	0
Sept.	157	20	0	0
Oct.	85	27	0	0
Nov.	82	20	10	0
March	64	17	7	0
April	77	10	3	0
May	51	3	0	0
June	22	0	0	0

ANOVA				
Source of variation	df	Mean square	F	P
Main effects	10	85 691	120	0.001
Date	8	35 716	50	0.001
Depth	2	285 591	403	0.001
Date \times depth interaction	16	28 631	40	0.001
Explained	26	50 577	71	0.001
Residual	135	709		
Total	161	8 762		

(b) *Libellula luctuosa* densities (1982–1983)

	Depth category (m)			
	<0.5	0.5–1.0	1.0–1.5	>1.5
July	134	7	0	0
Aug.	218	27	0	0
Sept.	83	10	0	0
Oct.	42	17	0	0
Nov.	40	17	0	0
March	32	23	0	0
April	47	20	0	0
May	51	3	0	0
June	33	0	0	0

ANOVA				
Source of variation	df	Mean square	F	P
Main effects	9	23 002	61	0.001
Date	8	14 756	39	0.001
Depth	1	88 981	236	0.001
Date \times depth interaction	8	11 618	31	0.001
Explained	17	17 645	47	0.001
Residual	90	376		
Total	107	3 120		

NOTE: ANOVA results include only those depth categories used at least once during the year.

Discussion

Comparative life histories

Both *L. lydia* and *L. luctuosa* are univoltine and exhibit

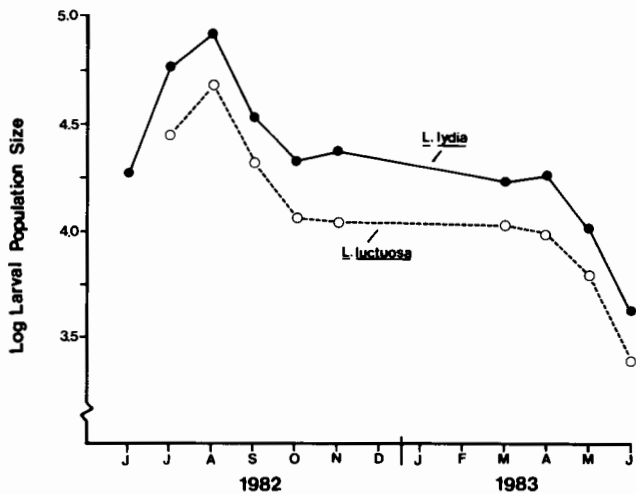


FIG. 5. Temporal changes in the larval population size of *L. lydia* (solid circles) and *L. luctuosa* (open circles). Population size on each date was calculated as the product of the mean ($n = 6$) density (no./m²) in each habitat and habitat area (m²), summed across habitats.

similar patterns of emergence, breeding, and larval development (Figs. 1, 2, 3). Their convergent phenologies are consistent with the idea that closely related dragonflies tend to have similar, rather than seasonally segregated, life histories (Sawchyn and Gillott 1974, 1975; Benke and Benke 1975; Ingram and Jenner 1976).

Dragonfly species vary considerably in the degree to which development among conspecifics is synchronized (Corbet 1964, 1980; Benke and Benke 1975; Wissinger 1988b). Within this context, *L. lydia* and *L. luctuosa* are both relatively asynchronous. *Libellula lydia* development appears to lack any of the mechanisms known to synchronize insect development (reviews by Corbet 1980; Tauber *et al.* 1986). Degree of asynchrony is more variable during the life cycle of *L. luctuosa*. Early development is nearly as asynchronous as in *L. lydia*, but later instars synchronize because (i) F-1 (and probably F-2) larvae diapause in fall and (ii) smaller larvae resume development before larger larvae in spring. The instar-specific delay in fall has been previously reported for only one other asynchronously hatching species (*Pachydiplax longipennis*; Eller 1963). Synchronization in spring is probably due to instar-specific responses to rising water temperatures (Corbet 1980).

Mean instar plots and survival curves illustrate that growth and mortality in these species occur in two seasonal phases: one in late summer–fall, and a second the following spring (Figs. 3, 5). This pattern of larval growth appears to be specific to asynchronous breeders, independent of latitude within the temperate zone (Lutz 1968; Benke and Benke 1975; Johnson and Crowley 1980; Ubukata 1981; Wissinger 1988b). Larvae of synchronous univoltine species hatch in spring, complete most or all of larval development before winter, and therefore have a negligible spring growth phase to their life cycle (Benke and Benke 1975; Deacon 1975; Wissinger 1988b). In contrast, seasonal patterns of mortality appear to depend more on latitude than on other life history characteristics. The pattern observed in this study is characteristic of many northern populations regardless of degree of synchrony (Ubukata 1981; Johnson 1986; Wissinger 1988c; but see

Lawton 1970). Mortality rates at lower latitudes are more linear (Benke and Benke 1975), perhaps reflecting greater winter activity of predators.

Asynchrony and phenologic priority

Field experiments with dragonflies demonstrate the negative impact that larvae of spring breeders can have on the survivorship of summer breeders (Benke 1978; Benke *et al.* 1982; Johnson *et al.* 1985). In all of these studies the earlier species breeds synchronously so that all larvae have a developmental size advantage over those of later breeding species. In this study, *L. lydia* mating began 2 to 4 weeks before that of *L. luctuosa*, and *L. lydia* had an average size advantage during larval development (Table 1). However, size asymmetries between these species are confounded by protracted recruitment periods. While some *L. lydia* larvae had a developmental head start over some *L. luctuosa*, others hatched at the same time or later than many *L. luctuosa* individuals. Thus, there were times during larval development when interspecific size ratios actually favored *L. luctuosa* (Table 1). In asynchronous species, intraspecific variability in the timing of development may swamp the effects of phenologic priority (Morin 1984).

Intraspecific resource partitioning

A striking feature of *L. lydia* and *L. luctuosa* populations is the enormous size range of larvae that co-occur at any time (Fig. 4). On average, the largest larvae were 3.1 and 4.9 times as large as the smallest conspecifics in the *L. luctuosa* and *L. lydia* populations, respectively (Table 1). Such intraspecific size differences are larger than all of the interspecific size differences for coexisting species recently culled from the literature by Polis (1984). Many conspecifics in *L. lydia* and *L. luctuosa* populations might overlap less in their use of prey resources than is commonly thought to accommodate interspecific coexistence (see also Keast 1977). The size structure in these populations also creates the potential for cannibalism, which is known to occur readily in the laboratory between many of the naturally co-occurring size combinations described in this paper (Wissinger 1988a). Only the subset of population theory that explicitly assumes intraspecific variation in the type and intensity of interactions seems appropriate for modeling the population dynamics of these species (see review by Lomnicki 1988).

Interspecific coexistence and size-structured populations

The size structure in *L. lydia* and *L. luctuosa* populations should also affect the potential for interspecific interaction. As with many arthropods (Wilson 1975), the range of prey sizes used by odonate larvae increases during ontogeny (Thompson 1978b). While same-sized larvae will overlap symmetrically, the diets of larger larvae will overlap more with those of smaller larvae than vice versa. Thus, coefficients of competition should not be the same for all co-occurring size combinations of these species. In addition, mixed competition–predation interactions (cf. Werner and Gilliam 1984) are possible, given that many of the size combinations found in this study will interact as predators and prey (Wissinger 1988a). Although it is not intuitively obvious whether non-static competition coefficients and (or) mixed competition–predation interactions will be stabilizing or destabilizing, the conditions for coexistence will no doubt differ from those predicted by classical competition theory (Abrams 1980; Lawlor 1980; Werner and Gilliam 1984; Wilbur 1980).

While the results of this study only indicate a potential for competition and predation, they imply that an understanding of how these ecologically similar species coexist will depend in part on experimentally disentangling a plethora of biotic interactions. Interpreting the relative importance of competition and predation in such experiments will be difficult unless the potential for complex interactions is anticipated in the design (Benke 1978; Reichert and Cady 1983).

Acknowledgments

I am grateful to the Horticulture Department of Purdue University, and in particular to the late E. M. Evans for my patent access to the study site. I thank Rich King for his help with collecting exuviae. Comments by Rick Howard, Peter Waser, and two anonymous reviewers improved an earlier version of this manuscript. This study was supported by a Purdue Research Foundation Fellowship, a Sigma Xi Grant-in-Aid, and a National Science Foundation Research Initiation and Support Grant, SER 77-06731, to Purdue University.

- ABRAMS, P. 1980. Some comments on measuring niche overlap. *Ecology*, **61**: 44–49.
- BENKE, A. C. 1969. Population dynamics and niche separation in an association of larval odonates. M.Sc. thesis, University of Georgia, Athens.
- 1970. A method for comparing individual growth rates of aquatic insects with special reference to the Odonata. *Ecology*, **51**: 328–331.
- 1978. Interactions among coexisting predators: a field experiment with dragonfly larvae. *J. Anim. Ecol.* **47**: 335–350.
- BENKE, A. C., and BENKE, S. S. 1975. Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology*, **56**: 302–317.
- BENKE, A. C., CROWLEY, P. H., and JOHNSON, D. M. 1982. Interactions among coexisting larval Odonata: an *in situ* experiment using small enclosures. *Hydrobiologia*, **94**: 121–130.
- BUTLER, M. 1984. Life histories of aquatic insects. In *The ecology of aquatic insects*. Edited by V. H. Resh and D. M. Rosenberg. Praeger, New York. pp. 24–55.
- CONNELL, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**: 661–696.
- CORBET, P. S. 1964. Temporal patterns of emergence in aquatic insects. *Can. Entomol.* **96**: 264–279.
- 1980. Biology of Odonata. *Annu. Rev. Entomol.* **25**: 189–221.
- CROWLEY, P. H., and JOHNSON, D. M. 1982. Co-occurrence of Odonata in the eastern United States. *Adv. Odonatol.* **1**: 15–37.
- DEACON, K. J. G. 1975. The seasonal regulation of *Leucorrhinia intacta* Hagen. M.Sc. thesis, University of Waterloo, Waterloo, Ont.
- ELLER, J. G. 1963. Seasonal regulation in *Pachydiplax longipennis* (Odonata: Libellulidae). Ph.D. dissertation, University of North Carolina, Chapel Hill.
- INGRAM, B. R., and JENNER, C. E. 1976. Life histories of *Enallagma hageni* and *E. aspersum* (Hagen) (Zygoptera: Coenagrionidae). *Odonatologica*, **5**: 331–345.
- JOHNSON, D. M. 1986. The life history of *Tetragoneuria cynosura* (Say) in Bays Mountain Lake, Tennessee, United States (Anisoptera: Corduliidae). *Odonatologica*, **15**: 81–90.
- JOHNSON, D. M., and CROWLEY, P. H. 1980. Habitat and seasonal segregation among coexisting odonate larvae. *Odonatologica*, **9**: 297–308.
- JOHNSON, D. M., CROWLEY, P. H., BOHANAN, R. E., WATSON, C. N., and MARTIN, T. H. 1985. Competition among larval dragonflies: a field enclosure experiment. *Ecology*, **66**: 119–128.
- KEAST, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition in two centrarchid fishes. *Evol. Biol.* **10**: 333–395.
- LAWLOR, L. R. 1980. Overlap, similarity, and competition coefficients. *Ecology*, **61**: 245–251.
- LAWTON, J. H. 1970. A population study on larvae of the damselfly *Pyrrosoma nymphula*. *Hydrobiologia*, **36**: 33–52.
- LOMNICKI, A. 1988. Population ecology of individuals. *Monogr. Popul. Biol.* No. 25.
- LUTZ, P. E. 1968. Life-history studies on *Lestes eurinus* Say (Odonata). *Ecology*, **49**: 576–579.
- MERRILL, R. J., and JOHNSON, D. M. 1984. Dietary niche overlap and mutual predation among coexisting larval Anisoptera. *Odonatologica*, **13**: 387–406.
- MORIN, P. J. 1984. Odonate guild composition: experiments with colonization history and fish predation. *Ecology*, **65**: 1866–1873.
- NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K., and BENT, D. H. 1975. Statistical package for the social sciences. 2nd ed. McGraw Hill, New York.
- POLIS, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *Am. Nat.* **123**: 541–564.
- PRITCHARD, G. 1964. The prey of dragonfly larvae (Odonata; Anisoptera) in ponds in northern Alberta. *Can. J. Zool.* **42**: 785–800.
- REICHERT, S. E., and CADY, A. B. 1983. Patterns of resource use and tests for competitive release in a spider community. *Ecology*, **64**: 899–913.
- SAWCHYN, W. W., and GILLOT, C. 1974. The life histories of three species of *Lestes* (Odonata: Zygoptera) in Saskatchewan. *Can. Entomol.* **106**: 1283–1293.
- 1975. The biology of two related coenagrionid dragonflies (Odonata: Zygoptera) in western Canada. *Can. Entomol.* **197**: 119–128.
- TAUBER, M. J., TAUBER, C. A., and MASAKI, S. 1986. Seasonal adaptations of insects. Oxford University Press, Oxford.
- THOMPSON, D. J. 1978a. The natural prey of larvae of the damselfly *Ischnura elegans* (Odonata). *Freshwater Biol.* **8**: 377–384.
- 1978b. Prey size selection by larvae of the damselfly, *Ischnura elegans*. *J. Anim. Ecol.* **47**: 769–785.
- UBUKATA, H. 1981. Survivorship curve and annual fluctuation in the size of emerging populations of *Cordulia aenea amurensis* Selys (Odonata: Corduliidae). *Jpn. J. Ecol.* **31**: 335–346.
- WALKER, E. M., and CORBET, P. S. 1975. The Odonata of Canada and Alaska: Anisoptera Libellulidae. Vol. 3. University of Toronto Press, Toronto, Ont.
- WERNER, E. E., and GILLIAM, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**: 393–425.
- WILBUR, H. M. 1980. Complex life cycles. *Annu. Rev. Ecol. Syst.* **11**: 67–93.
- WILSON, D. S. 1975. The adequacy of body size as a niche difference. *Am. Nat.* **109**: 769–784.
- WISSINGER, S. A. 1986. Comparative life histories and larval population interactions in a diverse assemblage of dragonfly larvae (Odonata: Anisoptera). Ph.D. dissertation, Purdue University, West Lafayette, IN.
- 1988a. Effects of food availability on larval development and inter-instar predation among larvae of *Libellula lydia* and *Libellula luctuosa* (Odonata: Anisoptera). *Can. J. Zool.* **66**: 543–549.
- 1988b. Life history and size structure of larval odonate populations. *J. North Am. Benthol. Soc.* **7**: 13–28.
- 1988c. Spatial distribution, life history, and estimates of survivorship in a 14 species assemblage of larval dragonflies (Odonata: Anisoptera). *Freshwater Biol.* **20**. In press.
- 1989. Seasonal variation in the intensity of competition and predation among pond-dwelling dragonfly larvae. *Ecology*, **70**. In press.