

**THE LIFE HISTORY OF *TETRAGONEURIA CYNOSURA* (SAY)
IN BAYS MOUNTAIN LAKE, TENNESSEE, UNITED STATES
(ANISOPTERA: CORDULIIDAE)**

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Data from 8 consecutive years of monthly sweep-net sampling in the littoral zone of Bays Mountain Lake are combined to show the life history of a "typical" generation of *T. cynosura* at this location (36° CN latitude, 550 m elevation). Population size peaks in mid-July, but declines by 60% before mid-August (mortality attributable to predation by both large dragonflies and sunfish). It then declines gradually through December, more steeply through the winter, and then gradually again until emergence in May. — Size-frequency distributions, and dry mass determinations for certain larvae, suggest that about 50% of the individuals in the penultimate instar in September are semivoltine; the others are fast-growing young-of-the-year entering the penultimate instar at a smaller size than members of the senior year-class. This size differential is maintained when larvae enter the final instar in October, and it appears that the smaller (junior year-class) individuals suffer more mortality during the winter, so that only about 25% of the emerging imagoes are univoltine.

INTRODUCTION

Since 1977, my colleagues and I have been studying the ecology of the odonate assemblage of Bays Mountain Park, Sullivan County, Tennessee, USA (82° 37'W, 36° 31'N). JOHNSON, CONEY & WESTFALL (1980) report 46 species of Odonata collected in this locale, 36 of which were taken as larvae. The major lentic habitat in the park is Bays Mountain Lake, a 15 ha shallow eutrophic reservoir in a forested watershed at 550 m elevation. Its littoral zone is composed of five habitats: submersed macrophytes, allochthonous detritus, emergent rushes, floating-leaved lotus, and sandy inlets. JOHNSON & CROWLEY (1980) describe these habitats in some detail, provide a vegetation map of the lake, and

estimate the area covered by each type in July 1979.

In July 1977 we established nine permanent sampling stations in the littoral zone of Bays Mountain Lake, one in the floating-leaved lotus, and two in each of the other habitats. An additional lotus station was added in July 1980, and two more submersed macrophyte stations, in July 1982. One standard 1 m sweep-net sample (0.33 m²) has been collected from each station near the mid-point of each month (except December 1982, and January and February of most years) since July 1977. All odonate larvae have been preserved in 70% alcohol, identified to the lowest feasible taxon using available keys (especially WESTFALL, 1984), and measured (head-width).

My intention is to continue to collect these monthly samples using standard techniques throughout the duration of our study. They provide background information to guide our more experimental research, and should gradually accumulate into a set of data on the long-term stability of odonate assemblages which may one day rival MACAN's (1974) twenty-year record for Hodson's Tarn.

Two papers (JOHNSON & CROWLEY, 1980; CROWLEY & JOHNSON, 1982) report rather extensive analyses of the first three years (July 1977 - June 1980) of sweep-net data from Bays Mountain Lake (and nearby Ecology Pond). In those papers we concluded that *Tetragoneuria cynosura* (we follow WESTFALL, 1984 rather than WALKER, 1966), the dominant anisopteran in Bays Mountain Lake, exhibited a semivoltine life history similar to that reported from Michigan (KORMONDY, 1959) and Pennsylvania (KORMONDY & GOWER, 1965), but different from the predominantly univoltine life history reported for North Carolina (LUTZ & JENNER, 1984; PAULSON & JENNER, 1971) and South Carolina (BENKE & BENKE, 1975). That conclusion has been questioned by Ulf Norling (personal communication) because it was based on arbitrary lumping of head-width measurements into instars (JOHNSON & CROWLEY, 1980, fig. 5) which he knew from experience (cf. NORLING, 1976) might obscure the phenomenon of cohort-splitting. Because *T. cynosura* has been the subject of much of our experimental research (JOHNSON et al., 1985; MOORE, 1985), and because the interactions between larval size-classes have proved to be especially important, I decided to see whether eight years of accumulated sweep-net data might provide sufficient information for a re-appraisal of its life history.

METHODS

The number of *T. cynosura* larvae collected in any single month (a total of 9 to 12 sweeps from five habitats) is not sufficient to make confident estimates of either population size or size-frequency distributions. But the combined collections for a given month in eight consecutive years (a total of 83 sweeps — 22 from submersed macrophytes, 13 from lotus, and 16 from each of the other three habitats) provides enough larvae to make reasonable estimates of population size as well as

size-frequency distributions with relatively few gaps. Such combined data do not provide much information about year-to-year variation, but may be used to describe the life history of a "typical" generation.

Total population size was estimated for each month by (1) obtaining the mean number of larvae per sweep for each habitat, (2) multiplying by 3 to estimate mean number per m², (3) multiplying by the area covered by a given habitat (JOHNSON & CROWLEY, 1980, tab. 1), (4) summing these products over all five habitats, and (5) multiplying the resulting estimate by 2 to adjust for inefficiency of sweep-net samples. These calculations make two important assumptions: (1) that estimates based on sweep-nets are about half what they would be if based on more quantitative methods, and (2) that areas covered by each habitat type have not changed dramatically during the eight-year period (cf. MACAN, 1964, 1974). The first is supported by comparison of monthly sweep-net estimates with those based on six random Gerking Sampler samples from each of the three major habitats (submersed, detritus, emergent) from July 1979 through August 1980 (unpublished data) — the median Gerking sweep ratio was 2.3, somewhat less than the value of 3.7 that can be obtained from data reported by LAWTON (1970). The second assumption is supported only by our visual impression that vegetation zones have remained relatively stable.

I used a "bootstrap" procedure (DIACONIS & EFRON, 1983) to estimate 95% confidence intervals for the population estimates. The several (13 to 22) actual values of number per sweep for each habitat were sampled at random, with replacement, to compose artificial estimates of density within habitats that had the same number of samples as originally available (step 1 above). These artificial density estimates were used to calculate artificial estimates of population size (steps 2-5). This process was repeated 1000 times on a microcomputer, the resulting estimates of population size were sorted, and 95% confidence intervals obtained by printing the 25th and 975th values in the sorted list.

Size-frequency distributions of head-width measurements were obtained for each month by simply combining all samples taken near the mid-point of each month over the eight-year period. It should be noted that the smaller instars are not adequately sampled by sweep-nets (LAWTON, 1970); therefore, samples during the period when small larvae are hatching (especially June) undoubtedly underestimate the frequency of the small size-classes. Since *T. cynosura* is a typical "spring species" (sensu CORBET, 1954), its synchronous oviposition results in a relatively discrete cohort (BENKE & BENKE, 1975), which rapidly grows into the range of sizes that are adequately sampled by the net. I have assumed that the July sample is relatively unaffected by size-selective sampling.

Inspection of the size-frequency histograms caused me to recover certain individual larvae from the preserved samples. These were re-measured, dried to constant weight at 60° C, and weighed on an electrobalance. The observed dry mass was divided by the range of masses predicted by two equations — $M = (cH + 0.1)^3$, where M is predicted dry mass (mg), H is measured head-width (mm), and $c = 0.4$ for minimum mass or 0.7 for maximum mass — which are known to enclose 96% of 771 individual observations on *T. cynosura* larvae whose head-widths and masses have been measured in connection with several experiments conducted at Bays Mountain Lake (unpublished data). The resulting proportion may be interpreted as an estimate of how much growth has been accomplished within a given instar. It can be used to distinguish individuals which have recently entered an instar from those that have been in it for some time, rather like the "phases" based on morphological changes described by NORLING (1976, 1984b).

RESULTS

Estimates of the total population of *Tetragoneuria cynosura* in Bays Mountain Lake for the mid-point of each month throughout a "typical" year are presented in

Figure 1. The population size peaks at almost two million in mid-July, but then declines by more than 60% before mid-August. After this dramatic drop, the population declines gradually through mid-December, more steeply during the winter months, and then gradually from mid-March through mid-May. Emergence has been reported from mid-April through early June (JOHNSON & CROWLEY, 1980, fig. 5) and the resulting new generation contributes the increase in population size observed between mid-May and mid-June.

Size-frequency histograms for *T. cynosura* head-width based on pooled samples from near the mid-point of each month are presented in Figure 2. In June there is a clear separation between newly hatched larvae (white) and those which have over-wintered in intermediate instars (gray). The former are probably under-represented due to inefficient sampling. Some of the latter have already entered the penultimate instar (about 4 mm head-width). By mid-July, most of the senior year-class (now shaded black) has entered the penultimate instar, where they are destined to spend the rest of the summer due to their well-known "long-day diapause" (LUTZ & JENNER, 1964; LUTZ, 1974a, 1974b). In September, the survivors of this group appear to be joined by a

distinctly smaller group of larvae which seem to represent a fast-growing part of the junior year-class, easily identified as early as July (mottled shading).

To test this hypothesis, I compared the dry masses of all individuals in the September samples, with head-widths between 3.5 and 4.5 mm, to the range of

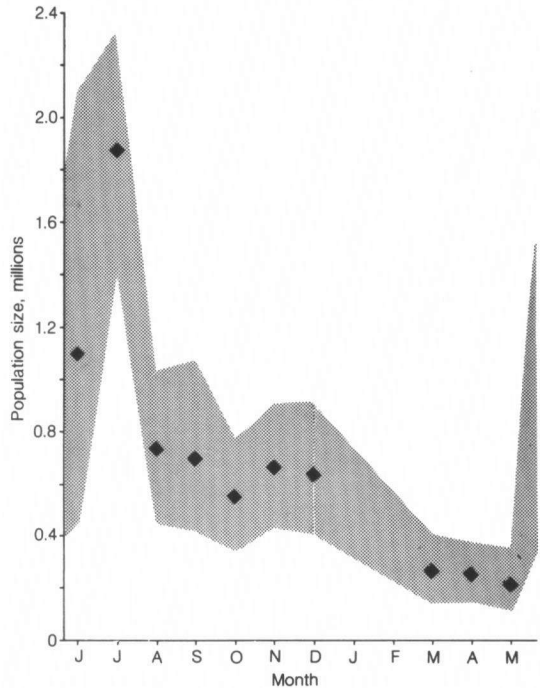


Fig. 1. Monthly estimates of population size for *Tetragoneuria cynosura* in Bays Mountain Lake from combined results of eight consecutive years (1977-1985) of sweep-net sampling (each estimate is based on 83 samples). Shaded areas include 95% confidence intervals obtained by "bootstrapping" 1000 estimates from the data set for each month.

dry masses expected for a given head-width (cf. Methods). A Median Test (SIEGEL, 1956) was used to test the null hypothesis that the proportion of expected growth accomplished was the same for individuals with head-widths above and below 3.7 mm (black and mottled respectively in Fig. 2, September). The alternative hypothesis was that those with head-widths more than 3.7 (black) would have accomplished a greater proportion of the growth expected, because they had been in that instar since June or July. The average proportions of expected growth accomplished by the two groups differed in the predicted direction (0.22 for the smaller group and 0.52 for the larger), there was very little overlap (only 3 of 30 observations) between the two groups, and the null hypothesis was rejected ($P(X^2_1 > 16.2) < 0.001$).

I consider the test described above to be relatively strong corroboration for the inference that the junior year-class exhibits cohort-splitting, probably based on attainment of some critical size early in the summer. NORLING (1984a) provides a particularly lucid discussion of this complex phenomenon. The *T. cynosura* population in Bays Mountain Lake seems to be a case of autumn cohort-splitting similar to those described in his figure 14.

Because the total numbers of individuals included in each size- or year-class in Figure 2 changed in very consistent patterns from month to month, I decided to

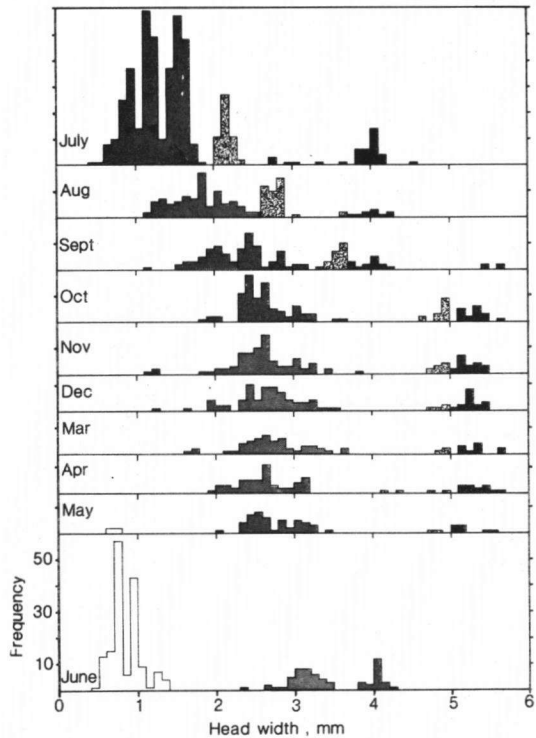


Fig. 2. Monthly size-frequency histograms for *Tetragoneuria cynosura* head-width in Bays Mountain Lake from combined results of eight consecutive years (1977-1985) of sweep-net sampling. Differential shading shows the year-class inferences used to calculate survivorship (Fig. 3 and text): black, senior year-class; — mottled, univoltine part of junior year-class; — gray, semivoltine part of junior year-class; — white, newly hatched larvae (May & June). Note that the transition from one year-class to the next is made between June (bottom) and July (top).

construct a survivorship curve based on these data (Fig. 3). The observed number in the junior year-class (both gray and mottled shading) provided an initial population (416) to which all subsequent numbers surviving were compared. A few minor "adjustments" were necessary to insure that survivorship declined monotonically for each category. Note also that mortality experienced before mid-July is not included, though HALVERSON (1983) has shown that mortality may be quite high in both the egg and early instar stages. For these reasons, as well as the fact that the data used are pooled collections made over an eight-year period, one should consider the survivorship curve in Figure 3 to be somewhat hypothetical. Nevertheless, it serves to illustrate certain points that deserve attention (cf. Discussion).

DISCUSSION

Two aspects of the life history of *Tetragoneuria cynosura* in Bays Mountain Lake are particularly intriguing when it is compared to other studies: (1) the very high mortality experienced from mid-July to mid-August (Figs 1, 3), and (2) cohort-splitting by the junior year-class (Fig. 2).

There are relatively few studies that have attempted to estimate survivorship curves for larval odonates (BENKE & BENKE, 1975; BENKE, 1978; LAWTON, 1970; MACAN, 1964;

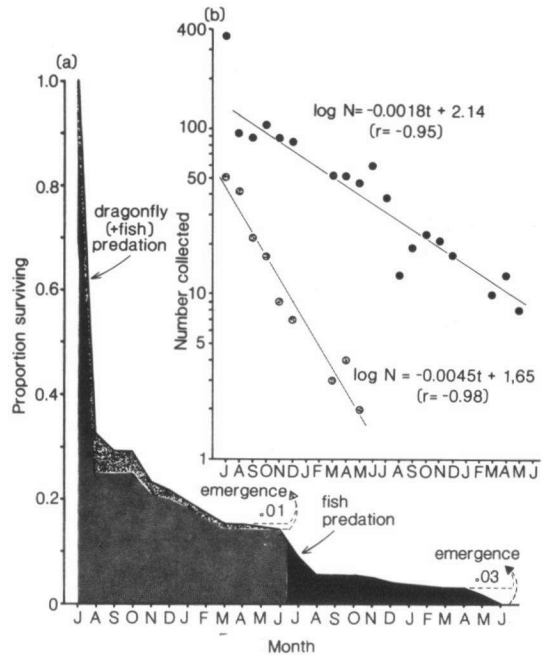


Fig. 3. *Tetragoneuria cynosura* survivorship in Bays Mountain Lake based on monthly size-frequency histograms (Fig. 2) from eight consecutive years of data combined. Differential shading shows the same year-classes inferred in Figure 2: (a) A somewhat hypothetical survivorship curve; note that all proportions refer to an initial number observed in mid-July — mortality among eggs and small larvae immediately post-hatching is not included. The proportion emerging after one and two years is indicated, as are periods when predation is known to be particularly important. — (b) Linear regression estimates of mortality rates per day (negative slopes) for the univoltine (mottled) and semivoltine (gray and black) parts of the cohort based on total numbers collected in each month (Fig. 2). Note that the first data point has been omitted from the semivoltine regression because mortality was much higher in the first month than thereafter.

UBUKATA, 1981; and KURATA, 1974). Most of these authors report relatively constant mortality rates (usually attributed to predation by dragonfly larvae and/or fish) throughout the warm season, and relatively little mortality over the winter (when predation by ectotherms is reduced). Only KURATA (1974) and UBUKATA (1981) report higher mortality during early instars, for *Aeshna juncea* and *Cordulia aenea amurensis* respectively. It seems clear that this is also the case for *T. cynosura* in Bays Mountain Lake (Figs 2, 3), and that the high mortality experienced by junior year-class larvae with head-widths less than 2 mm in mid-July (Fig. 2) is responsible for much of the decline in population size before mid-August (Fig. 1).

Analyses of the diets of late-instar dragonflies (*T. cynosura*, *Sympetrum vicinum*, *Celithemis elisa*, and *C. fasciata*) conducted by MERRILL (1981; cf. also MERRILL & JOHNSON, 1984) suggest that predation on smaller odonates was particularly high in July and early August of 1978 and 1979. A recent re-appraisal of Merrill's original slides suggests that nearly all of what Merrill reported as "Anisoptera" (MERRILL, 1981, tab. 3) during this period were indeed *Tetragoneuria* with head-widths less than 2 mm (C.N. Watson, personal communication).

MORIN (1984a, 1984b) has shown experimentally that fish predation can have a dramatic influence on both the abundance and species composition of littoral odonate assemblages. Analyses of the diets of large (> 150 mm) bluegill sunfish (*Lepomis macrochirus*) and redear sunfish (*L. microlophus*) in Bays Mountain Lake conducted by T.H. Martin (personal communication) suggest that predation on *Tetragoneuria* by redear sunfish was also quite high in July 1982, with the fish tending to concentrate on larvae with head-widths greater than 2 mm.

Rough estimates of *Tetragoneuria* consumption by fish and dragonfly populations during the month between mid-July and mid-August suggest that most of the mortality seen during this period in Figures 1 and 3 can be attributed to predation, with dragonflies responsible for most of the predation on the "smaller" members of the junior year-class (gray shading in Figs 2, 3), and sunfish, for that on the larger size-classes (mottled and black).

Increased exposure to predation by larger instars in dragonfly populations with semivoltine life histories is probably responsible for the higher mortality observed among early instars by KURATA (1974) and UBUKATA (1981), as well as for *T. cynosura* in Bays Mountain Lake (cf. also JOHNSON et al., 1985; MOORE, 1985). This risk may be much less (and more constant through time) in those situations where the population is either relatively small damselflies exposed to large dragonfly predation throughout a semivoltine life history (LAWTON, 1980; MACAN, 1964), or univoltine (BENKE & BENKE, 1975; BENKE, 1978). In fact, the linear regression estimate of daily mortality rate for the univoltine part of my *Tetragoneuria* population is remarkably similar (0.0045) to the range reported for another univoltine population (0.0033-0.0052, BENKE & BENKE, 1975, fig. 6). For the semivoltine part, the relatively constant daily

mortality experienced after mid-August of their junior year (0.0018) is not only less than half that experienced by their univoltine peers, but is an order magnitude less than that in the previous month (0.0200). This high risk of predation by larger con-specifics (or other species within a predator guild) seems to be a fairly general phenomenon (FOX, 1975; POLIS, 1981), and should provide strong selection in favor of any life-history traits (i.e., early oviposition or fast growth by small instars) that would enhance the opportunity to escape from the vulnerable size-class as soon as possible (cf. also WERNER & GILLIAM, 1984).

The life history of *T. cynosura* in Bays Mountain Lake has intriguing parallels with that of *Leucorrhinia dubia* in southern Sweden (NORLING 1984b). Both populations exhibit cohort-splitting in the summer/autumn preceding spring emergence. NORLING (1984a) suggests that this refine seasonal regulation by compensating for deficiencies in the more common "winter critical size" model. In both populations there is a suggestion that individuals which enter the final instar late also emerge later in the spring (Fig. 2, 5 of 13 black but 0 of 2 mottled emerge between mid-April and mid-May; see NORLING 1984b, fig. 3a.S. and fig. 8c). This is especially clear in Norling's data; it is quite uncertain in mine, because the smaller (and younger) members of the final instar seem to have experienced much greater mortality over the winter (about 70%) than either the larger (older) members of the final instar or their smaller peers (both about 30%). As a result, very few survive to emerge, but those that do are still present in mid-May after many of the larger individuals have emerged.

For those larvae that survive to mid-July of their first year, the probability of surviving to emergence seems to be dependent on size in July — about 8% for the larger univoltine part of the cohort, and about 4% for the smaller semivoltine part (Fig. 3). There appear to be some very important trade-offs involved in such cohort-splitting. An individual that hatches early enough and/or grows rapidly enough to complete a univoltine life history may risk higher mortality over-winter only to emerge relatively late, thus giving its offspring a slow start which would force them into a semivoltine life history. It is also likely that they would emerge at a smaller size, and thus have lower fecundity. Such complex interactions and opposing selection pressures on life-history adaptations may be profitably explored using a simulation model of size-structured populations with complex life-cycles such as that recently developed for damselflies (CROWLEY et al., 1986). The resulting hypotheses should be amenable to testing with field enclosure experiments.

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