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LIFE HISTORIES OF THREE SPECIES OF *LESTIDAE* IN NORTH CAROLINA, UNITED STATES (ZYGOPTERA)

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The life histories of *Lestes vigilax* Hagen, *L. disjunctus australis* Walker, and *Archilestes grandis* (Rambur), were studied in small, artificial ponds in western North Carolina. All three species were univoltine, but there were pronounced differences in their life cycles. *L. vigilax* overwintered as larvae in the F-3 and smaller instars, and emerged from late June to early August. The emergence consisted of larvae that hatched following a short egg stage the previous summer, overwintered, and emerged approximately one year after hatching. *L. disjunctus* apparently passed the winter in the egg, and hatching occurred the following spring. Larval development was completed in about two months, and emergence occurred from late July to early September. The larval development of *A. grandis* was similar to that of *L. disjunctus*, and emergence occurred from about mid-August to late September. *A. grandis* overwintered either in the egg stage or in very early larval instars. The emergence periods of all three species were temporally separated to a degree, a factor that is probably important in reducing competition in areas of coexistence.

INTRODUCTION

Members of the cosmopolitan family *Lestidae* are important carnivores in both temporary and permanent aquatic habitats. Tropical species pass the lengthy dry season as adults, and both egg and larval stages are of short duration (CORBET, 1964; KUMAR, 1972). Most lestids inhabiting temperate climates overwinter as eggs (SAWCHYN & GILLOTT, 1974a, 1974b), and the adults and larvae have a short existence, although some species have a short egg stage and pass winter in the more lengthy larval stage (LUTZ, 1968a; PAULSON & JENNER, 1971). In North America, the life histories and biology of several species of *Lestes* have been described at northern latitudes (GOWER & KORMONDY, 1963; SAWCHYN & CHURCH, 1973; SAWCHYN & GILLOTT, 1974a, 1974b). However, little information is available on the life histories of more southerly species, except for the studies on *Lestes eurinus* in North Carolina (LUTZ, 1968a, 1968b).

During a study of seasonal regulation in two coenagrionids (INGRAM, 1971, 1975), information was obtained on the larval development and emergence of three species of Lestidae. The present study describes the life histories of *Lestes vigilax* Hagen, *L. disjunctus australis* Walker, and *Archilestes grandis* (Rambur) in western North Carolina. Special attention was given to differences in the patterns of larval development and emergence.

THE STUDY AREA

The study was conducted at two permanent, artificial ponds near Highlands (Macon Co.) in the Blue Ridge mountains of southwestern North Carolina (35°5'N, 83°10'W). Schroder's Pond (elevation = 1285 m), approximately 10 years old, is located about 2.9 km NE of Highlands; the pond is about 1.0 ha in area with an average depth of about 1.0 m. McCord's Pond (elevation = 1012 m) is located in a cove approximately 4.0 km SW of Highlands. About 12 years old and 0.6 ha in area, this pond also had an average depth of about 1.0 m. Water was supplied to both ponds by several springs and a small stream. Both ponds were closely surrounded by small wooded areas, and the remainder of the margin contained mainly grasses, with isolated cultivated plants and a few trees. *Scirpus, Carex, Eleocharis, Juncus, Potamogeton,* and *Nitella* were common along the littoral area and at the land-water interface. *Potamogeton* was dominant at McCord's, whereas *Nitella* was most common at Schroder's. The most common odonates at both ponds were the coenagrionids *Enallagma aspersum* and *E. hageni*, followed by the lestids under study. *Ischnura posita, I. verticalis, Anomalagrion hastatum, Chromagrion conditum, Aeshna umbrosa, Epitheca cynosura,* and *Sympetrum vicinum* were also relatively common.

Using continuous recording thermographs, mean daily water temperatures for 1969 were low (3-8°C) from November to March and were highest in July (25-27°C). Temperatures during the warmer months were often slightly higher (1-2°C) at Schroder's than at McCord's (INGRAM, 1971). Daily late afternoon temperatures were also recorded with a mercury in glass thermometer during the summer months of 1968 and 1969 at Schroder's.

MATERIALS AND METHODS

Larval collections of *Archilestes grandis* were made during the summer of 1967 at McCord's Pond; this species was absent from the pond in subsequent years. *Lestes vigilax* larvae were also sampled at McCord's during 1968-1969. *L. disjunctus* was sampled during 1968 at Schroder's Pond. Collections were made with a long-handled dip net that was swept through aquatic vegetation and bottom debris. The samples were emptied into a white enameled pan containing water, and the larvae were removed from the pan with a Banta pipette.

The larvae were taken to the laboratory, and a dissecting microscope with an ocular micrometer was used to measure head width (maximum width of head) and to estimate relative wing-pad length (number of abdominal segments covered by the metathoracic wing-pads). These two characters permitted the separation of the last three instar classes (F = final, F-1 = penultimate, and F-2 = antepenultimate) in all three species. Larvae were generally returned to the ponds within 2 days of collection.

Patterns of emergence in *L. disjunctus* and *L. vigilax* were studied at Schroder's and McCord's, respectively, in 1968 and 1969. Exuvial collections were made from 100 dowels representing artificial emergence sites that were placed around the periphery of each pond. The dowels (0.5 cm diam., 90 cm length) were inserted into the substrate near the pond's margin at approximately 1 m intervals and extended about 50 cm above the water's surface. The total shoreline area covered by the dowels was about 30% and 50% at Schroder's and McCord's respectively. Exuviae were collected daily during the entire emergence periods in both years, and searches for exuviae were made both before and after the reported emergence periods.

A second method of collecting exuviae was used in 1969. Twenty strips of screen wire (50 cm length, 15 cm height) were placed at intervals of about 10 m around the margin of the pond. Each screen was stretched between 2 dowels that were attached to its ends. The dowels were inserted into the bottom about 10 cm from the edge so that the bottom of the screen touched the substrate and the upper portion of the screen extended about 10 cm above the water. The screens were oriented with their length parallel to the pond's margin. The screens served primarily as alternate emergence sites for larvae that might not utilize the dowels and would, otherwise, crawl onto the dense marginal vegetation where the chance of recovering exuviae was slight. The larger number of exuviae of *L. vigilax* collected from the screens than the dowels at McCord's indicated that the screens provided a more favorable emergence site for this species. In contrast, few exuviae of *L. disjunctus* were collected from the screens placed at Schroder's Pond. Other species apparently are not selective, as both screens and dowels were utilized at similar frequencies by *Enallagma aspersum* and *E. hageni* (INGRAM, 1971).

RESULTS

LESTES VIGILAX

Larval collections of *L. vigilax* were made from 5 May 1968 to 13 April 1969 to determine changes in instar composition (Figs. 1A and 1B). In the first larval collection on 5 May, about 30% of the larvae were in the F-2 and F-1 instars; most of the population was comprised of smaller individuals. By the next collection on 12 June, about 50% of the larvae had entered the final instar. Subsequent collections in June and in July were dominated by final instar larvae. Members of the new-year class were first collected on 7 August, indicating that the egg stage was of short duration. Growth of the new-year class continued into fall, but the population was largely stabilized during November and December. Larvae did not molt beyond the F-3 instar during the colder months, overwintering in this and smaller instars. By late March growth had resumed with the

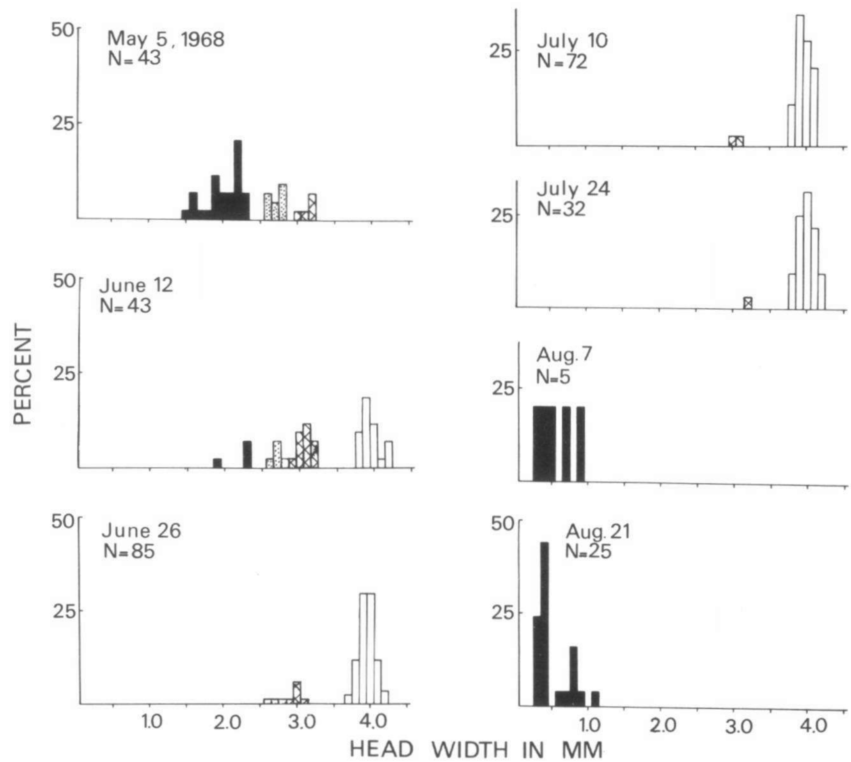

Fig. 1A. Head width frequency histograms of *Lestes vigilax* larvae collected in 1968-1969. N = sample size; clear bars = final instar; cross-hatched bars = F-1 instar; diagonally lined bars = F-2 instar; dark bars = smaller instars.

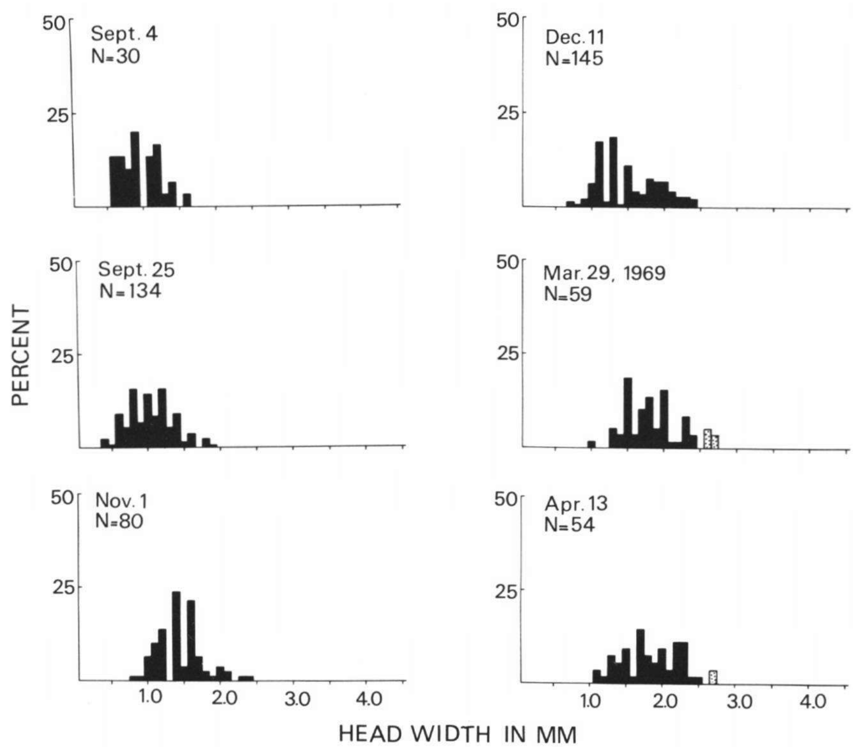

Fig. 1B. Fig. 1A continued.

entrance of some larvae into the F-2 instar. *L. vigilax*, therefore, had a univoltine life cycle, and each year's emergence consisted of larvae that hatched the previous summer, overwintered, and emerged approximately one year later.

The emergence pattern was similar in both years of observation, beginning on 30 June and ending on 7 August 1968 and beginning on 27 June and ending on 8 August 1969 from the estimates with the dowels (Fig. 2A-B). The 1969 emergence period lasted from 26 June to 12 August based on screen-collected exuviae (Fig. 2B). Although the timing and synchrony of emergence in 1969 was similar using either the dowel or screen estimates, the larger number of exuviae on the screens provided a more detailed record of the pattern. The screen estimates revealed that the number of emergences gradually increased from June to early July, reached a peak from 5 July to 27 July, and then declined and remained at low levels for the rest of the emergence period.

Exuviae from females were slightly more abundant, comprising 52.6% of 19

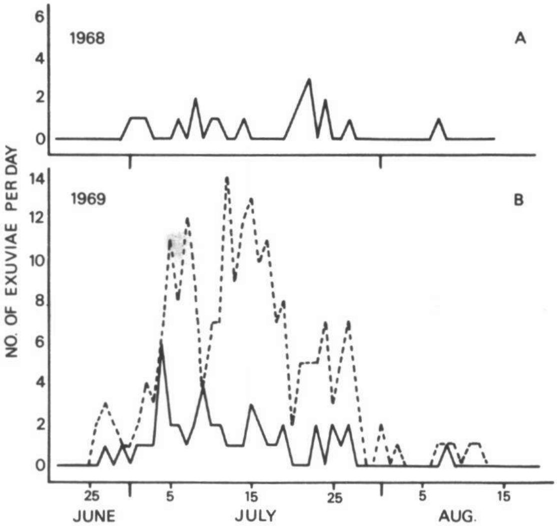

Fig. 2. Emergence patterns of *Lestes vigilax* in 1968 (A) and 1969 (B). Solid line = exuviae collected from dowels; dashed line = exuviae collected from screens.

exuviae in 1968 and 53.9% of 252 exuviae in 1969. Most of the exuviae collected late in the emergence period in 1969 were from females. After 27 July, when the number emerging per day dropped sharply, only 1 of 11 exuviae was from a male.

LESTES DISJUNCTUS

Larval collections of *L. disjunctus* were made from 14 June to 15 August 1968 (Fig. 3). No larvae were found in collections made in February and May. The larvae, which were first collected on 14 June, were very small, suggesting that they had recently hatched. Rapid changes in the instar composition of the larvae were revealed in subsequent collections. A few larvae entered the F-1 instar by 12 July, and a large portion reached the final instar by 26 July. Only larvae in the final instar were collected during August. The reduced number of final instars in the last collection indicated that the emergence period was nearly ended. Subsequent collections in September and October revealed no larvae.

Vegetation, primarily *Juncus*, on which females were observed to oviposit, was collected and inspected regularly in the laboratory for several months. No

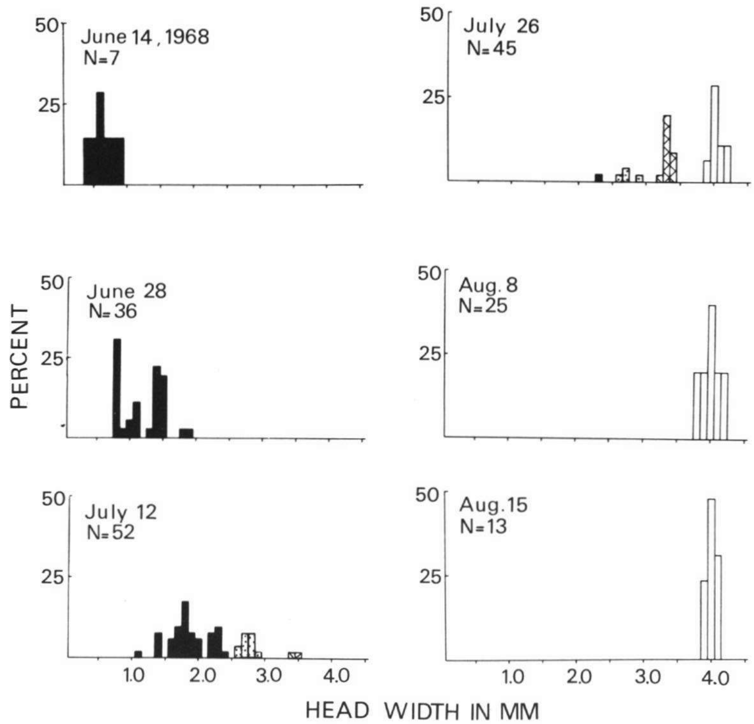

Fig. 3. Head width frequency histograms of *Lestes disjunctus* larvae collected in 1968. N = sample size; clear bars = final instar; cross-hatched bars = F-1 instar; diagonally lined bars = F-2 instar; dark bars = smaller instars.

larvae hatched from any of the vegetation, some of which was placed in water and some of which was not wetted. The failure of the eggs to hatch rapidly, together with the absence of larvae at the pond from approximately September to May, suggested that *L. disjunctus* overwintered in the egg and hatched in late spring.

Small numbers of exuviae were collected in both 1968 and 1969 (Fig. 4A-B). The first exuvium was collected on 29 July, and the last one was collected on 11 September 1968. The emergence period began and ended earlier in 1969; the first and last exuviae were collected on 11 July and 3 September respectively. However, the larva that emerged on 11 July was an apparent exception, since no other exuviae were collected for 12 days. The earlier emergence in 1969 than in 1968 was apparently related to warmer temperatures early in that year. Late

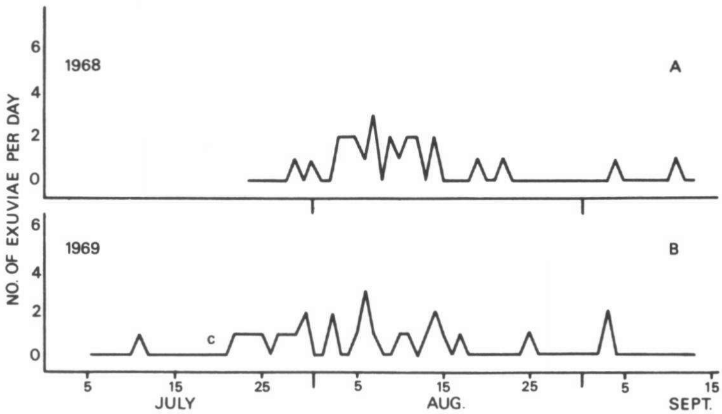

Fig. 4. Emergence patterns of *Lestes disjunctus* in 1968 (A) and 1969 (B).

afternoon surface temperatures were consistently higher (25-28°C vs. 20-23°C) from late June to late July in 1969 than in 1968. The warmer temperatures probably enabled the larvae to complete their development more rapidly.

In contrast to *L. vigilax*, most of the exuviae of *L. disjunctus* were collected from the dowels, and only three were found on the screens. The exuvial collections from both years were combined because of the small number collected (52), and 51.9% of the exuviae were from males.

ARCHILESTES GRANDIS

Larval collections of *A. grandis* were made during the summer of 1967 (Fig. 5). Although the number of larvae collected was small, it was deemed sufficient to indicate the basic type of life cycle. In considering the life cycle, the larger sizes of *A. grandis* larvae compared with those of the two species of *Lestes* should be noted (compare head widths of the last 3 instars in Figs. 1, 3, 5).

No larvae were found on 23 April. The larvae on 10 June were small, suggesting that they had hatched somewhat earlier in the spring. After 10 June, larval development was relatively rapid. Larvae entered the F-2 instar by 22 June and the F-1 instar by 21 July. Larvae in the final instar were first collected on 11 August, although several individuals in smaller instars were still present. In the sample on 5 September, all larvae but one were in the final instar, and the swollen and darkened wing-pads of most (71%) of the final instars indicated that emergence was near. After this date, no larvae were collected either in the remainder of 1967 or in subsequent years.

Only three exuviae were collected, one each on 16 August, 6 September, and 19 September. However, this limited evidence, together with the late season

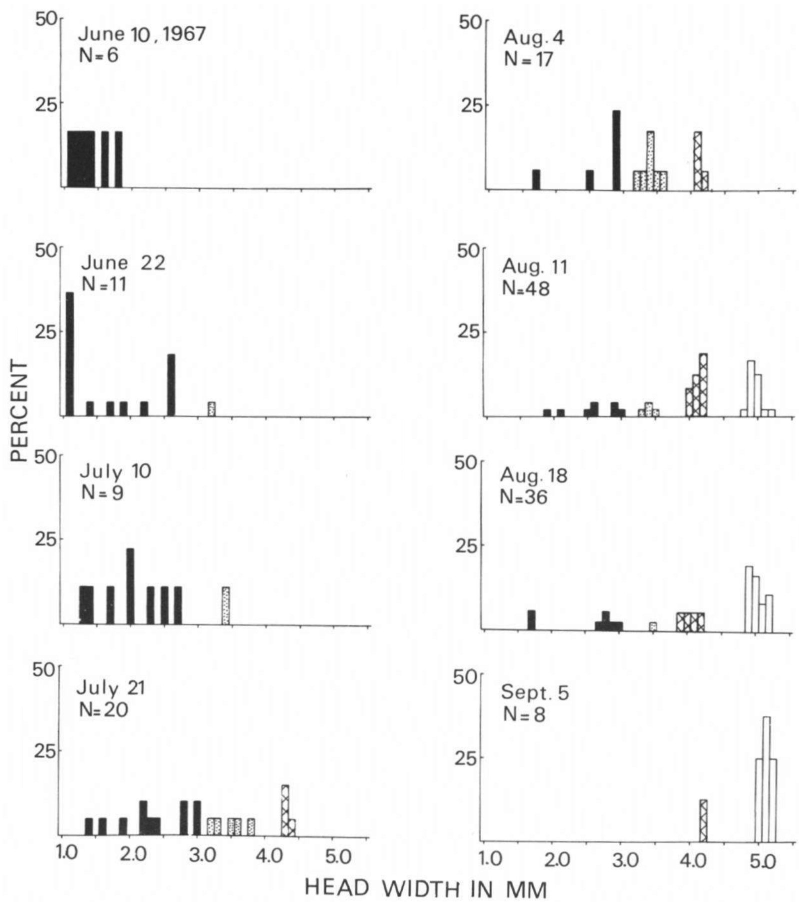

Fig. 5. Head width frequency histograms of *Archilestes grandis* larvae collected in 1968-1969. N = sample size; clear bars = final instar; cross-hatched bars = F-1 instar; diagonally lined bars = F-2 instar; dark bars = smaller instars.

entry of larvae into the final instar; indicates that emergence occurs late in the season, extending from about mid-August to middle or late September.

DISCUSSION

CORBET (1954, 1962) divided British Odonata into two ecological categories, "spring species" and "summer species" based on the role of diapause and the timing and synchrony of emergence. Spring species have an early emergence that is highly synchronized as a result of an overwintering diapause in the final instar. In summer species, winter is passed in stages other than the final instar, in which diapause does not occur, and emergence begins later in the season and is temporally dispersed. In North Carolina PAULSON & JENNER (1971) have shown that Corbet's categories represent only the two extremes of a continuum of odonate life cycle types. However, the three species of lestids in the present study were typical summer species, although the life cycle of *L. vigilax* differed greatly from those of *L. disjunctus* and *A. grandis*. Each of these univoltine species overwintered in stages other than the final instar, completed the final instar relatively quickly, and had a late-season emergence that was not highly synchronized.

L. disjunctus apparently overwintered in the egg stage and hatched the following spring. Larval development was completed in about 2 months, and emergence occurred in late summer. Comparable life cycles have been reported for other temperate zone *Lestidae* including *L. disjunctus disjunctus, L. unguiculatus, L. dryas,* and *L. congener* in Canada (SAWCHYN & GILLOTT, 1974a, 1974b), *L. rectangularis* in Pennsylvania (GOWER & KORMONDY, 1963), and *L. sponsa* in England (CORBET, 1956).

The larval development of *A. grandis* was similar to that of *L. disjunctus*, and indirect evidence suggested the occurrence of an overwintering egg stage. Since eggs were not collected, the mode of overwintering was based on the absence of larvae before and after the reported dates of collection and on the small size of the larvae found in June, apparently indicating they had recently hatched. However, BICK & BICK (1970) found that the eggs of *A. grandis* hatched in 15-16 days in Oklahoma, and presumably winter was spent in the larval stage. These observations suggest that the absence of larvae after the emergence period in the present study was due to the disappearance of the population from the pond rather than a prolonged egg stage. However, the presence of small larvae in late spring indicates that *A. grandis* overwintered either in the egg stage or in very early larval instars.

L. vigilax lacked a prolonged egg stage and overwintered in several larval instars. PAULSON & JENNER (1971) found that *L. vigilax* passed the winter in a wide range of larval instars and apparently did not cease development during the colder months, as several larvae molted shortly after collection at temperatures still at the level in nature. No larvae were observed to molt at pond temperatures in this study. *L. eurinus*, the only other lestid of the temperate zone known not to pass winter in the egg, overwintered in the larval stage in piedmont North Carolina (LUTZ, 1968a; PAULSON & JENNER, 1971), and at a site about 25 km north of Highlands (pers. obs.).

Although the life cycles of *L. vigilax* and *L. eurinus* (LUTZ, 1968a) were basically similar, the overwintering populations were quite different. *L. eurinus* overwintered in the F-3, F-2, and F-1 instars, whereas *L. vigilax* overwintered in instars F-3 and below, primarily in the smaller instars. Correspondingly, the emergence of *L. eurinus* (LUTZ, 1968a) occurred earlier in the year than that of

L. vigilax. The later emergence of *L. vigilax* may be partially related to the cooler temperatures in the mountains compared to those of the piedmont population of *L. eurinus*. PAULSON & JENNER (1971) found more advanced instars of *L. vigilax* in winter samples that included piedmont populations, and these larvae would presumably emerge earlier.

The emergence of *L. vigilax* occurred about one month earlier (late June to early August) at McCord's than that of *L. disjunctus* (late July to early September) at Schroder's in both years of study. Since the annual temperature cycle was similar at both ponds (INGRAM, 1971), thermal differences likely did not contribute to the later emergence of *L. disjunctus. A. grandis*, which coexisted with *L. vigilax*, had the latest emergence of the three species studied, beginning emergence in mid-August and probably extending at least until late September. The emergence periods of the three species, therefore, were partially separated temporally. Temporal separation of the life cycles is probably important in enabling species to coexist, as suggested for *Ladona deplanata* and *Libellula incesta* (BENKE, 1970).

The known flight season of *L. vigilax* extends from 1 May to 4 October in North Carolina (PAULSON & JENNER, 1971). While these dates include piedmont and coastal plain populations, which emerge both earlier and later in the season than mountain populations, adults flying later than the termination of emergence in this study were also reported from southern Canada (WALKER, 1953), Indiana (MONTGOMERY, 1948), and western North Carolina (WESTFALL, 1942); however, adult longevity would extend the flight season beyond the termination of emergence.

Adults of *A. grandis* have been reported during early fall in Ohio (WILLIAMSON, 1931), Indiana (MONTGOMERY, 1948), and Pennsylvania (FERRIS, 1951). This species was also observed near Highlands during late August and September after the present study (pers. obs.). In piedmont North Carolina, specimens were collected from late July (a teneral) to November, with most in September and October (pers. comm., R.D. Cuyler). In contrast, *A. grandis* was abundant and ovipositing by 15 June in Oklahoma (BICK & BICK, 1970). Some of the autumn records likely reflected the long adult life of this species (mean of 25 and maximum of 51 days) observed by BICK & BICK (1970), although the late season flight in the present study was not due to adult longevity. The early emergence and rapid hatching of eggs in the Oklahoma population indicate an overwintering larval stage. Possibly the life cycle has sufficient plasticity to pass the winter in either the larval or egg stage depending on local climatic conditions, since the flight season of the Oklahoma population differs considerably from that observed in other areas of the United States. Also, the wide distribution of *A. grandis*, from northern South America to the northeastern United States (MONTGOMERY, 1948), suggests the likelihood of life history variation.

The *L. disjunctus* populations in the present study represented the subspecies *australis* (pers. comm., M.J. Westfall, Jr.). However, the observed emergence from late July to early September corresponds more closely to the flight season reported for the subspecies *disjunctus*. WALKER (1952, 1953) noted that the flight season of *australis* was very different from that of *disjunctus*, the former having a long flight season with peak emergence in the spring, approximately two months earlier than *disjunctus*, which usually begins emerging in July and extends to fall. SAWCHYN & GILLOTT (1974b) observed a flight season from early July to mid-August of the subspecies *disjunctus* in Canada. In Indiana (MONTGOMERY, 1948) and North Carolina (pers. comm., D.R. Paulson) the flight season of *L. disjunctus* (presumably *australis*) began in early spring and extended into the fall. Paulson observed adults at a pond near coastal North Carolina on 12 December, a very late flight date, and also collected several larvae in the last three instars. These larvae apparently were destined to overwinter, since the absence of tenerals and exuviae indicated that emergence was terminated. However, no larvae could be found during the winter at a site in piedmont North Carolina where adults were commonly collected. The contrasting evidence on the life cycle of *L. disjunctus* suggests that further study is needed.

The similar degree of synchrony in the emergences of *L. vigilax* and *L. disjunctus* was not expected, since *L. vigilax* overwintered in a relatively wide range of larval instars, whereas *L. disjunctus* presumably spent the winter in the egg stage. The emergence of *L. vigilax* may be somewhat synchronized by having progressively higher temperature thresholds for development in successively later instars as reported for *L. eurinus* (LUTZ, 1968b). Rising spring temperatures would effect some degree of synchrony, since younger larvae would begin development first, followed progressively by succeeding, more advanced larvae. And, the length of emergence in *L. disjunctus* was considerably longer than that of other *Lestes* species which have an overwintering egg diapause (GOWER & KORMONDY, 1963; SAWCHYN & CILLOTT, 1974a, 1974b). Both of these factors apparently contributed to the similar, relatively unsynchronized emergences of *L. vigilax* and *L. disjunctus*. The sex ratios of both *L. vigilax* and *L. disjunctus* were near equality. Similar values were found in *L. eurinus* (LUTZ, 1968a), but *L. rectangularis* had a ratio of 2 males to one female (GOWER & KORMONDY, 1963).

The present study has shown basic similarities as well as differences in the life cycles of the three species of lestids in North Carolina and those of members of this family described in other studies. Additional research is needed to clarify the often conflicting evidence on the life cycles of *L. disjunctus* and *A. grandis*. The diverse life cycles exhibited by different species of Lestidae provide an excellent opportunity to study the effects of environmental factors on life history events and to broaden the complex picture of seasonal regulation revealed in previous investigations (LUTZ, 1968b; SAWCHYN & CHURCH, 1973; SAWCHYN & GILLOTT, 1974a, 1974b).

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