THE LIFE HISTORY OF *LESTES SPONSA* (HANSEMANN): LARVAL GROWTH
(ZYGOPTERA: LESTIDAE)

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The larval growth was monitored in 3 separate populàtions. *L. sponsa* typically has 10 instars; larval life lasted from between 68 and 83 days. The sex ratio is close to equality initially, becomes male biased, but is female biased at emergence. Females enter the final instar before males. The population with the fastest growth also showed the greatest degree of synchrony and produced significantly larger larvae than the other populations. It is suggested that food availability accounts for these differences.

INTRODUCTION

Lestes sponsa (Hans.) typically inhabits acid moorland pools in the British Isles, although it is also found in lowland ponds. It has a wide, Palaearctic distribution (LONGFIELD, 1949).

Early workers (e.g. MACAN, 1949, MACNEILL, 1951) supposed that larvae were not found in winter because of cryptic, mud-dwelling habits and it was left to CORBET (1956a) to clarify the basic life history of the species, now known to be similar to that of other members of the Lestidae in Europe (e.g. PIERRE, 1904, on *L. viridis* (Vander L.); WESENBERG-LUND, 1913, on *L. dryas* Kirby), North America (e.g. SAWCHYN & GILLOTT, 1974a, 1974b, on *L. congener* Hag., *L. unguiculatus* Hag., *L. disjunctus* Sel. and *L. dryas* again, but not *L. eurinus* Say, LUTZ, 1968) and Asia (UEDA, 1978, on *L. sponsa*). *L. sponsa* passes winter in diapause in the egg stage (CORBET, 1956b). In southern England eggs hatch in mid-April and larval growth is completed in two to three months (CORBET, 1956a).

The aim of the present paper is to investigate the life history in more detail, to look at larval growth rates in the field, the number of instars involved, the degree of synchrony in larval growth, and between-site variations in larval size and sex ratio throughout the season.

STUDY SITES

The growth of *L. sponsa* larvae was studied at two sites in Cheshire, England; in 1981 we studied a pond at Sound Heath (Nat. grid ref. SJ 619480) and in 1982, a pond at Malpas (Nat. grid ref. SJ 462450). We were also able to use unpublished data collected in 1967 by JHL from a pond at Brasside near Durham, northern England (Nat. grid ref. NZ 291451). Occasional samples were also taken from Brasside in 1974 (DJT) and Malpas in 1981 (JP).

The Brasside site was a small, weedy pond (now filled) lying in abandoned clay workings. Full details of the pond can be found in LAWTON (1971). The Sound Heath pond is a shallow (less than 0.5 m deep) peatbottomed pond dominated by *Typha latifolia* L. with very little open water. The Malpas pond is a flooded marl pit with a clay bottom about 1 m deep dominated by *Potamogeton natans* L.

METHODS

Larvae were sampled with a pond net, mesh size 0.3 mm used in a conventional way. The contents of the net was emptied into a white enamel tray from which the larvae were extracted. Each larva was placed in a separate glass tube containing filtered pond water and taken to the laboratory. Individuals were isolated since *Lestes* larvae are reported to be cannibalistic (FISCHER, 1961).

In the laboratory the head widths, wing bud lengths, hind tibia and body lengths of the larvae were measured where possible. Measurements were made using a binocular microscope with an eyepiece micrometer. The sex of larger larvae was noted.

RESULTS

Figure 1 a-c shows the frequency histograms of *Lestes* larval head widths for each of the sites on each sampling occasion. Figure 2a-b shows the combined data for Sound (2a) and Malpas (2b) plotted as wing bud length against head width.

These data indicate that *L. sponsa* typically has ten larval instars (counting the pronymph as instar 1). These instars separate fairly readily on head width (Fig. 1), but the later instars are more clearly defined from the plots of wing bud length against head width (Fig. 2).

The first date on which *L. sponsa* larvae were found in the pond at Brasside was 18 April when all animals collected clearly belonged to the first free instar (instar 2), mean head width 0.488 mm ($\pm$ 0.002 S.E.). The high degree of synchronization suggests that the hatch had taken place only a day or two earlier.

In Cheshire the first date on which larvae were sampled was 15 April (Malpas 1981) when all larvae were in instars 3 and 4. At Sound in 1981 second instar larvae were still present on the first sampling occasion (5 May) but most had reached instar 4 and one was in the fifth instar.
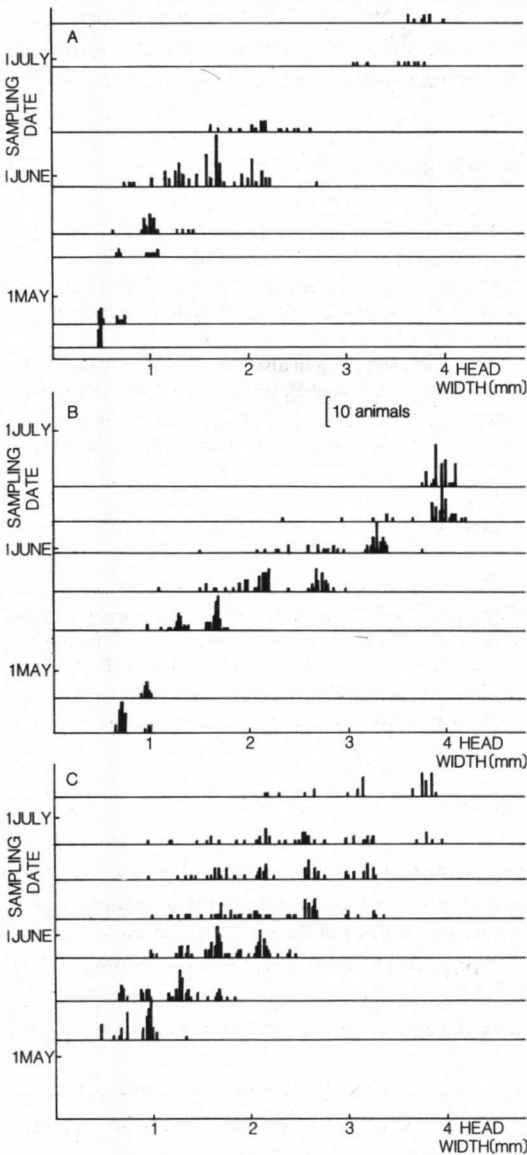
Fig. 1. Size frequency histograms of head widths of larval samples at: (a) Brasside; — (b) Malpas;   (c) Sound. All the Brasside samples were collected in 1967 except 29 May which was collected in 1974. All the Malpas samples were collected in 1982 except 15 and 25 April (1981). All the Sound samples were collected in 1981.

From a plot of mean head width against number of days after 15 April (Fig. 3), crude estimates of hatching dates can be made. From these estimates and from data on emergence, the best estimates of average larval duration at the three sites are 83 days (Brasside), 79 days (Sound) and 68 days (Malpas).

From Figures 1 and 3 it is clear that the growth rate of *L. sponsa* at Malpas was greater than at Sound or Brasside. It is interesting that the degree of synchrony is greatest also at Malpas, that is there is much less variation in mean head width on any sampling date.

Table 1 summarises the mean head widths and wing bud lengths of *L. sponsa* larvae of each sex for instars 6 to 10 at Sound and Malpas. Data are also included for final instar larvae at Brasside. As well as having a faster growth rate, the larvae at Malpas are significantly bigger (greater head widths) than those at Sound in the last three instars ($p < 0.02$ in each case). The differences in wing bud length are equally pronounced. From Figure 3 it was clear that growth rates at Brasside and Sound were similar, so that it is perhaps significant too that the head widths of Brasside larvae
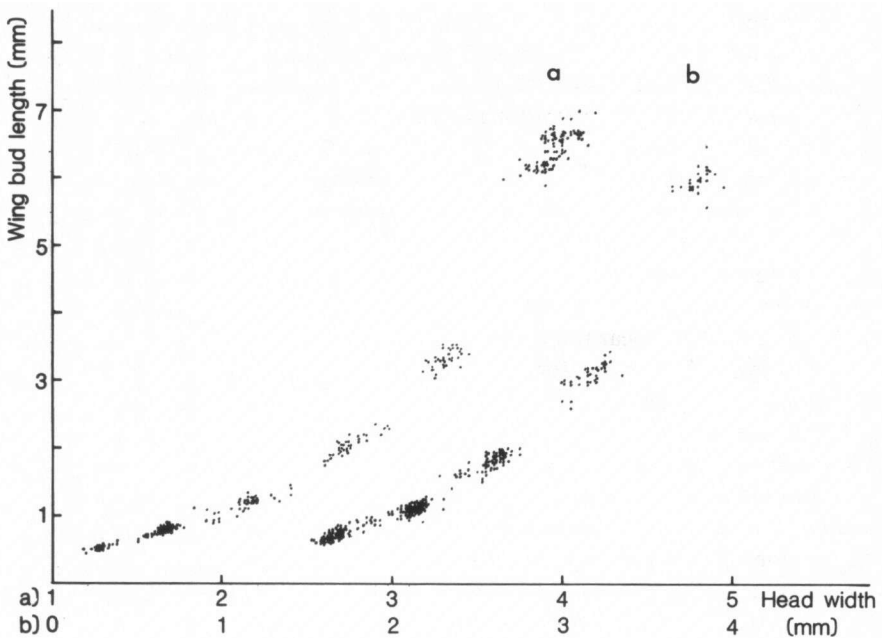
Fig. 2. The relationship between wing bud length and head width for samples of *Lestes sponsa* at: (a) Malpas (instars 5-10); — (b) Sound Heath (instars 6-10). Note that there are two scales on the abscissa.

Table I

Mean head widths and wing bud lengths with standard errors ($\pm$ 1SE) for *Lestes sponsa* larvae of each sex for instars 6 to 10 at Sound (1981) and Malpas (1982). (Also shown at the bottom of the table is the mean head widths for males and females in the final instar at Brasside, 1974)

	Sound 1981				Malpas 1982			
Instar	Head width (mm)		Wing bud length (mm)		Head width (mm)		Wing bud length (mm)	
	♂	♀	♂	♀	♂	♀	♂	♀
6	1.69±0.016	1.68±0.012	0.65±0.044	0.60±0.053	1.65±0.013	1.65±0.013	0.77±0.017	0.76±0.012
	(n = 34)	(n = 29)			(n = 27)	(n = 23)		
7	2.10±0.010	2.13±0.011	1.08±0.015	1.12±0.011	2.16±0.020	2.08±0.043	1.19±0.024	1.13±0.042
	(n = 33)	(n = 32)			(n = 30)	(n = 12)		
8	2.57±0.015	2.57±0.021	1.76±0.024	1.79±0.026	2.71±0.029	2.75±0.019	2.01±0.042	2.07±0.030
	(n = 34)	(n = 26)			(n = 15)	(n = 20)		
9	3.14±0.022	3.18±0.020	3.01±0.048	3.16±0.032	3.28±0.014	3.34±0.022	3.26±0.014	3.44±0.024
	(n = 16)	(n = 21)			(n = 19)	(n = 16)		
10	3.74±0.022	3.82±0.015	5.92±0.036	6.02±0.049	3.88±0.018	3.99±0.010	6.19±0.022	6.62±0.023
	(n = 8)	(n = 17)			(n = 28)	(n = 53)		

Brasside 1974: Mean head widths for final instar larvae: male 3.69 mm $\pm$ 0.026 (n = 6), — female 3.75 mm $\pm$ 0.018 (n = 9)

were closer to those of Sound than Malpas.

There were consistent sex differences in head width and wing bud length in the last three instars at both Sound and Malpas; females were larger than males. These differences were statistically significant ($p < 0.05$) for wing bud length, but not quite so ($0.10 > p > 0.05$) for head width.

Figures 4 and 5 indicate the larval sex ratio through the season. Figure 4 shows the percentage of males present at each sampling. The curves show the same pattern at both Sound and Malpas; the percentage of males reached a peak at around 60%, then declined steadily until sampling ceased. There was a similar decline between the last two instars at Brasside. At first sight there would appear to be two possible explanations for the falling proportion of males towards the end of larval life. The first is that males and females suffer differential mortality with males having a higher mortality rate; the second is that males emerge before females. We attempted to resolve this question by replotting the data as the percentage of males present in each instar on each sampling occasion (Fig. 5). If we consider the data for Sound, it shows (with the exception of one point for instar 7, and the whole of instar 10, both based on very small samples) the same picture as in Figure 4, but now more easily interpretable. When larvae first enter an instar, the sex ratio is female biased

Fig. 3. The relationship between mean head width and time in days after 15 April during the larval growth season. ● Malpas 1982; — O Malpas 1981; ☐ Sound 1981; — ■ Brasside 1967; — △ Brasside 1974.

when it is the modal instar of the sample, and becomes female biased again when most animals have moulted to the next instar. There were no males the first time final instar larvae were collected; as the first females emerged, the sex ratio became more male biased. At Malpas the picture is less clear; the growth rate was so fast in relation to the sampling intervals that only two points are available for each instar/sampling occasion combination.
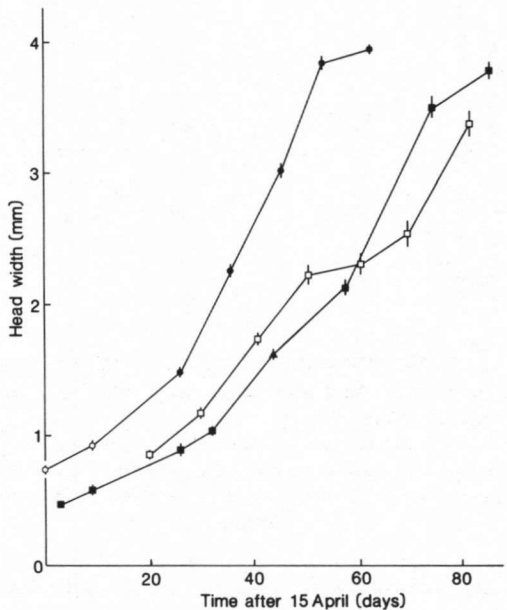
In summary, the sex ratio is close to unity at instar 6, and is female biased by instar 10, indicating that males may suffer greater mortality. Females enter the final instar before males and presumably emerge first.

We tested our data to see if animals in a given instar early in the season were the same size as animals present in that instar later on. We found no evidence at either of our main sites that animals differed in size within a given instar at different stages of the season.
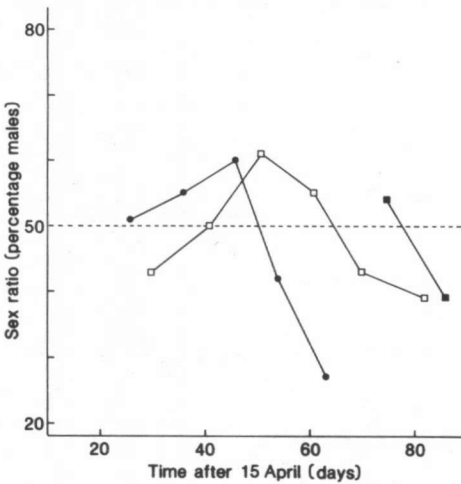
DISCUSSION

Fig. 4. The relationship between larval sex ratio (expressed as percentage of males) and time in days after 15 April during the larval growth season. ● Malpas; — □ Sound; — ■ Brasside.

Growth in the three different populations of *Lestes sponsa* was broadly similar, but differed in detail. The Malpas population showed a high degree of synchrony in growth which was not shown by the Sound population. It is clear from Figure 1 that eggs laid at Sound must have undergone a staggered hatching; larvae from both instar 4 and the final instar were present in the sample collected on 24 June 1981. That the hatching was so staggered at Sound is surprising in the light of Corbet's work on diapause in *Lestes* eggs (CORBET, 1956b).

Larval life lasted between an estimated 68 days at Malpas to 83 days at Brasside. This agrees with CORBET's (1956a) estimation of 71 days for larvae at a pond in Berkshire, southern England with hatching date of 15 April. Other estimates of larval life can be made from data in FISCHER (1966, 1967); her larvae hatched about 24 April and emerged some 90 days later. FISCHER (1972) was able to grow *L. sponsa* larvae from instar 2 to emergence in 38 days at 20° C in the laboratory given a plentiful food supply.

The degree of synchrony of larval development was less pronounced in our study and in CORBET's (1956a), than in work on three *Lestes* species on the Canadian prairies. There were seven instars present at once in one of our samples from Sound, at least five instars in one of Corbet's samples and four from the least synchronous sampling occasion at Malpas. SAWCHYN & GILLOTT (1974a, 1974b) never found more than three instars present in any sample for *L. disjunctus* and *L. unguiculatus* and found typically four instars for *L. congener*.

Sex ratios in Odonata have been reviewed by CORBET (1962) and LAWTON (1972). Lawton thought it would be "interesting to know at which point in development observed imbalances in larval sex ratio became apparent". His own data on *Pyrrhosoma nymphula* (Sulz.) and *Coenagrion puella* (L.) suggested that the slight excess of males which he observed in each case was apparent as soon as larvae of both species could be reliably sexed. This seems also to be the case with another population of *C. puella* studied by PARR & PALMER (1971). This was not the case, however, with *L. sponsa*. The data of LAWTON (1972) and PARR & PALMER (1971) are comparable with the form of presentation in Figure 4. *Lestes* larval samples showed an increase in proportion of males from near equality once larvae could be sexed, but this trend was reversed towards the end of the larval period. In all three populations studied the final instar larval sex ratio immediately prior to emergence was heavily female biased. Imbalances in sex ratio in *L. sponsa* then, seem to be the result of differential larval mortality in later instars of Zygoptera, a situation not found in earlier studies. GOWER & KORMONDY (1963) found a female biased sex ratio at emergence in *L. rectangularis* (29.8% males; p < 0.001), but LUTZ (1968) from larval collections and collections of exuviae at emergence found no significant departure from equality in *L. eurinus*.
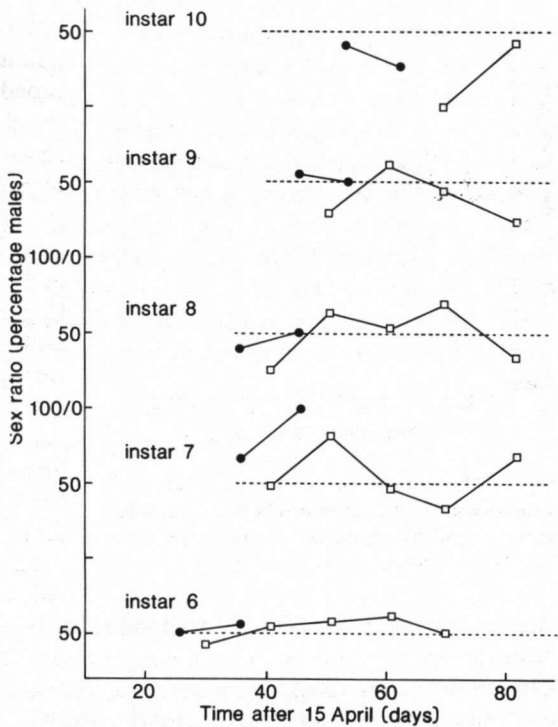

Fig. 5. The relationship between larval sex ratio (expressed as percentage of males) for each instar on each sampling occasion and time in days after 15 April during the larval growth season. ● Malpas; — ■ Sound.

Finally we would like to consider the sizes of larvae in the final instar at our two

main sites (summarized in Tab. I), the growth rates and the degree of synchrony in growth curves. LAWTON et al. (1980) showed that when larvae of *Ischnura elegans* (Vander L.) were maintained at a range of prey densities in the laboratory, those at high prey density had faster development rates than those at low prey density. Further, at very low densities the percentage increase in head width at the moult became markedly reduced. These changes in development rate and reduced percentage increase in head width occurred over a relatively narrow range of prey densities. The reduced growth rate, relative lack of synchrony in growth curve, and reduced size of larvae in instars 8 to 10, in particular, at Sound all point to a population which is under food stress in at least some part of its life cycle. The Malpas population on the other hand showed a rapid, relatively synchronized growth pattern and produced large larvae.

The growth curve from Brasside is based on much smaller samples than those from Sound and Malpas, so we are not able to comment on the degree of synchrony. Nevertheless, it is clear that the growth rate is slower and the larvae smaller than in the Malpas population. It is not clear from our limited data whether this reduction in growth rate/larval size at the more northerly Brasside population is the result of food availability. It is likely that there is some effect of temperature on feeding rate and consequently growth rate (cf. THOMPSON, 1978). We hope to show in a subsequent publication how temperature and prey availability interact to influence development rates in *L. sponsa* larvae in the laboratory.

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