

SEX RATIOS IN ODONATA LARVAE, WITH PARTICULAR REFERENCE TO THE ZYGOPTERA

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Larval sex-ratios were investigated in populations of *Pyrrosoma nymphula* (Sulz.) and *Coenagrion puella* (L.) from a point when larvae were approximately half-grown until just prior to, or including adult emergence. In both species there was a very small (averaging 52.0 and 54.4% respectively) but statistically significant excess of male larvae present throughout this period of development. These results are compared with other work on Odonata sex-ratios. Including the present study, an excess of male larvae is reported in eight of the available records for Zygoptera, and this imbalance is statistically significant in five of the records, involving two species. Another five records for the Zygoptera show an excess of female larvae, with the imbalance being statistically significant in two cases. There is an indication that sex-ratio imbalances involving an excess of females are larger than those involving an excess of males. These results are in direct contrast to the situation in the Anisoptera, in which all twenty-one of the available records show an excess of female larvae. The reasons for the difference between Anisoptera and Zygoptera in this respect are uncertain; nor are the causes of the sex-ratio imbalances in Odonata understood.

INTRODUCTION

A small, but consistent excess of female larvae in populations of Anisoptera at the time of adult emergence was demonstrated by CORBET (1962), and a possible selective advantage in this imbalance discussed by JOHNSON (1963). The only data available to Corbet on Zygoptera were for *Pyrrosoma nymphula* (Sulz.) in which the situation was the reverse of that found for the Anisoptera, with males forming 63.0 and 53.7 percent of the population at emergence in two

different years.

The present paper presents new information on larval sex-ratios in two species of damselfly, *Pyrrhosoma nymphula* (Sulz.) and *Coenagrion puella* (L.); in order to determine at which point in larval development an imbalance (if any) in the sex-ratio became apparent, larvae of both species were sampled throughout their development in the field. The results of this work are compared with other published information on sex-ratios in both the Anisoptera and the Zygoptera that has become available since CORBET's (1962) review.

METHODS

In newly hatched Odonata larvae there are no signs of the external genitalia, which develop gradually at successive moults (DEFOSSEZ, 1970). Preliminary observations during the present study suggested that initially, in both sexes, the external genitalia developed as two small points on the ninth abdominal segment and hence, that at first all larvae were male in appearance; female larvae then developed additional appendages on the eighth and ninth segments. The point at which female larvae could be reliably distinguished from male larvae was determined for both species (see results) and sex-ratios were only calculated for larvae larger than this critical size.

Pyrrhosoma larvae were collected from two small ponds (B and F) at Braside, adjacent to Durham City, County Durham. Descriptions of these ponds are given by LAWTON (1970, 1971). A sample of *Pyrrhosoma* larvae was collected from pond B in March 1966; thereafter pond B was sampled at approximately monthly intervals for two years between July 1966 and July 1968, whilst larvae in pond F were collected for just over one year, between February 1967 and May 1968. Sampling of larvae was carried out by means of a net on a stratified random basis (LAWTON, 1970, 1971). Exhaustive collections of exuviae were made daily over approximately half the area of pond B throughout the period of adult emergence in 1967 and 1968, and over the whole of pond F in 1967. Virtually all the larvae emerging from both ponds did so on emergent *Juncus* and *Eleocharis* stems close to the pond edge, and with practice exuviae were relatively easy to find. The collections therefore provided a very reliable estimate of the sex-ratio at the end of larval life.

Coenagrion larvae were collected from a small pond situated on Oxford University's Wytham Estate, Berkshire. A description of the pond, (pond 1) is given by ELTON (1966, p. 356). *Coenagrion* larvae were collected with a net between February 1967 and July 1968 at monthly or bi-monthly intervals, from randomly located sample points in the *Potamogeton* growing in the centre of the pond. Because of the nature of the habitat, most of the larvae emerged well out into the centre of the pond and reliable collections of exuviae could not be made during the emergence of *Coenagrion*.

All *Pyrrhosoma* and *Coenagrion* larvae were brought back to the laboratory for measurement, sexing (and in the case of *Coenagrion* to confirm identification) and returned to the pond at the sampling point within 24-48 h of collection.

RESULTS

The development of the external genitalia is summarised in Figure 1. Because females of both species were initially male in appearance (cf. above) the proportion of 'male-type' larvae was at first high. Some females could be identified in larvae greater than 4 mm long and in larvae of 6 mm and above the samples indicated a sex-ratio that was maintained throughout the rest of development. This suggests that all females and genuine males of both species could be distin-

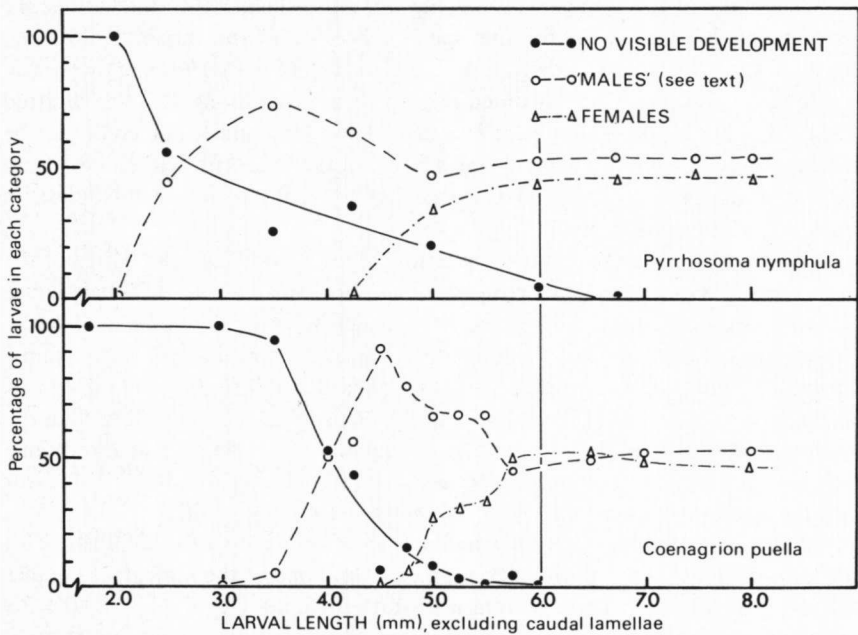


Fig. 1. The development of the external genitalia in larvae of *Pyrrhosoma nymphula* (Sulz.) and *Coenagrion puella* (L.) based on larvae collected in the field. The figure shows the proportion of larvae, in various size categories, that showed no development of the external genitalia, or were male or female in appearance. Larvae of both species can only be reliably sexed at a length (excluding the caudal lamellae) of 6 mm and above.

guished in larvae that were 6 mm or more in length. Larvae less than 6 mm long were therefore excluded from the analysis.

Pyrrhosoma larvae in ponds B and F showed the typical two year life-cycle described by CORBET (1957b), two generations or year-classes being present in any one year. Growth was extremely well synchronised and year-classes, designated by the year in which the larvae hatched, remained distinct throughout development (LAWTON, 1971). Sex-ratios could therefore be calculated for all the larvae in each year-class between late July (as they entered their second year of development) until emergence. Because the number of larvae collected on each sampling occasion tended to be fairly small, samples from two (or more) months have been pooled in order to provide more reliable estimates of the sex-ratio at various stages of larval development.

A majority of the *Coenagrion* larvae showed a one year life-cycle, hatching in July and emerging the following summer, although a part of each year-class grew more slowly and took two years to develop, merging with the more rapidly growing larvae of the next generation (Fig. 2). This is identical to the life-history reported by PARR (1970) for this species. Because of the variability in larval growth rates, sex-ratios in this species (unlike those for *Pyrrhosoma*) were calculated from samples which included two different generations, and also omitted from the analysis larvae that were less than 6 mm long and hence could not be reliably sexed. Differential growth rates between the sexes (for which there is, at present, no reliable evidence in Odonata larvae) could therefore introduce an error into these calculations.

Tables I and II summarise the sex-ratios found for both species. Three of the fifteen samples calculated for *Pyrrhosoma* showed a small excess of female larvae and the remaining twelve a small excess of males, with no obvious trends during development. Whilst none of the individual samples departed significantly from a sex-ratio of unity, the ratio of the total number of males to the total number of all the larvae collected (1274:2450 or 0.520) is just significantly greater than the expected ratio of 0.5 when the two are compared using the normal approximation to the binomial distribution ($0.05 > P > 0.02$) (BAILEY, 1959). It is clear that the sex-ratio imbalance in *Pyrrhosoma* was extremely small.

All the eleven samples for *Coenagrion* showed an excess of male larvae, with again no obvious trends during development. Only one of the individual samples showed a significant departure from a sex-ratio of unity (April 1970; $0.01 > P > 0.002$) although the ratio of the total number of males to the total number of all larvae collected (736:1325 or 0.544) is highly significantly different from an

Fig. 2. The life-history of *Coenagrion puella* (L.) in a pond on the Wytham Estate (Berkshire). The histograms are size-frequency histograms for various sampling dates (the base of each histogram being the data of sampling). Most larvae take one year to develop, but a proportion of each generation takes two years.

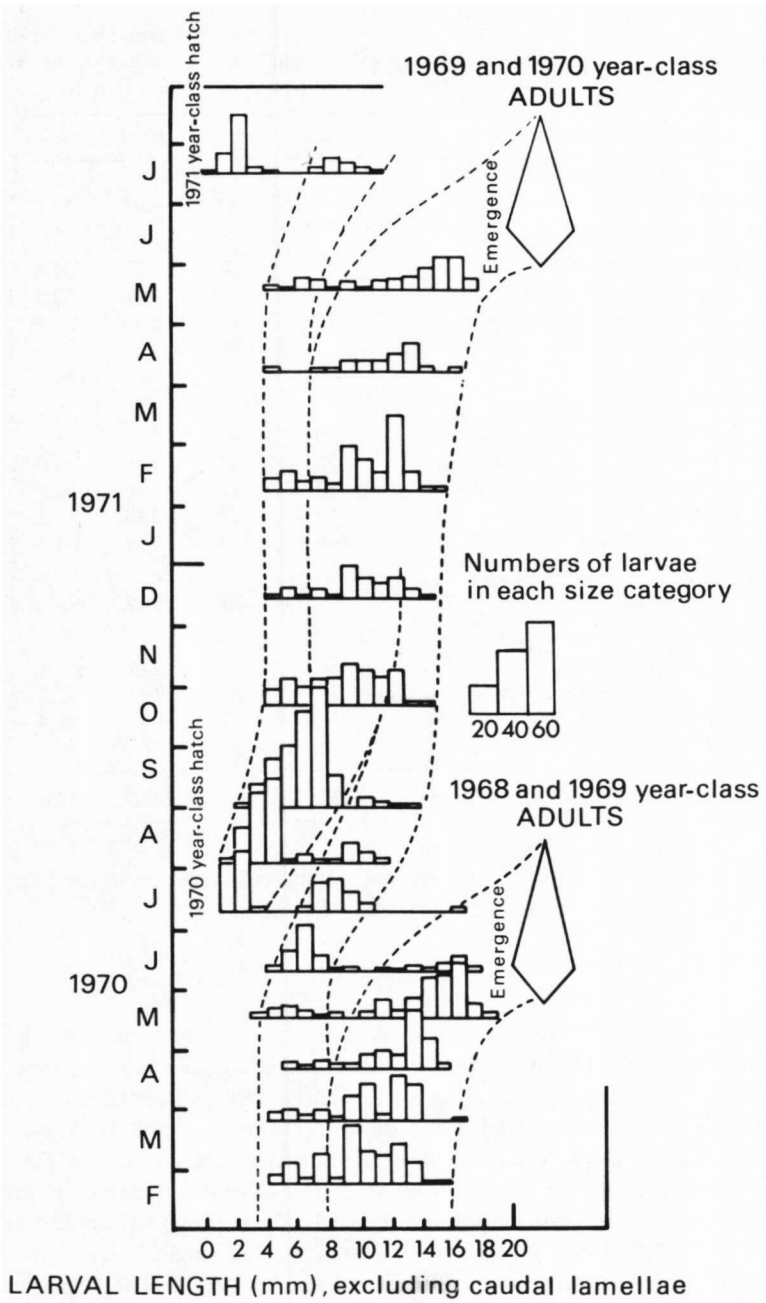


Table I

Sex-ratios in the larvae of *Pyrrhosoma nymphula*, in two different ponds at Brasside (County Durham), based on larvae collected with a pond-net, or on collections of exuviae at emergence; year-classes are designated by the years in which they hatched

Date of collection	♂	♀	Total	%♂♂
<i>1964 year-class, pond B</i>				
March 1966	126	119	245	51.4
<i>1965 year-class, pond B</i>				
July - September 1966	59	67	126	46.8
October - November 1966	73	67	140	52.1
December 1966 - March 1967	22	16	38	57.9
April - May 1967	No collection			
Emergence (May - June 1967)	70	68	138	50.7
<i>1966 year-class, pond B</i>				
August - September 1967	59	48	107	55.1
October - November 1967	36	40	76	47.4
December 1967 - January 1968	52	38	90	57.7
February - May 1968	67	63	130	51.5
Emergence (May - June 1968)	406	383	789	51.5
<i>1965 year-class, pond F</i>				
Emergence (May - June 1967)	75	74	149	50.3
<i>1966 year-class, pond F</i>				
August - September 1967	66	51	117	56.4
October - November 1967	78	63	141	55.3
December 1967 - February 1968	41	42	83	49.4
March - May 1968	44	37	81	54.3
Totals	1274	1176	2450	52.0

expected ratio of 0.5 when the two are compared using the normal approximation to the binomial distribution ($0.002 > P > 0.001$).

DISCUSSION

Tables III and IV summarise information which has become available since CORBET's (1962) review of Odonata sex-ratios. The conditions imposed by Corbet for reliability have been relaxed slightly, but samples of less than 100 individuals have been omitted; (the only exception are CORBET's own data (1962) on *Pyrrhosoma* where $n = 97$). In some instances the data in Tables III and IV represent pooled samples from several years and/or habitats; where this was done by the original author the data have been presented unchanged e.g. PARR & PALMER (1971). In other instances, the original data have been pooled for presentation in the present work e.g. JOHNSON (1968); pooling has

Table II

Sex-ratios in the larvae of *Coenagrion puella*, in a pond on the Wytham Estate (Berkshire), based on larvae collected with a pond-net; samples contain larvae of more than one generation because of variations in their rates of development

Date of collection	♂	♀	Total	%♂♂
<i>1968 and 1969 year-classes</i>				
February 1970	74	68	142	52.1
March 1970	69	48	117	59.0
April 1970	63	36	99	63.6
May 1970	85	76	161	52.8
June - July 1970	62	61	123	50.4
<i>1969 and 1970 year-classes</i>				
August 1970	101	82	183	55.2
October 1970	75	63	138	54.3
December 1970	42	35	77	54.5
February 1971	75	74	149	50.3
April 1971	32	31	63	50.8
May 1971	58	42	100	58.0
Totals	736	616	1352	54.4

Table III

A summary of the available information on sex-ratios in larval Anisoptera; only data published since, or not included by CORBET (1962) are included and small samples have been excluded. (Species are arranged in order of their departure from a sex-ratio of unity)

Species	Sampling method	n	%♂♂	References
<i>Oplonaeschna armata</i>	Exuviae at emergence	130	37.7	JOHNSON, 1968
<i>Sympetrum vicinum</i>	Ditto	261	37.9	KORMONDY & GOWER, 1965
<i>Leucorrhinia rubicunda</i>	Ditto, 1960	438	40.0	PAJUNEN, 1962
<i>Tetragoneuria cynosura</i>	Ditto	269	45.4	KORMONDY, 1959
<i>Leucorrhinia dubia</i>	Ditto, 1959	2295	45.6	PAJUNEN, 1962
<i>Oplonaeschna armata</i>	Larval collections (half-grown individuals)	182	46.8	JOHNSON, 1968
<i>Leucorrhinia dubia</i>	Exuviae at emergence, 1960	1398	47.1	PAJUNEN, 1962
<i>Leucorrhinia rubicunda</i>	Ditto, 1969	350	48.3	PAJUNEN, 1962
<i>Anax junius</i>	Ditto	164	48.2	TROTTIER, 1966

only been carried out if the individual samples all showed a similar imbalance in the sex-ratio.

The records for the Anisoptera larvae again all show a consistent excess of females and there seems little doubt that this is a general phenomenon for which there are now twenty-one records involving some fifteen species. The situation in the Zygoptera is more complex and the proportions of male larvae were therefore analysed for significant departures from an expected proportion of 0.5. In all, five records (involving five species) showed an excess of females (as in the Anisoptera) and in two of these the departure was statistically significant, whilst eight records (five species) showed an excess of male larvae (the opposite of the situation found in the Anisoptera) and in two species (involving five records) the departures were again statistically significant. There therefore appears to be a considerable difference between the Zygoptera and the Anisoptera in this respect.

Consideration of the records for the Zygoptera (irrespective of their statistical significance) provides some indication that the largest departures from equality in the sex-ratio are observed in those species with an excess of females and that (with the exception of Corbet's records for *Pyrrhosoma*) the size of the departures from an equal number of both sexes tend to be rather smaller in those situations involving an excess of males. Clearly, however, more extensive data are required to establish this point with any certainty. Finally, it is obvious that only the more substantial departures from equality in either direction, whatever their statistical validity, are likely to be of much biological significance.

Sex-determining mechanisms in nearly 400 species of Odonata are reviewed by KIAUTA (1969), who showed that in almost all cases they are of the XO-XX type, in which the male is the heterogametic sex. Any imbalance in the primary sex-ratio under this system is extremely unlikely (HAMILTON, 1967). Because of this, and because recent theoretical considerations by LEIGH (1970) suggest that differential adult mortality between the sexes (of the type seen in Odonata; CORBET, 1952, 1962; PARR, 1965) cannot provide a means of selection for imbalance in the neonate sex-ratio, it would be interesting to know at which point in development observed imbalances in larval sex-ratio become apparent. In the present study, the slight excess of male larvae was observed as soon as larvae of both species could be reliably sexed, and persisted with no obvious change until emergence. Similar data (PARR & PALMER, 1971) suggest that this may also be true in another population of *Coenagrion puella*; comparable data are not available for any other Zygoptera nor for any Anisoptera, although 180 second-year larvae of *Oplonaeschna* collected by JOHNSON (1968) showed an excess of female larvae, which was also observed in larvae at emergence one year later (Table III).

In many insects, the homogametic sex is reputedly the more viable under adverse conditions, for example at high population densities (KLOMP, 1964).

Table IV

A summary of the available information on sex-ratios in larval Zygoptera; small samples have been excluded from the analysis. (Species are arranged in order of their departure from a sex-ratio of unity. Sex-ratios have been analysed using the normal approximation to the binomial distribution; cf. BAILEY, 1959)

Species	Sampling method	n	Number of ♂♂	%♂♂	d	P	References
<i>Lestes rectangularis</i>	Adults and exuviae at emergence	104	31	29.8	4.12	.001>P	GOWER & KORMONDY, 1963
<i>Ischnura verticalis</i>	Exuviae at emergence, 1961	189	65	34.4	4.29	.001>P	KORMONDY & GOWER, 1965
<i>Enallagma ebrium</i>	Exuviae at emergence, 1961	209	92	44.0	1.73	0.1>P>0.05	KORMONDY & GOWER, 1965
<i>Lestes eurinus</i>	Collections of larvae	783	377	48.2	1.04	P>0.1	LUTZ, 1968
<i>Enallagma cyathigerum</i>	Exuviae at emergence	1889	943	49.9	0.07	P>0.1	PARR & PALMER, 1971
<i>Ischnura elegans</i>	Collections of larvae	1404	722	51.4	1.07	P>0.1	PARR & PALMER, 1971
<i>Lestes eurinus</i>	Exuviae at emergence	296	154	52.0	0.70	P>0.1	LUTZ, 1968
<i>Ischnura verticalis</i>	Exuviae at emergence, 1962	344	181	52.6	0.97	P>0.1	KORMONDY & GOWER, 1965
<i>Pyrhosoma nymphula</i>	-	2450	1274	52.0	1.98	0.05>P>0.02	Present study
<i>Pyrhosoma nymphula</i>	Exuviae at emergence, 1953	753	404	53.7	2.00	0.05>P>0.02	CORBET, 1962
<i>Coenagrion puella</i>	-	1352	736	54.4	3.27	.002>P>.001	Present study
<i>Coenagrion puella</i>	Collections of larvae	659	375	56.9	3.55	.001>P	PARR & PALMER, 1971
<i>Pyrhosoma nymphula</i>	Exuviae at emergence, 1951	97	61	63.0	2.54	.02>P>.01	CORBET, 1962

Consistent with this generalisation would be the implication by GARMAN (in CORBET, 1962) that female Odonata may be more viable than males. It is therefore possible that the tendency for female larvae to outnumber males in Anisoptera and some Zygoptera is a reflection of the marginally greater viability of the homogametic sex. However, this simple explanation fails to take into account the different patterns of sex-ratio imbalance demonstrated for the Anisoptera and the Zygoptera. Nor does the available evidence linking changes in larval population density to changes in sex-ratio support the idea that sex-ratio imbalances may be related simply to the greater viability of females under stress – in this case high population densities. Thus the number of adult *Pyrhosoma* emerging from pond B in 1968 was approximately ten times higher than in the previous year (LAWTON, 1970), although there was no obvious change in the sex-ratio, and whilst a particularly large emergence in *Anax imperator* was associated with a slight increase in the proportion of females (CORBET, 1957a), changes in the sex-ratios of two species of Zygoptera (from an excess of females in one year to an excess of males in the following year), although based on rather small samples, were apparently associated with opposite changes in abundance of the two species (KORMONDY & GOWER, 1965). On present evidence, variations in the sex-ratios of Odonata do not, therefore, appear to be correlated in any simple way with changes in population density, a result consistent with most of the data summarised by ANDERSON (1961) for other animals of male heterogamety.

An alternative hypothesis to explain the sex-ratio imbalance of Anisoptera is that of JOHNSON (1963) who argued that equal adult numbers of both sexes, in a situation where the sexes have an unequal mating expectancy constitutes an inefficient breeding-system and could serve as a basis for the selection of unequal adult sex-ratios; the mechanism suggested is for selection of higher rates of survival in female larvae, leading to a greater proportion of females at emergence.

Theoretical considerations apart, several features of dragonfly biology present problems for this hypothesis, not least the uncertainty about what happens to the adult sex-ratio between emergence and reproduction. Only a small part of the total adult emergence may actually reproduce and there may be differential mortality and/or dispersal of adult males and females prior to reproduction (BICK & BICK, 1961; CORBET, 1952, 1957a; PAJUNEN, 1962), which will mask or alter considerably small differences in sex-ratios of the type frequently observed at emergence.

Those Zygoptera which show an excess of male larvae in the population prior to and at emergence would appear to present further difficulties for Johnson's hypothesis; this is particularly true in the case of *Pyrrhosoma* which has also been shown to have higher rates of mortality in adult females than males (CORBET, 1952, 1962), which is one of the major reasons given by Johnson for the reduced mating expectancy of adult females. It is, of course, possible that major differences between species in adult territorial and reproductive behaviour are significant in this respect, but speculation of this nature merely reinforces the impression that on present information attempts to explain larval sex-ratio imbalances in Odonata, in terms of adult breeding structure, are premature and that the biological significance of even the more substantial sex-ratio imbalances is not understood.

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