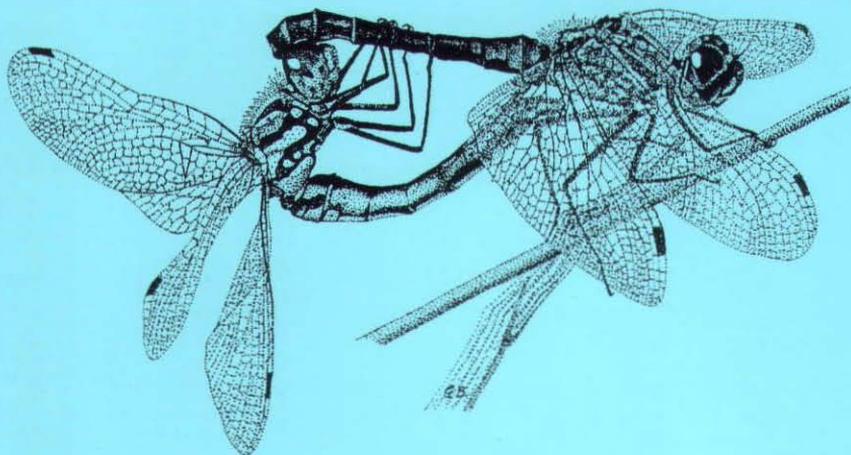




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Front cover illustration: Black Darter *Sympetrum danae* at Stoke Heath, Dorset, 4 August 1989, by Gill Brook.

The recent expansion of the Small Red-eyed Damselfly *Erythromma viridulum* (Charpentier) in The Netherlands

ROBERT KETELAAR

Dutch Butterfly Conservation, P.O. Box 506, 6700 AM, Wageningen, The Netherlands
 robert.ketelaar@vlinderstichting.nl

Introduction

In 1999, the Small Red-eyed Damselfly *Erythromma viridulum* (Charpentier) was found in Essex (Dewick & Gerussi, 2000). In 2000 and 2001, the species was recorded from many more sites and now appears to have colonized an extensive area within south-eastern England. During the last three decades, the expansion of *E. viridulum* has been recorded on the European continent (e.g. Nederlandse Vereniging voor Libellenstudie (NVL), 2002; De Knijf & Anselin, 2001; Brock *et al.*, 1997). This article describes the recent expansion of *E. viridulum* in The Netherlands.

Early Records

In the period before 1970, the occurrence of *E. viridulum* in The Netherlands was erratic, with a few records scattered over the country (Figure 1). The first record of *E. viridulum* in The Netherlands was a single male observed by C. Willemse in 1917 near Heerlen in the south-eastern part of country. In the following six decades the species remained a very rare damselfly with records in 1936, 1951, 1968, 1971 and 1972. In 1936, one male and one teneral female were captured near Wageningen on different dates in July (Geijskes, 1937), suggesting a possible breeding population. However, *E. viridulum* was not found again here in the following years despite the request of Geijskes in his article to keep looking for the species. In 1971, *E. viridulum* was again recorded near Wageningen, in the river forelands of the Rhine. Seven males and two females were collected by J. Belle, marking the first documented population of *E. viridulum* in The Netherlands.

Looking back at the records of the recording scheme in The Netherlands, it seems most likely that *E. viridulum* became established in the country during the early years of the seventies. This view is supported by the discovery of the species at three localities in the southern part of The Netherlands during a summer camp of CJN (a youth organisation for nature studies) in 1972. Unfortunately, not many recorders were active in those years, so a more precise date for the first permanent colonization is not possible. Although no further records are available until 1976, it appears likely that *E. viridulum* was present in the intermediate years.



Figure 1. Distribution of the Small Red-eyed Damselfly in The Netherlands in the period 1900-1969.

Recent Colonization

In the late seventies, it became clear that *E. viridulum* was expanding its range in The Netherlands. More than ten individuals were recorded from several locations in 1976 and 1977. This was the start of one of the most spectacular colonizations since dragonfly recording started in The Netherlands (around 1850). During the eighties, *E. viridulum* was found at many sites throughout the country (Figure 2). The swift and rapid colonization accelerated during the early nineties and, by 1995, *E. viridulum* had become the most abundant species of Odonata in some parts of The Netherlands. It now occurs in all parts of The Netherlands, including all the Waddensea Islands (Figures 3 and 4). The concentration of records in the western part of The Netherlands is a consequence of intensive searching of the abundant suitable habitat in that region.

To illustrate the scale of this increase, 75,938 individuals of *E. viridulum* were recorded during the nineties, making this species the ninth most abundant species in The Netherlands during the decade. In contrast, the population of *E. najas* was smaller with 65,792 individuals recorded (Table 1). Over the same period, *E. viridulum* was recorded from 1708 kilometre squares, ranking 19th of 65 species in terms of occupied kilometre squares.

Table 1 Number of individuals recorded of the ten most abundant species of Odonata in The Netherlands in the period 1990–2000. (Source: National Dragonfly Database; Dutch Society for Dragonfly Studies (NVL), EIS-Netherlands and Dutch Butterfly Conservation).

<i>Ischnura elegans</i>	Blue-tailed Damselfly	453,503
<i>Enallagma cyathigerum</i>	Common Blue Damselfly	436,664
<i>Lestes sponsa</i>	Emerald Damselfly	220,373
<i>Sympetrum danae</i>	Black Darter	161,062
<i>Coenagrion puella</i>	Azure Damselfly	125,262
<i>Coenagrion pulchellum</i>	Variable Damselfly	124,361
<i>Libellula quadrimaculata</i>	Four-spotted Chaser	77,658
<i>Pyrrosoma nymphula</i>	Large Red Damselfly	76,020
<i>Erythromma viridulum</i>	Small Red-eyed Damselfly	75,938
<i>Erythromma najas</i>	Red-eyed Damselfly	65,792

Habitat choice

In The Netherlands, *E. viridulum* typically inhabits small, eutrophic waters with abundant aquatic vegetation. It is found in agricultural ditches, ponds, fen waters, disconnected river branches, loam pits and chalk quarries. Unlike *E. najas*, it tends to favour waters with small aquatic plants, preferably floating mats of green algae, dense stands of Spiked Water-milfoil (*Myriophyllum spicatum*) and Rigid Hornwort (*Ceratophyllum demersum*). However, *E. viridulum* has a broad habitat spectrum and the

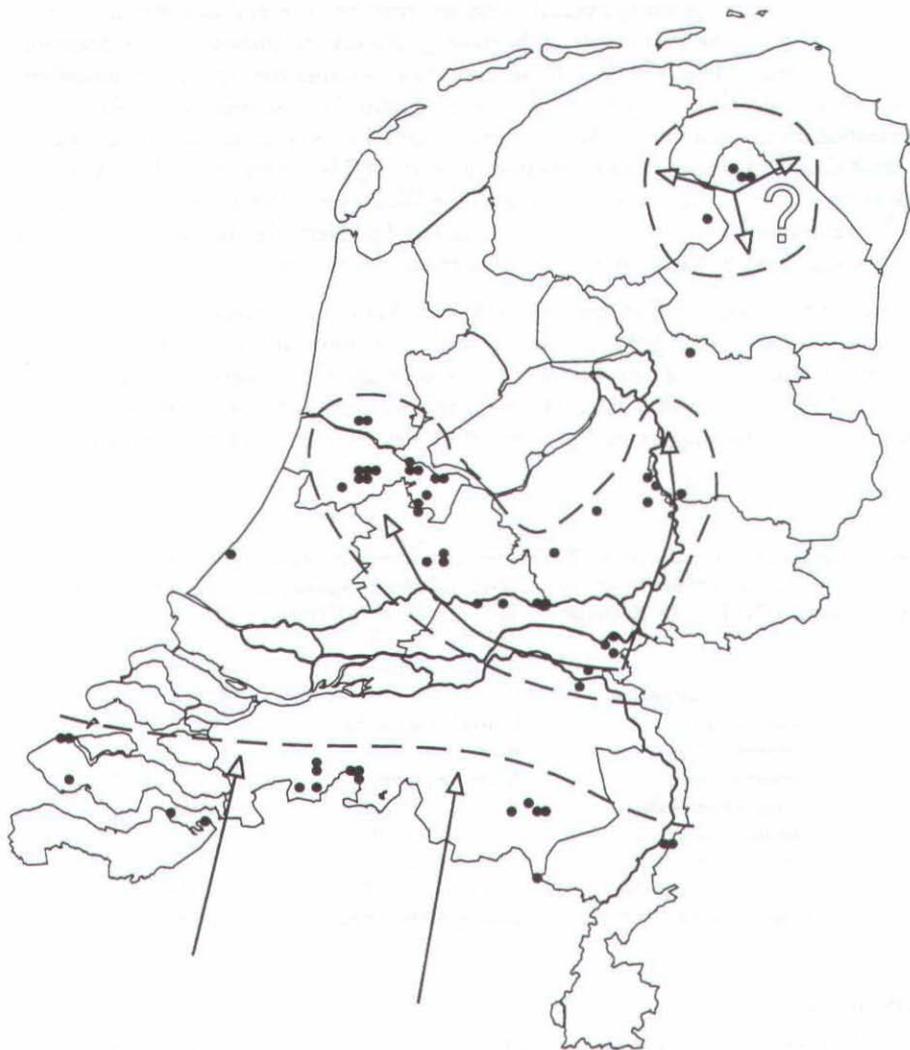


Figure 2. Distribution of the Small Red-eyed Damselfly in The Netherlands in the period 1970–1989. Arrows indicate the possible colonization of *E. viridulum* in The Netherlands via three routes.

species can also occur, albeit less frequently, on acid moorland pools (with abundant *Sphagnum* spp.), shorelines of large lakes, dune pools and running water. Except for brackish water, extremely acid bogs and large rivers, *E. viridulum* appears to be able to colonize all types of fresh water habitats where there is abundant aquatic vegetation.

Phenology

E. viridulum flies in The Netherlands during the summer. The first records usually occur at the end of May, and the numbers peak during the last two weeks of July and first two weeks of August. During June and the beginning of July, *E. viridulum* can occur together with *E. najas*, sometimes causing confusion for recorders. The last individuals are seen in the first week of October. In recent years, the flight seasons of both species of Red-eyed Damselflies seem to have developed more overlap: *E. viridulum* flies earlier and records of *E. najas* in August are no longer a rarity. This indicates that every Red-eyed Damselfly requires careful identification. Details of the identification are given by Wasscher (1999).

Pattern of expansion

It is intriguing to see that in the late seventies and early eighties *E. viridulum* had populations throughout the country (Figure 2). It might be expected that there would be a clear expansion from south to north. Although the distribution map for the period 1970–1989 shows a slight concentration in the southern and central part of The Netherlands, large populations had also established by 1976 in the northern part of the country.

However, a detailed look at the map reveals some remarkable observations, providing a possible theory as to how the expansion took place. The first population of *E. viridulum* was recorded along the river Rhine near Wageningen and then, in 1951 and 1976, new sites were found near Deventer not far from the river IJssel, a branch of the Rhine. The valley of the Rhine is well known for records of southern species occurring north of their normal range because of its favourable climatic conditions. For the Scarlet Darter *Crocothemis erythraea* (Brullé), the Rhine-valley appears to have been an important route during its expansion to the north (Ott, 1996). The Dutch records indicate this might also be the case for *E. viridulum*. The central part of The Netherlands may have been colonized from these early populations along the Rhine and its branches.

A second origin for the present Dutch population probably came from the south. In 1972, *E. viridulum* was recorded from three locations near the border with Belgium and, until the early nineties, appears to have been restricted to a rather small stretch along the border. A gap between these populations and those probably originating from Rhine populations can be seen in the distribution presented in Figure 2.

The origin of the records from the north of the country remains a bit curious. The first record here was made in 1968 and since successive records from 1970–1990 were made



Figure 3. Distribution of the Small Red-eyed Damselfly in The Netherlands in the period 1990–2001.

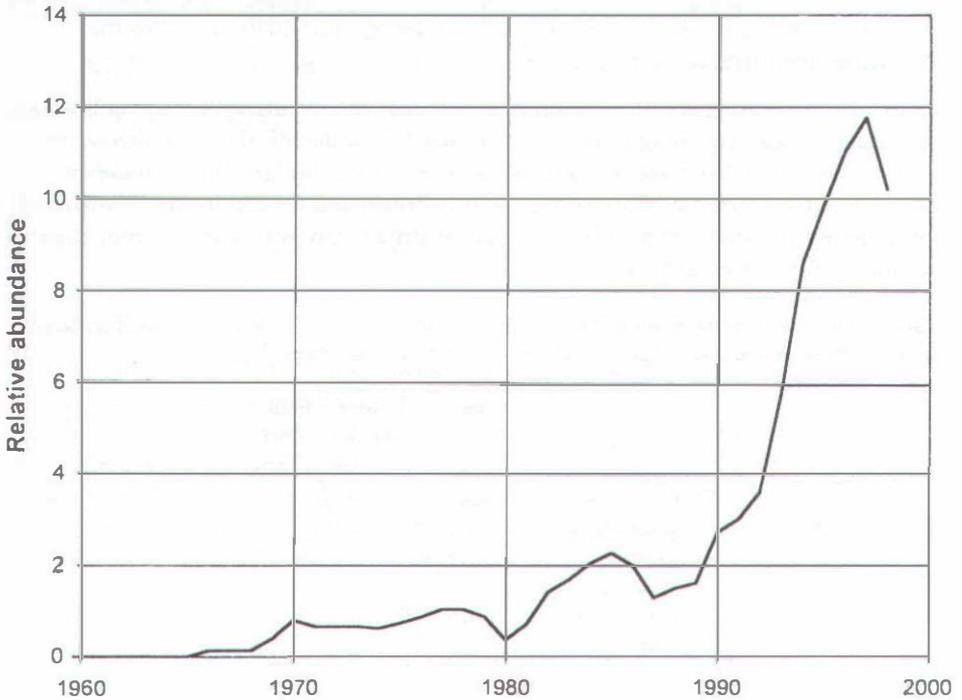


Figure 4. Three-year running average of the relative abundance of the Small Red-eyed Damselfly in The Netherlands in the last century. Relative abundance is the percentage of kilometre-squares with records of dragonflies in which the Small Red-eyed Damselfly is recorded.

in the vicinity of this record, it is tentatively suggested that all these populations originate from a single colonization event in the late sixties.

Summarizing, it is suggested that the expansion of *E. viridulum* took place via three routes: an expansion northwards from Belgium, an expansion north-westwards via the Rhine valley and a possible expansion from an outpost in the north of The Netherlands. The first two routes can be tested by a close examination of German and Belgian records, the latter will probably remain suggestive.

Colonization of Waddensea Islands

In 1995 and 1996, *E. viridulum* was recorded from six out of seven Waddensea Islands (Figure 3 and Table 2), where dune pools and agricultural ditches were occupied. The establishment of populations on all of these islands is very likely, except for Rottumerplaat and Röttumeroog where no fresh water is present. However, a record for

2001 from Rottumeroog (L. Luyten, pers. comm.) proves that the dispersal observed in 1995 and 1996 was no single event and that wandering individuals may cross the Waddensea regularly.

From a British perspective, this colonization is of particular interest because it involved dispersal over sea. Assuming colonization occurred from the mainland (or alternatively, from nearby islands) at maximum a distance of 26 km was bridged by *E. viridulum*. This is similar to the shortest distance between Great Britain and the continent (30 km). It is therefore possible that new populations in Great Britain may also originate from repeated colonization from the continent.

Table 2 First record of the Small Red-eyed Damselfly on the Dutch Waddensea Islands. The islands are sorted from west to east and are all included on the distribution maps (Figures 1–3).

	Year	Distance from mainland (km)
Texel	1996	3
Vlieland	1995	26
Terschelling	1995	15
Ameland	1995	8
Schiermonnikoog	1995	7
Rottumerplaat	1996	12
Rottumeroog	2001	12

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Thanks to Dick Groenendijk for critically reading of the manuscript and providing useful suggestions. It was the idea of Adrian Parr to write this article and he helped me with lots of technical things to materialize his idea.

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Growth and autumnal decline of feeding in captive-reared first-year larvae of the Azure Hawker *Aeshna caerulea* (Ström)

DAVID CLARKE

Burnfoot, Cumwhitton, Brampton, Cumbria CA8 9EX

Introduction

In temperate latitudes, larvae of Odonata show a decline in rate of development and food intake in late summer–autumn in preparation for surviving adverse winter conditions. I was able to characterize this by monitoring the production of faecal pellets by larvae of the Azure Hawker, *Aeshna caerulea* (Ström). Faecal pellet production correlates with prey intake (Corbet 1999: p.105). The results appear to confirm expectations that seasonal factors are involved in the regulation of the life-history of this species. The study also enabled comparisons to be made with field observations of larval growth-rates.

Methods

Four first-year larvae of *A. caerulea* collected in 1998 from NW Scotland (58°N, 5.5°W) were reared at Carlisle (55°N, 3°W) from very early instars through to cessation of feeding in October. They were collected from the field on 27 May, presumably having recently hatched from eggs laid during the preceding summer. When I received them two days later, they were between 2.06 and 2.56mm in length. Their instar numbers were not known, but were probably a mixture of 2 and 3 – counting the prolarva as 1 (see Smith *et al.*, 2000: pp.5–6).

The larvae were kept individually in transparent containers in about 150ml of water (20ml at first) with a little *Sphagnum* moss. The water, from rainwater sources, was renewed weekly. They were exposed to the normal daylight regime of 55°N, receiving light indirectly from a south-facing window of an unheated room where their containers were kept. Whilst no data are available for comparison, it is likely that the daily temperature range in captivity was less extreme than in the field, with perhaps a slightly higher mean temperature. A daily supply of live invertebrate food was provided, and always such that there was an excess over the apparent need. Prey items initially had been tiny ostracods. A wider range of Crustacea and dipteran larvae and pupae was provided once the larvae could tackle larger food. In September and October prey items were almost exclusively *Daphnia* spp.

The growth of all four larvae of *A. caerulea* was recorded and, at the end of the season,

collection of faecal pellets was used as an additional monitoring technique. Counts of faecal pellets were made each day in early evening from 8 September to 24 October. The results, shown in Figure 1, have been smoothed by calculating a moving average over three days, with the output per larva averaged over the four individuals.

Results

a) Decline of feeding (Figure 1)

The most noteworthy feature of the data is the sudden onset of a progressive decrease in feeding activity, apparently triggered independently of food availability. Each larva underwent a moult during the first half of September (on 6th, 9th, 14th and 15th respectively). This appears to have a temporary effect on pellet-production that is noticeable in the graph, which includes the last three dates. Soon thereafter the graph shows a very clear decline in pellet production, commencing just a few days after the autumnal equinox on 21 September. Although this was not measured, I observed that the pellet size also decreased markedly in the final few days before cessation of feeding. I attempted to stimulate increased feeding by raising the number of 'available' prey by at least 50 per cent on 4 October (arrow (a) in Figure 1), and again on 17 October (arrow (b)), but with little evident response. By 24 October all four larvae had virtually ceased feeding.

b) Growth and moulting

By 24 October, three larvae had moulted 7 times, one 8 times, since originally received. I consider that they were now variously in either instar 9 or 10. In the notation in which the final instar is F (or F-0), these equate to instars F-6 and F-7 (calculated on an average body length increase of c.20 per cent per moult, which I have found generally consistent in captive-rearing).

Although the light and temperature regimes at Carlisle will have differed slightly from those of the field source, it is interesting to note that the final size achieved by the captives at cessation of feeding was c. 10–12mm in overall length. This was comparable to their equivalents in wild populations at the field source. Smith *et al.* (2000) have made extensive studies of the sizes of larvae of *A. caerulea* in the field and there has been much consistency between their findings and my data from captive rearing.

Discussion

Corbet (1999: section 4.3.7.4 and Figures 4.26 and 4.27) discusses seasonal variation in energy consumption by larval Odonata. Earlier work by Corbet (1962: Chapter IV) gave much impetus to the study of life history patterns and Norling (1984) reviews some subsequent work on the over-wintering strategies of Odonata of temperate latitudes. Norling stresses the major role of photoperiod (either long or short day length) in controlling growth and hibernation. This operates through the regulation of periods of diapause: arrested development not directly related to the onset of adverse conditions.

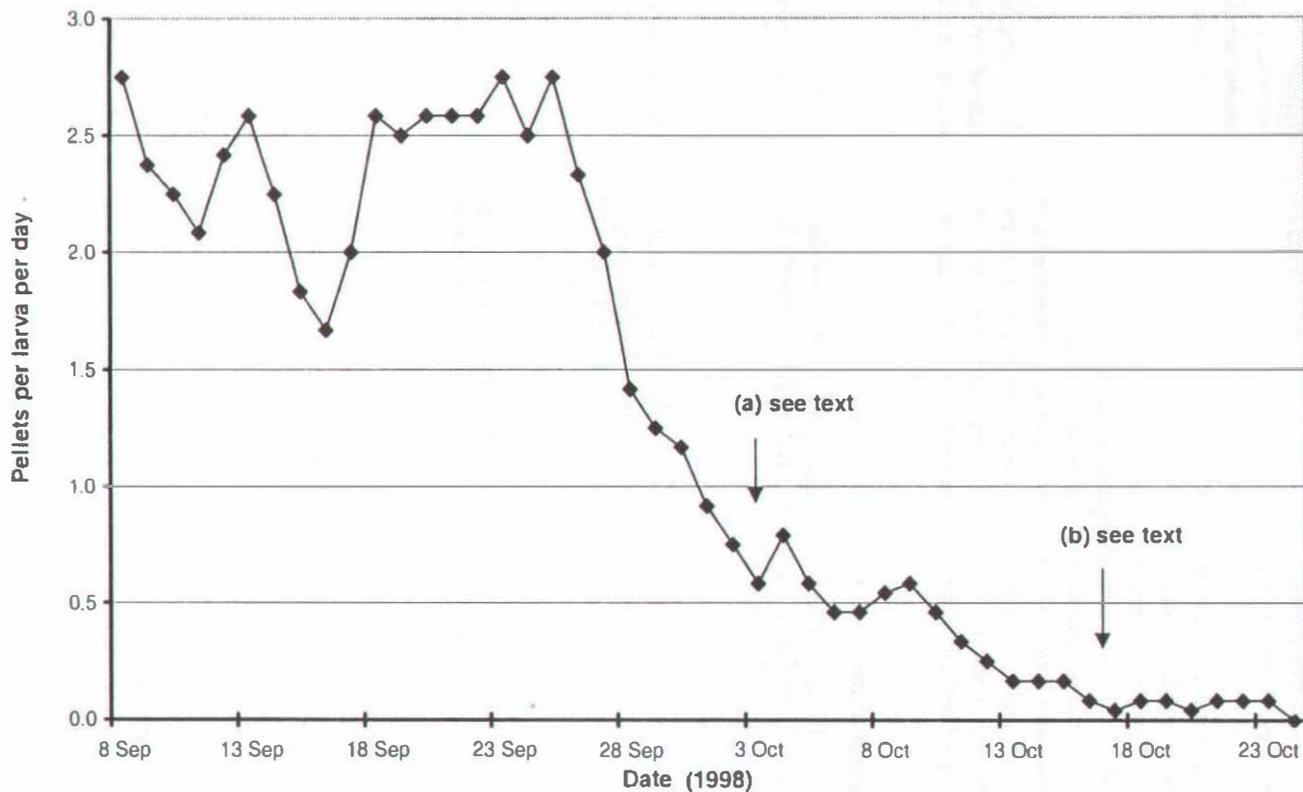


Figure 1. Faecal-pellet production by four captive first-year larvae *Aeshna coerulea* (results averaged over four larvae; plotted as a three-day moving average).

Although studies had concentrated on later instars, Norling refers to populations of the Common Hawker, *A. juncea*, in northern Sweden as appearing to show photoperiod-induced diapause in all larval instars except the first four (which included the prolarva). *A. caerulea* was not included in the work cited but, having an arctic-alpine distribution that overlaps the northern range of *A. juncea*, it might be expected to have similar regulatory mechanisms. In Scotland, at sites studied by Smith *et al.* (2000) and by myself (Clarke, 1994), *A. caerulea* usually appears to hibernate as a larva for three successive winters. More extreme conditions elsewhere in its range may well extend the duration of the larval phase and hence the frequency of diapause phenomena. Norling (1984) also discusses the general vulnerability of larvae in later stages of the moult cycle, leading up to casting the skin (ecdysis). The moults of the captives shortly before decline of feeding will have ensured that all began the winter rest period at a stage well removed from that part of the cycle.

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The dragonflies of a Cambridgeshire pond and its surroundings in 2001

NORMAN W. MOORE

The Farm House, 117 Boxworth End, Swavesey, Cambridge CB4 5RA

Introduction

In theory, keeping records of the adult dragonflies which occur on a nearby pond throughout the flying season should be easy. In practice, it is difficult, because engagements of all sort – including fieldwork elsewhere – prevent one from visiting the pond on many days. However, for a number of reasons I was able to visit my pond at Swavesey in Cambridgeshire on most days during the flying season (30 April to 15 November) of 2001. As a result my records for that year are more complete than for any previous year since the pond was dug in 1983 (Moore, 1987) and thus seem worth recording. An additional reason for publishing the records for 2001 is that the flying season followed the wettest winter ever recorded and it was interesting to discover whether this had had any noticeable effect on the dragonfly fauna of the pond. This paper provides a summary of my observations, which are related to other observations made on the pond since 1983 (Moore, 1987, 2002 and unpublished). The nature of the pond's dragonfly fauna is outlined, and the value and limitations of such studies is discussed.

Methods

The pond is *c.* 38m long and *c.* 13m wide at its widest point. It lies in an enclosure in a grass field, which is bordered on the west side by a plantation of hardwood trees. The pond is surrounded by a narrow strip of grassland, which is sheltered by banks made from the clay dug out when the pond was constructed in 1983. Beyond the clay banks, which support rough grassland and bushes, are two other strips of grassland which lie 7–11m from the pond's edge. They are enclosed from the field by a hawthorn and blackthorn hedge (see Figure 1).

Transects (Moore, 1953) were made on 114 days during the 200-day flying season of the dragonflies on the pond. On some days two or more transects were made. The transect round the water's edge was *c.* 95m long, that in the grasslands outside the banks *c.* 120m in total, and that in our garden, which is *c.* 120m away from the pond, was *c.* 110m long. Fourteen supplementary transects were made on land between the pond enclosure and the garden between 4 May and 3 June. The part on the south side of the enclosure hedge was *c.* 55m long and that on the east edge of the plantation was *c.* 90m long.

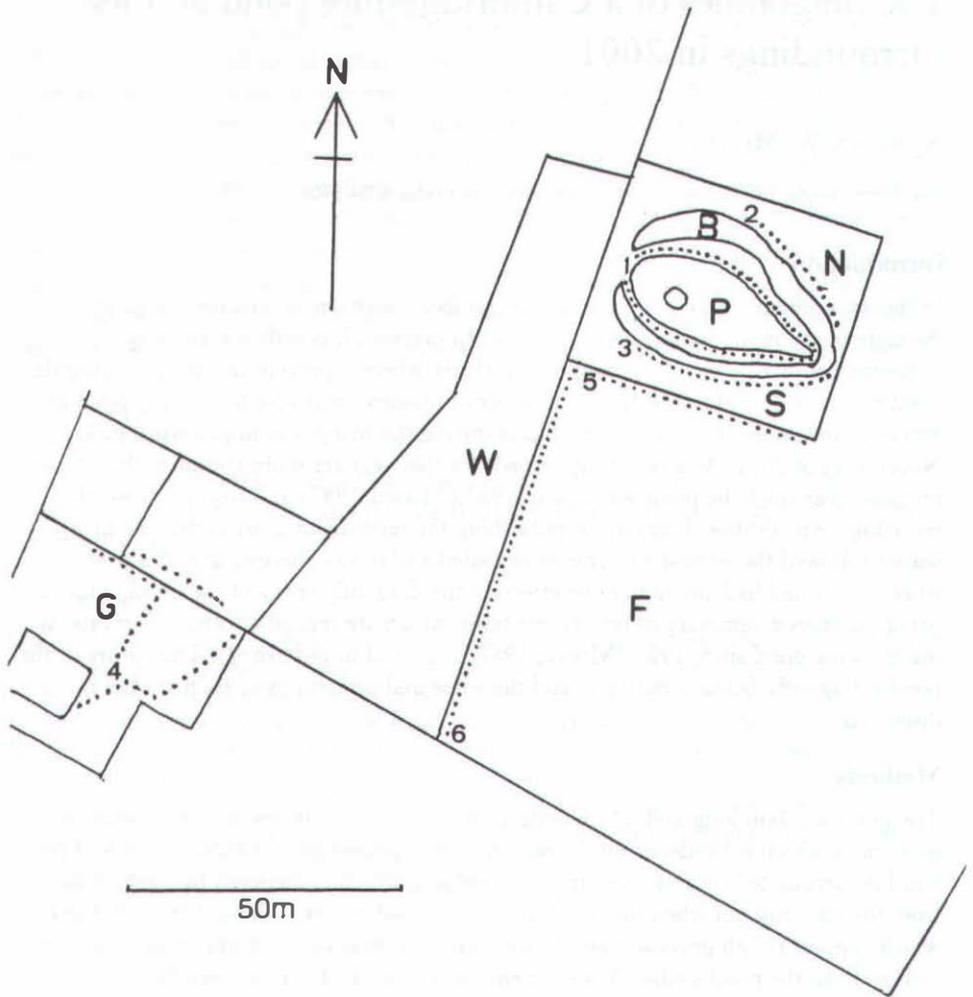


Figure 1. Sketch map of the pond and its surroundings showing positions of transects.

Key

- B – bank, F – field, G – garden, N – north grassland, P – pond, S – south grassland, W – plantation
1 – transect round pond's edge
2 – transect in north grassland
3 – transect in south grassland
4 – transect in garden
5 – supplementary transect by hedge
6 – supplementary transect by plantation

Records were kept of the times of day when the transects were made and of weather conditions so that the significance of the numbers of dragonflies observed could be assessed.

On all transects adult, teneral and immature insects were counted. The immaturity of insects was assessed by their colour. Virtually all transects were made between 0930h and 1630h GMT, most within an hour or so of solar noon so as to obtain comparable results for adult males (Moore & Corbet, 1990). As a result of the timing of transects many tenerals of species which emerge early in the morning must have been missed. There was not enough time to search for exuviae.

The order of the species in the tables is the order in which I first saw them in the flying season of 2001.

Results

The observations made throughout the 2001 flying season are summarised in Tables 1 to 5.

Table 1 shows that adults of 13 species were present at the pond for more than a month.

Table 1. The durations of the teneral and adult flying seasons of the dragonfly species on the pond in 2001.

Species	Dates	
	Teneral	Adult
<i>Pyrhosoma nymphula</i> (Sulzer)	30.04 – 23.05 ^a	07.05 – 21.06
<i>Coenagrion puella</i> (L.)	08.05 – 27.06 ^b	16.05 – 20.07
<i>Libellula quadrimaculata</i> L.	11.05 – 25.05	21.05 – 17.07
<i>Ischnura elegans</i> (Vander Linden)	20.05 – 19.07 ^c	21.05 – 10.08
<i>Brachytron pratense</i> (Müller)		21.05 – 22.06
<i>Enallagma cyathigerum</i> (Charpentier)	27.05	22.05 – 21.08
<i>Anax imperator</i> Leach		05.06 – 08.08
<i>Lestes sponsa</i> (Hansemann)	12.06 – 01.07	03.07 – 03.09
<i>Sympetrum striolatum</i> (Charpentier)	14.06 – 22.08	01.08 – 15.11
<i>Sympetrum sanguineum</i> (Müller)	22.06 – 09.07	02.07 – 27.09 ^d
<i>Aeshna cyanea</i> (Müller)	28.06 ^e	01.08 – 25.09
<i>Aeshna grandis</i> (L.)		03.07 – 24.08
<i>Aeshna mixta</i> Latreille		01.08 – 11.10

Note:

- a all but one emerged 30.4 to 12.5
- b all but one emerged 8.5 to 18.6
- c two periods of emergence: 20–22.6 and 29.6–19.7
- d all but one insect observed from 2.07 to 28.8
- e exuvia

Table 2. The largest number of adult males observed by water on a transect in the week indicated. (The months are divided into quarters each represents approximately one week.)

Species	May	June	July	Month August	September	October	November
<i>P. nyrphula</i>	1 8 7 6	3 1 1					
<i>C. puella</i>	26 64	83 46 20 28	33 5 4				
<i>L. quadrimaculata</i>	2	4 3 1 2	3 1 1				
<i>I. elegans</i>	1 2	3 3 5 5	4 4 3 2				
<i>B. pratense</i>	1 2	1 1					
<i>E. cyathigerum</i>	1	1 1	6 2	6 2 1			
<i>A. imperator</i>		1 1	1 1	1 1			
<i>L. sponsa</i>			1 3 1 2	4 4 2 3	1 a		
<i>S. striolatum</i>				5 4 4 4	3 a 3 2	3 4 3 3	2 1 1
<i>S. sanguineum</i>			4 ^b 3 1 3	2 3 3 1	a 1 ^c		
<i>A. cyanea</i>				1 1 2 1	1 a 1 1		
<i>A. grandis</i>			1 1 1 1	1 2 1	a		
<i>A. mixta</i>				3 ^d 1 3 3	2 a 1 3	2 1	

Notes:

- a no observations were made between 4 and 16 September
 b included two immature coloured insects holding territories by water
 c an isolated record on 27 September – presumably an immigrant
 d all three insects were by the edge of water not flying over it

In addition, a female *Libellula depressa* L. was seen in our garden on 13 May and it, or another, on the far side of the hedge surrounding the pond on 20 May. Single male *Erythromma najas* (Hansemann) were seen at the pond on 27 May and 5 June. On 20 June I got a glimpse of a noticeably small male *Erythromma*, which may have been our first *Erythromma viridulum* (Charpentier), but unfortunately I was unable to confirm its identity. Male *Calopteryx splendens* (Harris) visited the pond on 6 and 13 July.

Oviposition was observed in all the species shown in Table 1 except *B. pratense*. A pair of this species was observed in copulation near the edge of the pond. Teneral of nine species were observed. A chance find of the exuvia of an *A. cyanea* showed that at least ten species emerged from the pond in 2001. There was nothing unusual about the dates of the flying seasons of adults or tenerals, or about the relationship between them.

Table 2 shows the changes in the sizes of the populations of adult territorial males by water throughout their flying seasons. *C. puella* was the only abundant species. The low numbers of each aeshnid species are to be expected since the pond is quite small and the Highest Steady Density (Moore, 1964) of these species is low: there is only room for one or two males at any one time. Only in *C. puella* did the observed population density approach the known Highest Steady Density of the species (Moore, 1991).

The data show that *P. nymphula*, *C. puella*, *L. quadrimaculata*, *I. elegans*, *L. sponsa*, *S. striolatum*, *S. sanguineum*, *A. cyanea* and *A. mixta* were observed in every week of their flying season, whereas *B. pratense*, *E. cyathigerum*, *A. imperator* and *A. grandis* were not. Table 3 confirms the difference between the two groups: the species which were present

Table 3. Presence of adults on days when transects were made under optimal conditions.

Species	Number of days in flying season when transects were made under optimal conditions	Number of days in flying season when adults were recorded on transects made under optimal conditions
<i>P. nymphula</i>	14	14
<i>C. puella</i>	16	16
<i>L. quadrimaculata</i>	16	16
<i>I. elegans</i>	23	21
<i>B. pratense</i>	9	7
<i>E. cyathigerum</i>	25	11
<i>A. imperator</i>	17	6
<i>L. sponsa</i>	21	19
<i>S. striolatum</i>	23	23
<i>S. sanguineum</i>	13	12
<i>A. cyanea</i>	14	12
<i>A. grandis</i>	17	9
<i>A. mixta</i>	17	16

each week occurred on every or practically every fine day, whereas the species which were not recorded in each week did not appear on some of the days when conditions were ideal.

The data in Table 4 give an indication of the extent to which adult, teneral and immature insects used the sheltered grassland between the banks and the hedge, and our garden. The records in this table were made at different times of the day and under a variety of weather conditions. Variations in these make detailed comparisons between species impossible. Thus the figures given in Table 4 only give a very rough indication of the use of grasslands and the garden by dragonflies. However some conclusions can be drawn.

As was to be expected, records of tenerals were virtually confined to the water's edge. The eight records of teneral *P. nymphula* in the grassland shows that some tenerals of this species do not fly far from their breeding place on their maiden flight.

Very few immature insects were observed in the grasslands or in our garden. The immature insects observed near the water's edge probably consisted mainly of maturing insects which were finding their way back to their breeding place.

More adult insects than tenerals or immatures used the grasslands and garden. The insects in the grasslands must have been there for different reasons. Some would have been feeding or resting insects, which were away from water because of weather conditions or the time of day. Some males would have been insects which had been expelled from the water's edge as the result of territorial encounters.

The dragonflies in the grasslands must have come mainly from the pond. Members of the seven species observed in the garden could have come from other sources as well: all but *P. nymphula* and *S. sanguineum* had been observed in our garden before the pond had been constructed.

The supplementary information obtained from the transects made between the pond enclosure and our garden between 4 May and 3 June was as follows. Four teneral, 13 immature and four adult *P. nymphula* were seen by the hedge, and one teneral, three immature and two adult by the plantation. Also female *L. depressa* and an immature *C. puella* were seen by the hedge and an immature *L. quadrimaculata* and an adult *C. puella* were seen by the plantation.

In Table 5 a comparison is made between the dragonfly fauna of our pond as observed in 2001 with those of previous years. All the species recorded in 2001 had been observed in previous years. Nearly all the breeding species had been recorded every or nearly every year in the 17 year period. However the numbers observed have changed. Notably the pioneer species have either disappeared (*Orthetrum cancellatum* (L.)) or have declined (*I. elegans* and *S. striolatum*). *L. sponsa* and *E. cyathigerum* have also apparently declined.

The records for 2001 and 2000 are very similar. No unusual effects of the exceptionally wet winter of 2000–2001 are yet discernible.

Table 5. The dragonfly fauna of the pond in 2001 compared with previous years.

	Number of years	The largest number of territorial		
	species recorded	males recorded		
	1984–2000	2001	2000	1984–2000
<i>P. nymphula</i>	15	7	5	5 (1995, 2000)
<i>C. puella</i>	17	83	54	113 (1993)
<i>L. quadrimaculata</i>	17	4	1	3 (1990, 1993)
<i>I. elegans</i>	17	5	7	30 (1988)
<i>B. pratense</i>	7 ^x	2	2	2 (2000)
<i>E. cyathigerum</i>	17	6	9	30 (1988)
<i>A. imperator</i>	16	1	1	1 (all years present)
<i>L. sponsa</i>	17	4	6	14 (1987)
<i>S. striolatum</i>	17	5	5	13 (1999)
<i>S. sanguineum</i>	15	6	7	7 (2000)
<i>A. cyanea</i>	16	2	2	2 (1986, 1987, 1993)
<i>A. grandis</i>	17	2	1	2 (1985, 1988)
<i>A. mixta</i>	17	3	2	5 (1999)
<i>C. splendens</i>	6	1	0	1 (1992, 1994, 1996, 1997, 1999)
<i>C. pulchellum</i>	3	0	0	1 (1993, 1994, 1997)
<i>F. najas</i>	3	1	0	1 (1985, 1990, 1996)
<i>L. fulva</i>	2	0	0 (female)	0 (females 1985, 2000)
<i>I. depressa</i>	13	0 (female)	1	2 (1997)
<i>O. cancellatum</i>	7	0	0	3 (1984)

Note:

x *B. pratense* has been recorded every year for the last eight years except for 1995.

Discussion

The data show that this medium sized pond near the edge of the Cambridgeshire Fens has an unusually rich dragonfly fauna, which has changed relatively little in 18 years. It consists of a high number of *C. puella* and much lower numbers of 12 other species. In 2001 the pond was continuously occupied by adults of nine species and sporadically by four others. All these species except for one were seen to oviposit in the pond. In addition, very low numbers of three other species visited the area of the pond briefly but showed no reproductive activity. What is the nature of the pond's dragonfly fauna? To what extent were the insects observed home grown and to what extent immigrants from neighbouring habitats?

The pond is not linked directly by a stream or ditch to other aquatic habitats, however all the 19 species recorded on it do breed within four kilometres. They should be easily capable of dispersing to the pond. That most could and did was shown by 13 species appearing during the first summer after the pond's construction. Only prohibitively time-taking marking of teneral insects could provide an accurate answer to their question about the nature of the pond's fauna. In the absence of marking data only a tentative assessment is possible.

The nine species which were recorded regularly throughout their seasons, which oviposited and were observed as teneral insects almost certainly had resident populations, although these may have been augmented by immigrants.

The four species (*B. pratense*, *A. imperator*, *E. cyathigerum* and *A. grandis*) which showed reproduction behaviour, but were present irregularly throughout their flying seasons were probably dependent to a greater extent on immigrants. This was almost certainly the case with *E. cyathigerum*. The pond appears to provide a suboptimal habitat for this species, and there are relatively few breeding records at it. However there are vast populations of this species in the gravel pits three kilometres to the north-west. It seems likely that the pond's population consists largely of immigrants from this source.

The nature of a pond's fauna is important from the conservation point of view. The conservation of a species in the long run must depend on the conservation of sites which are optimal for it. Small ponds, owing to their size, are unlikely to provide optimal habitats. However, ponds such as that described in this paper should not be considered merely as receptacles for surplus individuals from optimal sites. They are an important back-up for optimal sites, for example if these are damaged by a pollution accident. Conceivably a large number of suboptimal habitats whose populations interact could, on their own, maintain a species for a long time.

As noted in the Introduction, it is extremely difficult to carry out as detailed a study even as the very incomplete one described in this paper. However, experience with this pond shows that very incomplete surveys can be useful if continued over several years. Studies of a wide range of ponds have been published, but generally they cover shorter periods of time. If more, necessarily incomplete, but long-term studies could be made we could gradually build up a natural history of dragonfly ponds. Among other things this would provide valuable information about the relationship between species richness and size of pond, and about the effects of isolation from nearby dragonfly habitats. I am still unable to say whether the long-term stability of the dragonfly fauna of my pond depends on the quality of the habitat or the availability of immigrants to it. If we had more pond studies we could begin to answer this and similar questions.

Summary

Throughout the 2001 flying season transects were made round the edge of a

Cambridgeshire pond, in sheltered grassland nearby and in a garden 125m away. Adults, teneral and immature insects were counted.

Fifteen species were recorded, in 13 of which reproductive activity was observed. Teneral of nine species were observed. Only *C. puella* was abundant.

In the grasslands, eight species of adults, and five each of teneral and immature insects were observed.

The species present in 2001 were similar to those observed from 1984 to 2000.

The extent to which the different species were regular breeders and/or immigrants from neighbouring habitats, and its relevance to conservation, is discussed.

The limitations and value of surveys of this kind are discussed.

Acknowledgement

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Voltinism of the Common Blue Damselfly *Enallagma cyathigerum* (Charpentier) in a Scottish loch: a preliminary study

PHILIP S. CORBET & S. H. CHOWDHURY

PSC: Department of Biological Sciences, University of Dundee DD1 4HN, UK

(Present address: Crean Mill, St Buryan, Cornwall TR19 6HA, UK)

SHC: Department of Zoology, University of Chittagong, Bangladesh.

Summary

During 1986–1987 a larval population of *Enallagma cyathigerum* was sampled repeatedly from a *Littorella* sward near the margin of a small Scottish loch (Rohallion Loch) to determine the species' voltinism and to characterize ontogenetic changes in external morphology. Size-overlap between hatching cohorts made it difficult to trace cohort development but results support the inference that most larvae were developing as semivoltine summer species, spending their second (last) winter in stadia F-1 (mainly) and F-0, while a few larvae showed the potential to complete development in either one or three years. Extrapolation backwards from the last three stadia revealed that larvae completing development passed through about 15 stadia (including the prolarva). Regular, heavy stocking of Rohallion Loch with insectivorous fish (including trout) invited comparison with observations by Macan in a tarn in the Lake District with attributes, including aquatic macrophytes and a predominantly semivoltine population of *E. cyathigerum* occupying *Littorella*, resembling those of Rohallion Loch. In Rohallion Loch, larvae of *E. cyathigerum*, though known from research in North America to be vulnerable to predation by fish, were maintaining dense populations in the presence of fish, probably by obtaining refuge in *Littorella* swards. We emphasize the need to discover secure morphological characters for distinguishing small larvae of *E. cyathigerum* from those of other coenagrionids.

Introduction

Happening upon a dense, easily accessible larval population of the Common Blue Damselfly, *Enallagma cyathigerum* (Charpentier), and believing at the time that we possessed the means to distinguish larvae of this species from other coenagrionids in UK (Chowdhury & Corbet, 1987), we undertook a year-long sampling programme to investigate the voltinism of this species in a small loch that offered a potentially informative comparison with an earlier long-term study by Macan (1974) of the same species in a very similar habitat. The following account presents the results of our investigation, which we regard as preliminary in that it had to be concluded after only one year.

Methods

All observations were made at Rohallion Loch, Perthshire, UK (56°32'N, 3°32'W; O.S. Grid Reference NO 048387; depth away from margins c. 1–2m; area c.4.25ha). A dam at the NE corner retains the water that forms the loch. All samples of larvae were taken near a gravel landing beach close to a fishermen's hut on the N shore. Here, in 1987, woodland comprising mainly *Salix* (height up to 4m), *Betula* and *Picea* (8–10m) and *Fagus* and *Quercus* (20m) came to within c. 10–20m of the loch margin, where Yellow Iris (*Iris pseudacorus*), Sharp-flowered Rush (*Juncus acutiflorus*) and Bogbean (*Menyanthes trifoliata*) occupied a band 5–10m wide, and Bottle Sedge (*Carex rostrata*) grew offshore, in a band of similar width. Along the dam *Equisetum* grew amongst the *Carex rostrata*. In the northeast part of the loch were large floating patches of Amphibious Bistort (*Persicaria amphibia*), White Water-lily (*Nymphaea alba*) and submerged *Myriophyllum*. Carpeting the bottom to within c. 1m of the water's edge near the sampling site were several large patches of Shoreweed (*Littorella uniflora*) forming a dense sward extending at least 5m, and perhaps a much greater distance, away from the shore. Here the *Littorella* sward lay between c. 10cm and 1m beneath the water surface, allowing the possibility that some leaves would be exposed at times of low water. All larvae of *Enallagma cyathigerum* used for our analyses were obtained from a rectangular patch of *Littorella*, c.4 × 5m in area, located c. 4m from the gravel shore at the north side and c. 4m from a stand of emergent *Carex rostrata* at the NW side. During the study period the *Littorella* harboured a rich and diverse fauna, which included Acarina, *Asellus*, Coleoptera, Corixidae, *Cyclops*, pea mussels, sticklebacks (*Gasterosteus aculeatus* L.), tadpoles and larvae of Chaoboridae, Ephemeroptera and Trichoptera. Fish in the loch comprised Brown Trout (*Salmo trutta* L.), Rainbow Trout (*Salmo gairdneri* Richardson), Tench, (*Tinca tinca* (L.)) at 'low density' and small Perch (*Perca fluviatilis* L.) at 'medium density' (Factor, 2000). Of these only Rainbow Trout have been stocked by the Estate, the annual regime being: 100 in March, and then 50 each month until 1000 in October. No records of water temperature are available; the sampling site, featuring south-facing shallows, will have been among the warmest places in the loch. Because we could make only a few, intermittent visits to Rohallion Loch, we tried to time them during the expected period of main growth of *E. cyathigerum* and also to extract from them the greatest amount of information likely to reveal the pattern of seasonal development and ontogenetic change in external morphological characters.

Larval collections were made using a triangular-frame hand-net with square mesh (one side of a square 1mm) with a straight leading edge 40cm wide. In 1986 exploratory collections were made on 24 September, 6 October and 16 November, from amongst *Juncus acutiflorus*, *Myriophyllum*, leaf litter and three patches of *Littorella*. On all three occasions *E. cyathigerum* larvae were encountered in numbers only in the *Littorella*, being present in two of the three patches in September and October, and in all three in November. Accordingly all subsequent samples were taken from the same rectangular

Table 1. *Enallagma cyathigerum* larvae in Rohallion Loch. Attributes of standardized samples taken from *Littorella* and used for analysis (body length (BL), head width (HW) and lengths of wing sheaths (WS) and caudal lamellae (CL)).

Sample Number	Date	No. of larvae examined	No. of F-1 larvae	No. of F-0 larvae	No. of larvae in each stage of metamorphosis	No. of exuviae (and stadium)	Attributes measured
1	6-Oct-86	214	9	8			BL
2	6-Jun-87	157	7	5	W2 (3) W3 (1) W4 (1)	3 (F-1) 1 (F-2)	BL, HW, WS
3	13-Jul-87	194	0	7	W2 (3) W3 (0) W4 (2)		BL, HW, WS
4	28-Aug-87	240	36	0			BL, HW, WS, CL
5	18-Sep-87	261	17	4			BL, HW, WS, CL
6	6-Oct-87	279	24	22			BL, HW, WS, CL

patch of *Littorella*, described above. On 6 October and 16 November the size-frequency distribution of *E. cyathigerum* larvae was wide and closely similar. For our analysis of growth we chose the sample on 6 October and five more taken in 1987, as detailed in Table 1. Each of these six samples was obtained by making five parallel and adjacent net sweeps through *Littorella*, each sweep being the width of the net (40cm) and 5m long, starting away from the shore and finishing c. 1m from the adjacent *Carex*. On 6 October 1987 dense wefts of brownish filamentous alga covered the *Littorella* leaves, making it more difficult than usual to detect larvae, especially the smaller ones. During some visits we made concurrent collections in the same place using a net with finer mesh, but this did not significantly extend the size range of larvae collected; so we have omitted such collections from the analyses.

All larvae collected were retained and examined alive within 48h under a binocular microscope (Nikon 201095, at a magnification up to $\times 140$), being provisionally distinguished from larvae of the Blue-tailed Damselfly, *Ischnura elegans* (Vander Linden) by their lack of dorsal spots on the thorax and abdomen (see Chowdhury & Corbet, 1987: Figure 1A). At the same time certain dimensions were measured, to the nearest 0.1mm, as listed in Table 1, body length (BL) being treated as the distance between the anterior margin of the head (excluding the antennae) and the posterior limit of the abdomen (thus excluding the caudal appendages, CL), and head width (HW) being the widest part of the head. Also recorded were: the extent (expressed as the number of abdominal segments they covered) of the wing sheaths (WS), which permitted unequivocal diagnosis of the penultimate and final stadia, designated F-1 and F-0

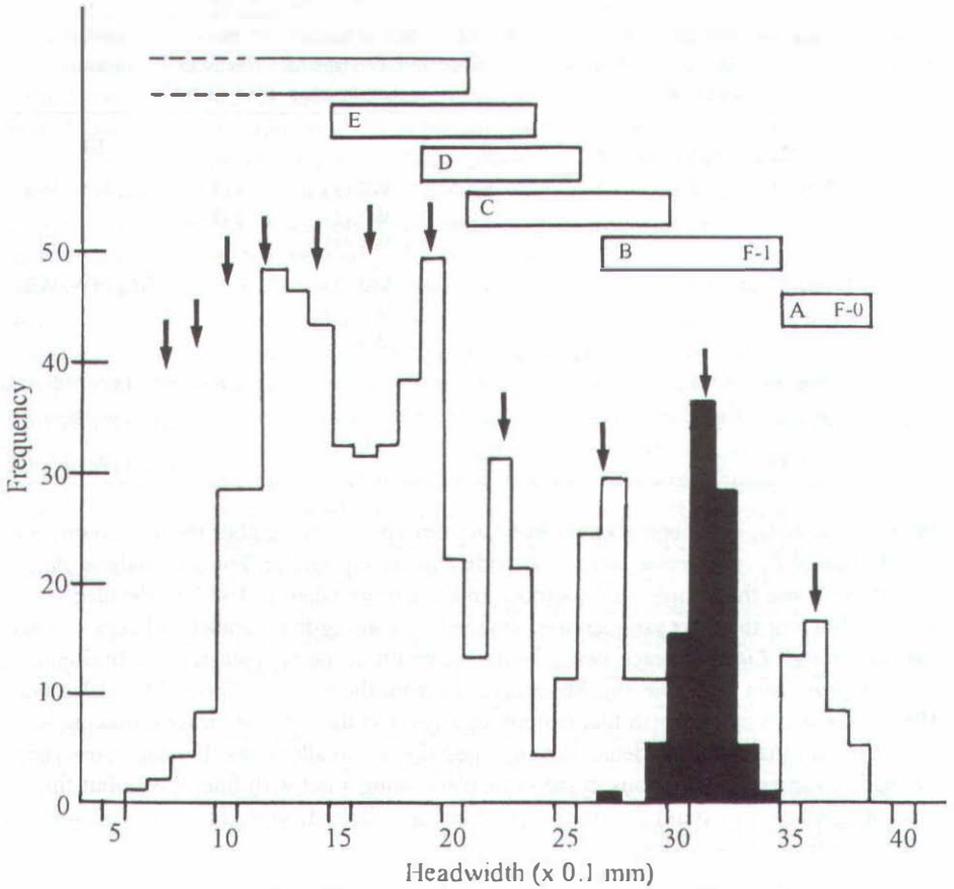


Figure 1. *Enallagma cyathigerum* larvae in Rohallion Loch. Head width (HW) frequency distribution for all larvae examined (N=694). Each horizontal bar above indicates the range of HW embraced by a category of WS coverage, the letter within the bar corresponding to the number of abdominal segments over which the WS extend (see Table 2). Bars A and B represent stadia F-0 and F-1 respectively. Bar C probably corresponds to stadium F-2 and bars D-E probably represent stadia F-3 and F-4 respectively. In D the WS cover segment 1; in E no WS rudiments are visible externally. The HW ranges for stadia F-1 and F-2 overlap slightly. Vertical arrows indicate the frequency modes that probably correspond to preceding stadia, being derived from extrapolation backwards from F-1 assuming a growth ratio at ecdysis of 1.1825. HW entries in F-1 are shown in black.

respectively; and signs of metamorphosis (designated W2, W3 and W4), as indicated by the progressive parting and swelling of the wing sheaths (as defined by Corbet & Prosser, 1986). If larvae were teneral, soft and/or pale and if exuviae were present, this was also noted as signifying recent ecdysis.

Larval samples were then preserved for subsequent microscopical examination during which the specific identity of all larvae was checked using the presence of the parasetal palpal spine (PPS) prescribed by Gardner (1954b: p.162) for distinguishing F-0 larvae of *E. cyathigerum* from those of other British coenagrionids and the subject of a recent comparative study by May & Corbet (2001).

The presence of adult Odonata was recorded as weather permitted, namely on 3 July 1987.

Results

Larvae of all sizes examined lacked segmental dark-brown spots on the thorax, thus conforming with *E. cyathigerum* (Chowdhury & Corbet, 1987: p.375) but some larvae (BL < 10mm) showed slight segmental spotting on the abdomen. Using strong incident lighting, the PPS was clearly distinguishable at a magnification of $\times 40$ or less in larvae of HW 1.9mm (c. stadium F-4) and above. If the PPS was sclerotized, it was clearly visible at $\times 15$ in larvae within the same size range. For smaller larvae, down to the smallest examined (HW 0.6mm, stadium c. 4, or F-11), a compound microscope was needed (ocular $\times 10$; objective Phase 2 20 DL 0.4 160/0.17). The PPS was well developed in all larvae examined (N = 694; stadia c. 4 to F-0) except in one F-1 larva that possessed a very small PPS on the right palpus (May & Corbet, 2001: Figure 2C) and none on the left palpus. WS first became detectable at HW 1.5–2.0mm (c. stadium F-4).

Figure 1 records the relationship between HW and length of WS in the 694 larvae for which these attributes were recorded. WS length and HW permit unequivocal recognition of stadia F-0 and F-1 (Table 2) but the ranges for HW of stadia F-1 and F-2

Table 2. *Enallagma cyathigerum* larvae in Rohallion Loch. Attributes of the last three stadia.

Stadium	Body length (BL) ¹	Head width ¹	Sample size	Caudal lamellae (CL) ¹	Wingsheaths ²	CL:BL ³
F-2	66–133	20–29	98	35–51	>1 <2	43
F-1	110–154	27–34	93	42–56	>2 <3	37
F-0	145–179	35–38	42	48–60	3.3–4.0	33

¹ Range in units of 0.1 mm.

² Range (abdominal segments covered).

³ Approximate percentage of overall length contributed by caudal lamellae (based on medians).

overlap. The modal growth ratio between modal HW of F-1 and F-0 (1.1825) allows one to estimate the approximate number and dimensions of earlier stadia by extrapolation backwards (Figures 1 and 2), bearing in mind that total stadium number can vary widely, even among siblings (Corbet, 2002). Such extrapolation reveals that stadium 2 would equate to *c.* stadium F-13 (HW 0.41mm) and that the smallest larva collected (HW 0.6mm) would be about stadium F-11 or stadium 4, counting the prolarva as stadium 1. These estimates are consistent with the report that the HW of stadium 2 of *Enallagma ebrium* (Hagen) is 0.35–0.36mm (Fontaine & Pilon, 1979: p.85). Figure 2 records the correlation between HW and BL during larval development.

On 3 July 1987, during sunshine and a brisk warm southwesterly breeze, many mature males of *E. cyathigerum* were flying among stems of *Iris* and *Juncus* on land within 5–10m of the water's edge. A few males were flying over the *Carex rostrata* zone within 1–2m of the landward edge, where a tandem pair was seen. Along the outer (lochsides) edge were many males, some in tandem. Unpaired males were settled on lochsides vegetation and one was on a water-lily leaf. No copulating pair or ovipositing female was seen. A teneral female rose from the *Carex rostrata* on its maiden flight towards the shore.

In a sheltered woodland clearing at the eastern end of the loch were males of *E. cyathigerum* (immature), *Ischnura elegans* (immature) and the Large Red Damselfly, *Pyrrosoma nymphula* (Sulzer) (mature). A tandem pair of *E. cyathigerum* was over grass on the landward side of the trees, flying away from water *c.* 70m from the water's edge at the larval sampling site. No adult Odonata were seen at the loch during samples 3–6. At Rohallion Loch on 30 June 1984, Betty Smith (personal communication) recorded >1000 adults of *E. cyathigerum* and >200 adults of *Ischnura elegans*.

Other species of odonate larvae obtained during routine sampling at Rohallion Loch comprised the Emerald Damselfly, *Lestes sponsa* (Hansemann) (*c.* stadium F-6) in sample 2.

Discussion

Our use of the PPS to distinguish larvae of *Enallagma cyathigerum* requires amplification. Parr, who also used the presence of the PPS to distinguish larvae of *E. cyathigerum* from those of *Ischnura elegans* and *Coenagrion puella* in a population in south Lancashire, UK, noted (Parr, 1970: p.175) that small larvae of *Ischnura elegans* and *Coenagrion puella* often have a spine resembling the PPS but that it is 'never as well developed and obvious' as in *E. cyathigerum*. Gardner (1954a: p.20) had already remarked that the PPS was present in the first few stadia of British coenagrionids, to disappear after about stadium 7. The presence of the PPS in small larvae of *I. elegans*, one of the other two coenagrionids known to occupy Rohallion Loch, means that we cannot exclude the possibility that some of the 'small' larvae that we assigned to *E. cyathigerum* on the basis of the PPS were

actually *I. elegans*. (Small larvae of *Pyrrhosoma nymphula* are readily distinguishable by their banded caudal lamellae.) We have so far been unable to examine small larvae known to be *I. elegans* and so cannot comment further on this possibility except to say that, in general appearance, all larvae we examined seemed to be conspecific. So, until we are able to examine the appearance of the PPS in small larvae of *I. elegans*, we shall assume that all larvae in the samples we analyzed (i.e. those listed in Table 1) were indeed *E. cyathigerum*. Larval samples deriving from this study have been deposited as voucher material at the Freshwater Biological Association laboratory at Ambleside, UK. We note that our reservations regarding diagnosis apply to any field work in which larvae have been assigned to *E. cyathigerum* on the basis of the key to F-0 larvae by Gardner (1954b). There is an urgent need to terminate this uncertainty, especially as *E. cyathigerum* and *I. elegans* frequently occupy the same sites in western Europe, e.g. in Britain (Parr, 1969) and in southwestern Germany (Sternberg & Buchwald, 1999: p.301).

WS first appear (in F-4), rather later than expected from a study of other species (see Corbet, 1999: p.213). For example, WS are first detectable in F-6 in *Enallagma vernale* Gloyd, (Rivard & Pilon, 1978), a taxon provisionally regarded as a subspecies of *E. cyathigerum* (Donnelly, 1989; Westfall & May, 1996: p.385). The percentage of overall length contributed by the caudal lamellae (Table 2) changes greatly during ontogeny, declining progressively from about 85 in stadium c. F-10 to 33 in F-0.

Most published accounts we have seen on the larval ecology of coenagrionids in Britain omit mention of how larvae of *E. cyathigerum* were distinguished from those of other species. An exception is the report by Parr (1970) referred to above. Future precise work on the larval ecology of British coenagrionids will benefit greatly from critical studies of the external morphology of early stadia, with especial reference to the presence and appearance of the PPS (see May & Corbet, 2001).

The overlap in HW between stadia F-1 and F-2 (Table 2) may reflect the existence of supernumerary stadia (see Corbet, 1999: p.209). The distributions in Figure 3 suggest a seasonal variation in HW of F-1 that would be consistent with the existence of supernumerary stadia (Corbet *et al.*, 1989; Aoki, 1999). Nevertheless the growth ratio between modal HW in F-1 and F-0 (1.1825) allows one to estimate the approximate number and dimensions of earlier stadia by extrapolation backwards (Figures 1 and 2). Our resulting estimate of 15 stadia (including the prolarva) equates with the total recorded for this species by Balfour-Browne (1909) but exceeds the usual value of 11–13 (rarely 15) (including the prolarva) recorded by Sternberg & Buchwald (1999: p.308).

The intermittent, wide deviations in the correlation between BL and HW (Figure 2) may be caused by extension and telescoping of the abdomen associated with ecdysis; and they emphasize the limitations of using BL as a criterion of larval size. The decline in the percentage of overall length contributed by the caudal lamellae has been reported for two

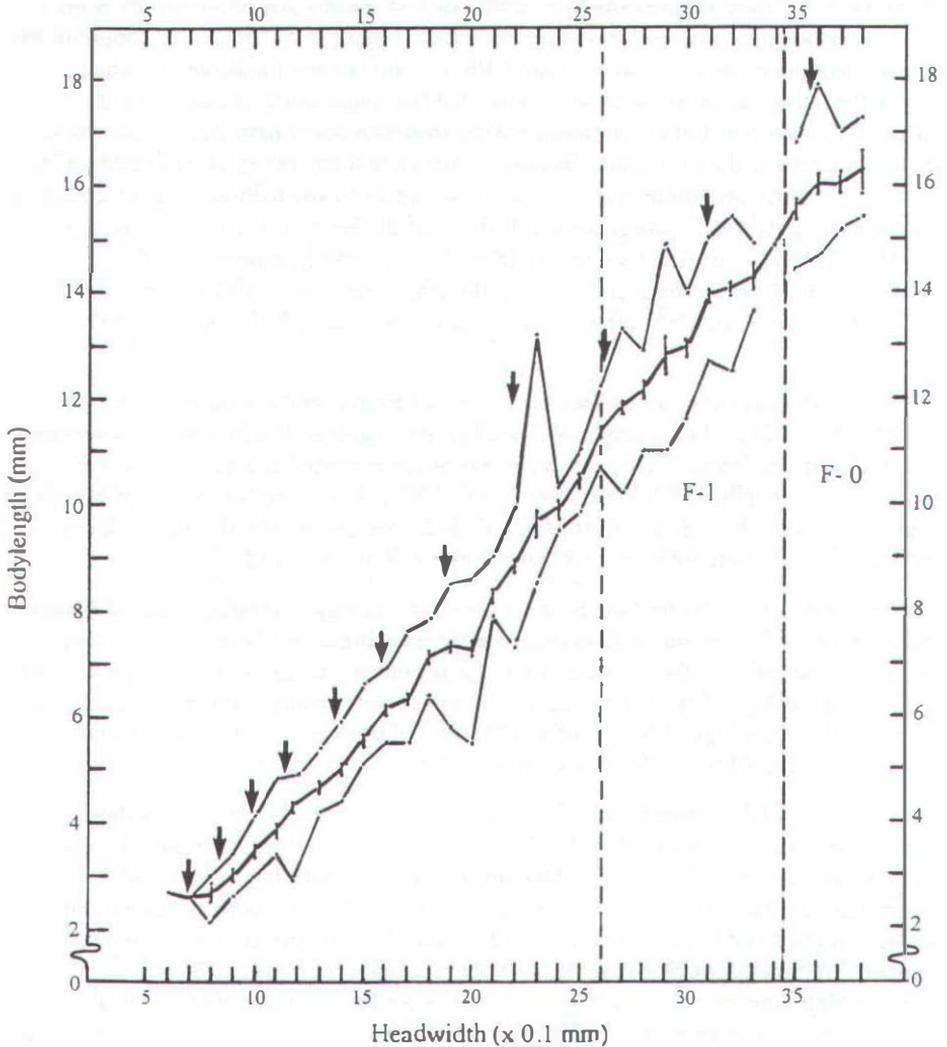


Figure 2. *Enallagma cyathigerum* larvae in Rohallion Loch. Relationship between head width (HW) and body length (BL) (thick line) and the extent of the standard deviation for all larvae examined for these variates (N=694). Vertical arrows indicate the notional positions of stadia as portrayed in Figure 1.

species of *Coenagrion* (Gardner, 1954a; Corbet, 1955) and for *Pyrrosoma nymphula* (Gardner, 1950). It is evidently a common feature among coenagrionid larvae.

The extent of the flying season shown (as duration of oviposition) in Figure 3 has been inferred from the recorded general flying season for this species (see below), from the presence at Rohallion of many mature adults on 30 June 1984 (E. Smith, personal communication), and from our observation (reported above) of many mature adults there on 3 July 1987. In southwestern Germany (48–49°N) this species often has the longest emergence period of any odonate, beginning in early May and extending to September (Sternberg & Buchwald, 1999: p.303). Emergence is also temporally dispersed, lasting more than 116 days in the Upper Rhine region (c.48°N) (Schiel, 1996: p.84), where EM_{50} may be reached only on the 50th day of the emergence period. Near Braunschweig, Germany (c. 52°N), EM_{50} was reached after about 25 per cent of the emergence period (Schulz, 1995: p.76). The maturation period has been recorded as averaging 10–12 days but varying between 7 and 30 days (Sternberg & Buchwald, 1999: p.303). The flying season, like the emergence period, is unusually protracted, mature adults being active by water in southwestern Germany from mid May until mid September and occasionally until the beginning of October (Sternberg & Buchwald, 1999: p.303). In Britain the flying season is somewhat shorter, from early June to early September (Brooks, 1999: p.88) but is still considerably longer than that of most other odonates. In Cheshire, UK (c.53°N), the average and maximum longevity of mature males was 12 days and 5–6 weeks respectively (Parr, 1976). In the laboratory mature females survive longer than males (Cordero, 1994). In Hodson's Tarn, a habitat in the Lake District of northwestern Britain (c.54°N) broadly resembling Rohallion Loch (Macan, 1964), emergence occurred from mid May until mid July, being concentrated in June and showing a slight peak in the second half of that month. The latest recorded emergence was on 13 August, and adults disappeared in September. We may expect the flying season at Rohallion Loch to resemble that at Hodson's Tarn. In the Norfolk Broads, southeastern Britain (c.52°N), *E. cyathigerum* had a longer emergence period (mid May until the end of August; mainly mid May to July) than any other species of sympatric odonate, and a longer flying season (end of May until end of August) than any other sympatric species except *Ischnura elegans* (Johansson, 1978). Some investigators have recorded two broad peaks of emergence (e.g. Macan, 1964; Sternberg & Buchwald, 1999: p.303) and this invites comparison with the two peaks of abundance of adult males reported in mid June and mid July by Parr (1976) in Cheshire, UK, and in mid June and mid August in Bavaria (c.48–50°N) by Kuhn & Burbach (1998: p.103). At Rohallion Loch, F-0 larvae showed signs of advanced metamorphosis only in early June and mid July (Table 1). If, at lower latitudes and in a suitable habitat, another emergence peak appears very late in the season, this may represent the emergence of larvae that hatched (from eggs) in spring of the same year and are thus bivoltine (see Burbach, 2000). The knowledge that in the laboratory, when maintained at 25°C, *E.*

cyathigerum can complete larval development in 61 days (Schulz 1995: p.76) makes bivoltinism a distinct possibility in habitats where prey availability and temperature permit. In southwestern Germany (c. 48-50°N), *E. cyathigerum* is reported as being typically univoltine (Kuhn & Burbach, 1998).

On the assumption that embryonic development is completed in 2-3 weeks at 25-30°C (Schulz 1995: p.76), we assume that eggs begin to hatch after about 4 weeks or more in Rohallion Loch, that is in early July (Figure 3: star symbol next to sample 3) and that the resulting larvae appear as the junior cohort during the summer, first becoming evident in our samples in August (Figure 3: sample 4) and then conspicuous by mid September (Figure 3: sample 5, reference point a). The long period during which hatching can take place is consistent with the wide variation in size in the larval population at all times of year, even in what is evidently the junior cohort (e.g. sample 4). We find it plausible to trace this cohort to sample 6 (Figure 3: b), whereupon, after overwintering at a modal HW of 1.35mm (stadium c. F-6) until sample 2 (Figure 3: c), the cohort exhibits rapid growth during the summer, attaining a modal HW of 1.9mm (c. stadium F-4) by mid July (Figure 3: d) and 2.65mm (c. stadium F-2) by late August (Figure 3: e). Between late August and mid September many larvae enter stadium F-1 (Figure 3: f) and a small proportion enter F-0, though apparently not proceeding to metamorphosis. It is in this stadium-distribution that the population overwinters for the second time. Although a few larvae overwinter in F-0, it appears that the main entry to F-0 is delayed until the next spring, the life cycle being mainly that of a semivoltine summer species (*sensu* Corbet, 1954). So the emergence period, as evidenced by the presence of metamorphosing F-0 larvae during June and July (Figure 3: samples 2 and 3), and the long flying season, is clearly protracted, giving rise to the long duration of oviposition and hatching of eggs. By analogy with the source of the second emergence peak in the Emperor Dragonfly, *Anax imperator* Leach (Corbet, 1957: p.39) and *Pyrrosoma nymphula* (Corbet & Harvey, 1989: p.143) we note the possibility that the two emergence peaks falling about two weeks apart in several populations of *E. cyathigerum* (see above) may represent the emergence of larvae that overwintered in F-0 and F-1 respectively. Having regard to what is known about methods of seasonal regulation in other temperate-region Odonata (see Corbet, 1999: pp.230-234), a plausible assumption is that in this population of *E. cyathigerum* a photoperiodic response in late summer and autumn is inhibiting metamorphosis in F-0 larvae and (less rigorously) ecdysis in F-1 larvae. The fact of emergence having been recorded in late August by Burbach (2000) suggests that, if there is an autumnal inhibition induced by photoperiod, it does not become effective much before late August (allowing for the time taken to complete metamorphosis). Although a semivoltine cohort can be traced without difficulty from the distributions in Figure 3, cohort-overlap seems a distinct possibility, perhaps leading to univoltinism in a small proportion of larvae, this proportion probably varying according to prey availability and temperature during the spring and summer, such that a few of the F-1 larvae evident in sample 4 (late August) may be able to enter

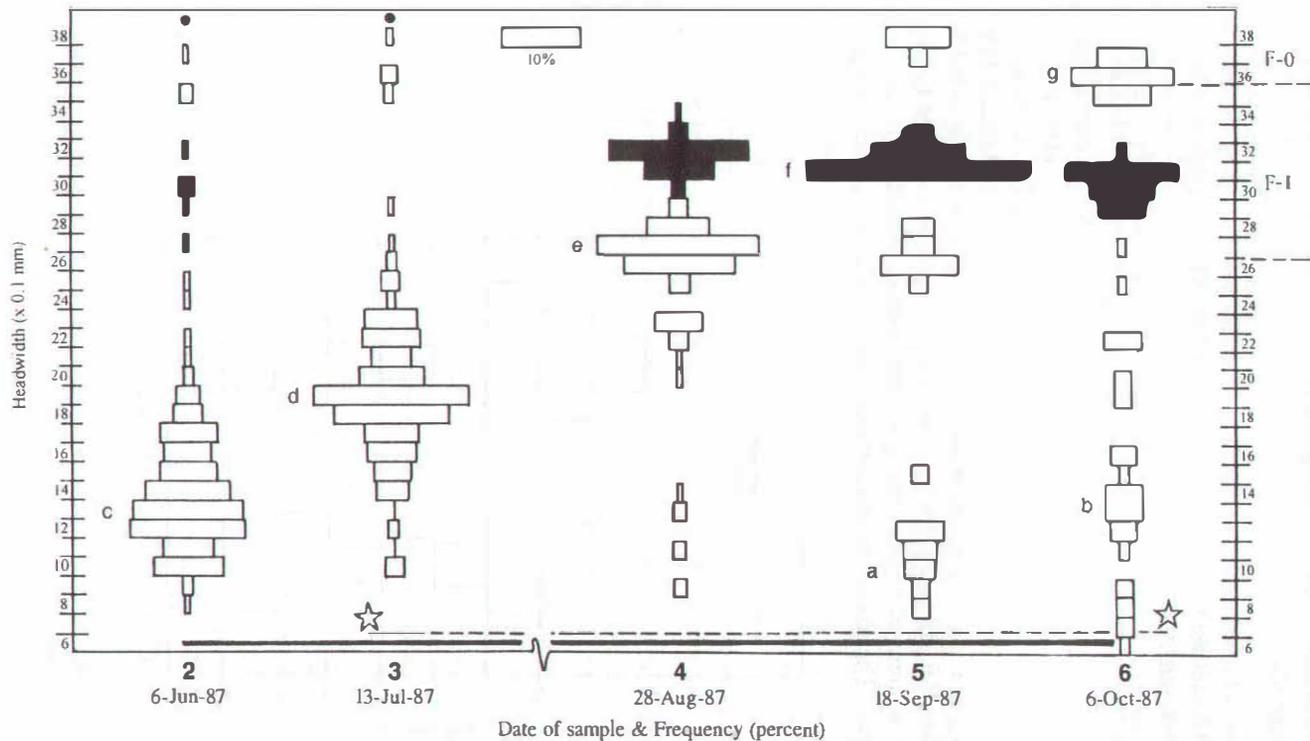


Figure 3. *Enallagma cyathigerum* larvae in Rohallion Loch. Headwidth (HW) frequency distributions for samples 2–6. Temporal intervals between samples do not necessarily represent the real intervals between them. Entries for stadium F-I are shown in black. A filled circle just beneath the upper horizontal frame shows a time when final-stadium larvae were undergoing metamorphosis (see Table 1, column F). The thick dark line just above the lower horizontal frame shows the inferred duration of oviposition, and the broken line above it, marked with a star at each end, shows the inferred duration of egg hatching. Lower-case letters a-g represent reference points for tracing the growth of a larval hatching cohort from shortly after hatching (a) until just after entry to the final stadium (g) (see text).

F-0 and proceed to metamorphosis and emergence before their development is inhibited by autumnal photoperiods.

That a similar pattern of development prevailed in 1986 (the year preceding the samples shown in Figure 3) is indicated by Figure 4 which shows the BL distributions of larvae in early October 1986 and 1987. They are broadly similar.

On the basis of our results, we infer that the life cycle of *E. cyathigerum* in Rohallion Loch can be summarized as follows. After an extended period of hatching during the first summer of the aquatic stage, larvae pass their first winter at a modal HW of *c.* 1.25mm (*c.* stadium F-7), coexisting with a senior cohort in F-1 and F-0. In their second summer, larvae of the junior cohort grow rapidly, from *c.* 1.25 to *c.* 3.05mm HW (*c.* stadia F-7 to F-1), entering their second winter as the senior cohort, mostly in F-1 but also (as a minority) in F-0. All larvae that pass their second winter in F-1 enter F-0 in their third summer, whereupon metamorphosis and emergence ensue, though not persisting into August. The size of the smallest members of the junior cohort during

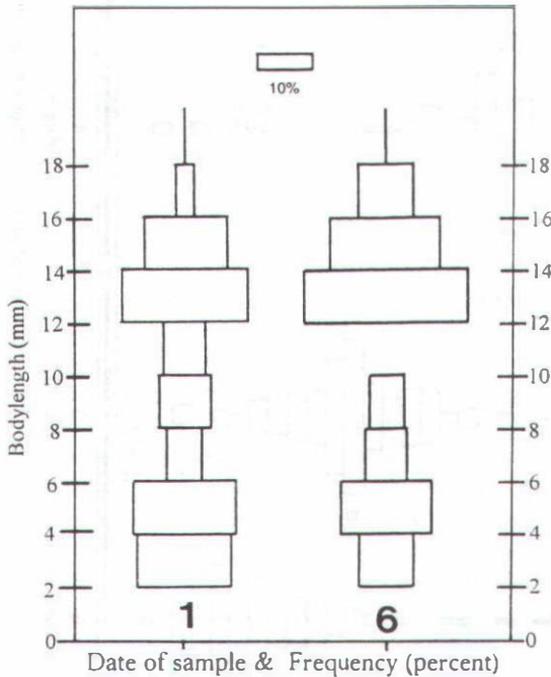


Figure 4. *Enallagma cyathigerum* larvae in Rohallion Loch. Body length (BL) frequency distributions of samples 1 and 6. For attributes of samples see Table 1. The horizontal scale bar at centre top equates to 10 per cent.

their first winter (Figure 3: sample 6) exposes the possibility that some such larvae might fail to attain F-1 by the end of their second summer and therefore require three, not two, years to complete a generation.

Our conclusions conform well with those of Macan (1974) derived from his detailed, long-term study of this species in Hodson's Tarn (c. 54° N), a habitat broadly resembling Rohallion Loch in both its dimensions and endowment of aquatic macrophytes (Macan, 1964: p.325; 1975). In Hodson's Tarn, larvae from the eggs hatching earliest grew fast enough to be able to emerge the next year (univoltinism), but most eggs hatched later, producing larvae that did not grow much until the following summer (i.e. their second summer), equipping them to emerge the next year, during their third summer (semivoltinism). As we did, Macan found that size-overlap between cohorts made it difficult to trace cohort growth. The size-distributions of larvae in October in Hodson's Tarn and Rohallion Loch were similar. Thus in Hodson's Tarn a few larvae were univoltine, most were semivoltine and a few required three years to complete a generation, emerging in their fourth summer. More larvae required a generation time of three years at higher densities (Macan, 1964: p.332). Tighter comparison is difficult because Macan did not distinguish the two last stadia; nor did he specify the dimension he measured, beyond referring to it as 'length' (Macan, 1964: p.331). Our results are consistent with the conclusion by Schultz (1995), from laboratory studies, that *E. cyathigerum* larvae grow rapidly and exhibit unsynchronized development.

There are two other respects in which comparison between our results and those of Macan is informative, bearing in mind that Macan's study site, Hodson's Tarn, closely resembles Rohallion Loch. Apart from the similarities already mentioned, it is likely that the seasonal march of water temperature (Macan 1966) was also closely similar on account of its close correspondence with the pattern in Dykehead Pond (c. 57° N), a habitat not far from Rohallion Loch (Corbet & Harvey, 1989: p.136). Both habitats showed an annual range of near-surface water temperature of between about 0 and 22°C.

A second respect in which our findings resemble those of Macan (1964) in Hodson's Tarn is in the microhabitat distribution of larvae among plant zones. In both waterbodies, larvae of virtually all sizes occurred mainly in *Littorella* swards, real or artificial. During our first exploratory samples we discovered that very few larvae were to be found elsewhere (e.g. in marginal *Carex*) and that thereafter larvae of all sizes were consistently found in high numbers in the *Littorella*. Macan (1964: p.349) found the smallest larvae to be ubiquitous in Hodson's Tarn but most abundant in *Littorella* swards in shallows near the shore, and least abundant amongst *Carex*. Macan inferred that large larvae moved from the *Littorella* into *Myriophyllum* before emergence. Clearly larvae must leave *Littorella* swards before emergence, which may explain the under-representation of F-0 larvae in samples 2 and 3 at Rohallion (Figure 3). In Upton Broad, southeastern UK (c. 53° N) (where there was no *Littorella*) by September the great

majority of smaller larvae of *E. cyathigerum* were inhabiting open mud, while larger larvae were in marginal reedbeds (Johansson, 1978). Larvae started to leave the open mud habitat in March, presumably entering the reedbeds, so that by June only a few large larvae remained in mud.

A third respect in which our findings merit comparison with those of Macan (1964) in Hodson's Tarn is the co-existence of *E. cyathigerum* with insectivorous fish. In Hodson's Tarn, the density of larval *E. cyathigerum* was scarcely affected by the introduction of 500 Brown Trout, when *Littorella* was present in shallow marginal zones. Macan noted that artificial *Littorella* (see Macan, 1972), which was available to larvae in the tarn, was thicker than the real plant and that it harboured more larvae. After introduction of Trout to Hodson's Tarn (where these fish were known to be consuming larvae of *E. cyathigerum* (Macan, 1967)) more larvae were found in *Littorella* and fewer among *Myriophyllum* (Macan, 1966); and larvae were reduced in numbers when vegetation disappeared (Macan, 1977b). These findings are not readily reconciled with the report that in Germany *E. cyathigerum* larvae are vulnerable to predation by fish and that, in the presence of odonate larvae and sticklebacks, *E. cyathigerum* suffered the highest predation from the fish (Steiner *et al.*, 2000). Sticklebacks co-existed with *E. cyathigerum* in Rohallion but we did not record their gut contents. The co-existence of *E. cyathigerum* and Brown Trout in Hodson's Tarn and Rohallion Loch is also at variance with the report that in southwestern Michigan *E. cyathigerum* is confined to fish-free lakes (McPeck, 1989; 1998). Correlated with this distribution in Michigan is the behaviour of larvae in the presence of a predator. Larvae from fish-free lakes are exposed to odonate (anisopteran) larvae as the dominant predators and have developed rapid swimming as an antipredation response, in contrast to congeneric species from lakes containing fish which remain immobile in the presence of a predator. Escape by swimming allows a larva to escape from an anisopteran predator but renders it more vulnerable to predation by fish. Interestingly, *E. cyathigerum* larvae in Europe have been reported as swimming actively in response to a predator's attack (Schulz, 1995: p.91), although in another investigation larvae reduced their activity slightly (i.e. stopped abdomen waving) in the presence of fish (Steiner *et al.*, 2000). Our laboratory findings were that *E. cyathigerum* larvae originating from Rohallion Loch showed no significant depression of feeding rate when exposed to an active invertebrate predator (Chowdhury & Corbet, 1988) and we noted the possibility that larvae might gain immunity from predation by virtue of their occupancy of the *Littorella* sward. This inference would be consistent with the vigorous populations of *E. cyathigerum*, most of which were occupying *Littorella*, co-existing with Brown Trout in Hodson's Tarn and Rohallion Loch. Our laboratory findings do not exclude the possibility that larvae in Rohallion may reduce some facets of their activity in the presence of fish, although Schultz (1995), from laboratory observations, records that larvae of *E. cyathigerum* flee from attack by predators and actively search for food – behavioural traits that would seem to increase their vulnerability to predation by fish. In view of the inferred importance of *Littorella* as a refuge from fish, it is noteworthy that at

Hodson's Tarn Macan (1964) observed a female *E. cyathigerum* climbing (under water) down a Spike-rush (*Eleocharis*) stem until she reached a *Littorella* plant, in the leaf of which she laid at least 49 eggs. Macan (1977a: p.14) noted that larvae hatched from eggs laid in 'deep' water in Hodson's Tarn where *Littorella* extended to a depth of perhaps 2m. Aquarium studies of *E. cyathigerum* larvae in the presence of *Littorella* might be informative. Likewise, a comparison between the antipredation behaviour of *E. cyathigerum* in western Europe and North America might throw light on the apparent anomalies we have noted.

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Migrant and dispersive dragonflies in Britain during 2001

ADRIAN J. PARR

10 Orchard Way, Barrow, Bury St Edmunds, Suffolk IP29 5BX

Summary

The year 2001 was in some respects a quiet one, with fairly low numbers of many of the traditional migrant species recorded. Indeed there were no reported sightings of Yellow-winged Darter, *Sympetrum flaveolum* (L.) during the course of the year, for the first time in nearly a decade. However, there were several reports of *Anax parthenope*, and an interesting record of *Orthetrum brunneum* from Guernsey in the Channel Islands, the first confirmed sighting for our region. The outstanding records of 2001 must be the sightings of literally hundreds of *Erythromma viridulum* at new sites in southeast England, predominantly near the coast of East Anglia. This would appear to result, at least in part, from a substantial immigration from the Continent during late July and August.

Account of Species

Significant British records reported to the BDS Migrant Dragonfly Project during 2001 are outlined below. Information on complementary events in Ireland can be found on the DragonflyIreland website (Nelson *et al.*, 2001). A report on events in Britain during 2000 was published by Parr (2001).

Calopteryx virgo (L.) – Beautiful Demoiselle

2001 – One individual was observed apparently flying in off the sea at Lizard Point, Cornwall, on 27 August, during a day when there was much bird and some visible insect migration (MT).

Ischnura pumilio (Charpentier) – Scarce Blue-tailed Damselfly

2001 – An *aurantiaca* phase female was examined in the hand at Farlington Marshes, Hampshire, on 29 July (AT). This species has a good dispersive capacity (Cham, 1991), so the individual may well have originated from the colonies in the New Forest area some 25–30km away, although with migratory species such as *Anax parthenope* and *Sympetrum fonscolombeii* appearing in southern England at this time, a more distant origin is also possible.

Erythromma najas (Hansemann) – Red-eyed Damselfly

2001 – One at Yafford, Isle of Wight, on 14 July (DD) was the first record for the island. This species is known to be currently expanding its range in Britain (e.g. Brooks & Lewington, 1999).

***Erythromma viridulum* (Charpentier) – Small Red-eyed Damselfly**

2001 – The species was first discovered in Britain as recently as 1999, when colonies were identified in Essex (Dewick & Gerussi, 2000). During the following year a further stronghold was found on the Isle of Wight (D. Dana in Cham, 2001). In 2001, there was further consolidation of the populations within these regions, but the year was also notable for a large number of records from new areas, principally near the coast between Kent and Norfolk, but also from a few sites well inland. A full analysis of these spectacular events has been published by Cham (2002) and it would appear that many of the new records might have originated from fresh immigrations from the Continent.

During the last days of July and into August, several sites for *E. viridulum* were discovered in coastal Suffolk. A single individual caught on the beach at Sizewell on 31 July (PC) would appear to be an immigrant and it seems possible that other Suffolk records could also have included immigrants. A further, more clearly defined, migration event took place in mid August. On the afternoon of 13 August, five individuals were observed at a pond at Folkestone, Kent (NJ, JR). The main influx appeared to start on 14 August, when 170 appeared during the course of the day at Eccles-on-Sea, Norfolk (NB), and a further 100+ were discovered at the well-watched site of Winterton Dunes, Norfolk. On 15 August, 60+ *E. viridulum* were present near Waxham, Norfolk, with smaller numbers nearby at Horsey (PHe). Twenty or more were also recorded at Fingringhoe Wick, Essex, with similar numbers near Ipswich, Suffolk. In the days following these initial observations, a noticeably decline was observed at many, although not all, of these sites. Around this time, records of *E. viridulum* from inland areas started to occur, perhaps indicating further dispersal from the coastal sites. Most inland sightings came from a zone within 20km of the coast, but notable sightings were made near Bedford (starting on 24 August), near Luton (28 August), at Littlebury Green, north-west Essex, and at Pitstone, Buckinghamshire (Cham, 2002).

Although rigorous proof that *E. viridulum* can breed successfully in Britain is still lacking, there seems little doubt that this is indeed the case. Many observations of oviposition during 2002 suggest that this species is well on the way to successfully colonizing south-east England. It will be of considerable interest to monitor future expansion, although the role of continuing immigration, as opposed to local dispersal, will become increasingly difficult to determine.

***Aeshna cyanea* (Müller) – Southern Hawker**

2001 – There was an unconfirmed report of one from Ramsey, Isle of Man, on 1 July that, if definite, would be the first record for the island. Another was caught at a UV light at Rugby, Warwickshire, on the night of 7 October.

***Aeshna mixta* Latreille – Migrant Hawker**

2001 – A male was caught at a UV light on the night of 30 July at Bradwell-on-Sea, Essex (SD). On 14 August, up to 1000 were present at Great Yarmouth Cemetery,

Norfolk, with some 300 still present the following day. These Norfolk sightings coincide with the influx of *E. viridulum* that was observed just a few miles to the north.

Anax parthenope Sélys – Lesser Emperor Dragonfly

2001 – Although 2001 was generally an unspectacular year for immigrant Odonata from southern Europe, *A. parthenope* was recorded on a number of occasions during the season. Reports came primarily from the regions of southern Cornwall and the coastal Kent/Sussex border, two areas of Britain where this species has been recorded in most recent years. At least two separate influxes took place, one in late July and the other in late August. Complementing the British records were four or five sightings (including a female) from Counties Wicklow, Waterford and Wexford in south-east Ireland made during the last days of July and the first few days of August (Nelson *et al.*, 2001). The first record for this species in Ireland occurred as recently as 2000 (Parr, 2001).

The following British records have been well documented and a small number of additional reports are being investigated further (Parr, 2002a):

26 July–18 August	One or more males seen intermittently at Dungeness RSPB Reserve, Kent (SB)
28 July–5 August	Male at Marazion, Cornwall (DF, PHi)
29 July	Male at Eglarooze Reservoir, Cornwall (LT)
25 August–2 September	Male photographed at Barrow Gurney Reservoirs, Somerset (RM)
26 August	Male at Castle Water NR, Rye Bay, East Sussex (PT)
4–7 September	Male photographed at Bake Farm, Cornwall (KP)

Following observations of oviposition at Bake Farm during 1999 (Pellow, 2000) there were hopes that successful breeding might occur, as had been observed previously in Cornwall (Pellow, 2000). However, the only record of *A. parthenope* at Bake Farm during 2000 was of a single mature male seen during late July and into August (Parr, 2001), and the only record there during 2001 was the late-season male referred to above. With no exuviae found, it would appear that this latest breeding attempt has had little or no success.

Cordulia aenea (L.) – Downy Emerald

2001 – Following the record in Parr (2001) of one seen in Staffordshire, c.65km from known breeding sites, one was seen on 17 July 2001 at Ludham Marshes, Norfolk, c.15km from the only Norfolk site for this species (DH).

Libellula depressa L. – Broad-bodied Chaser

2001 – In what was otherwise a late season, an early record from Portland Bill, Dorset, on 24 April might perhaps refer to an immigrant, especially since an example of the migratory Dark Swordgrass moth, *Agrotis ipsilon* (Hufnagel), had been trapped at the same locality on the preceding night (MC). One at Heysham NR, Lancashire, on 6 July was unusual for the site, and indeed the area in general. Since it was present in the company of *S. fonscolombi*, it too could have been a migrant.

***Orthetrum brunneum* (Fonscolombe) – Southern Skimmer**

2001 – A male was caught at La Grande Mare, Vazon, Guernsey sometime around 10 July (CD; Long, 2002). This represents the first confirmed record for Britain and the Channel Islands. The species has its strongholds in southern Europe, but is known to currently be expanding its range to the north (Parr, 2002b). Sightings of unfamiliar blue dragonflies at the same site during 1999 and 2000 (CD) may also refer to this species, as there are no recent records of other *Orthetrum* (or indeed *Libellula*) species from Guernsey (Merritt *et al.*, 1996), although *O. cancellatum* is established on some of the other Channel Islands. Further investigations are required in order to ascertain the precise status of this species on Guernsey.

***Orthetrum cancellatum* (L.) – Black-tailed Skimmer**

2001 – On 7 July at Heysham NR, Lancashire, two males appeared in quick succession, apparently from the south-east (PM). They stopped briefly, then left to the west. These were the only records of the year from that site, which is near the north-western limit of the range for this species in Britain.

***Sympetrum striolatum* (Charpentier) – Common Darter**

2001 – Little of note was reported during the year. Counts throughout the summer and autumn at two localities in Somerset both showed peaks on 4 September and 28 September (TW), perhaps indicative of some general movements.

***Sympetrum fonscolombei* (Sélys) – Red-veined Darter**

2001 – Although several records were forthcoming, particularly from the species' strongholds in Cornwall, events during 2001 were relatively quiet by recent standards, and no counts reached double figures. This contrasts with the significant influx seen during the previous year (Parr, 2001). A regular pattern of migratory abundance, with major influxes occurring roughly every other year, does now seem to be developing (Parr, 2002c).

The first records for the year occurred during spring at several of the regular sites for the species. On 17 May a male was at Marazion, Cornwall, and on 26 May one was seen at Spurn NNR, East Yorkshire. One (an immature) was seen at Bake Farm, Cornwall, on 10 June and another was noted on the Lizard, Cornwall, on 11 June. On 30 June, two exuviae were found at Dungeness, Kent (JGB). Clearly, some of these early season records refer to British-bred individuals. During July records of very low numbers of mature adults were received from not only these regular sites, but also from single localities in Hertfordshire, Lancashire and County Durham, and from several further locations in southern Cornwall. Since some of these sites had also held *S. fonscolombei* during 2000, these records may include further British-bred individuals. However, fresh immigration also seems likely, given the concentration of records into two distinct periods (early and late July), the latter coinciding with reports throughout the country of more obvious migrants. A few new records occurred during August (single sites in Cornwall,

Norfolk and Warwickshire) but late season sightings were very sparse, and there was little sign of the autumn emergence of locally bred individuals that have characterized recent years. No autumn emergence was observed at Bake Farm, Cornwall, where immatures have been recorded late in the season during other recent 'quiet' years. A total of six individuals accidentally caught in beetle flight traps set between 5 September and 5 October near Llandarcy, Glamorgan (BMNH) may be indicative of a nearby breeding site. The last record for the year was from the Lizard, Cornwall, when a single individual was trapped along with several migrant moths in a UV moth trap on the night of 25 October, under conditions favourable for immigration from the south.

Oviposition was only positively observed at two sites during the course of the year (at Bake Farm, Cornwall and Rainton Meadows, Durham), although it may have been missed elsewhere. Given the likelihood of further major immigrations in the near future, *S. fonscolombei* seems likely to remain a familiar, if rather local, species.

Sympetrum danae (Sulzer) – Black Darter

2001 – Although Suffolk currently lacks an established breeding population, there was an unconfirmed report of six from the coast near Sizewell on 26 July. The species was also noted from two sites on the Isle of Wight: Afton Down on 9 September (SKJ) and Alverstone on 12 September, apparently the second and third records for the island. It would seem that greater than normal dispersal within Britain, or else some limited immigration from abroad, might have taken place.

Sympetrum sp.

2001 – An immature male *Sympetrum* showing several characteristic features of the Vagrant Darter, *Sympetrum vulgatum* (L.), including the dark mark on the frons extending down the inner margins of the eye (Askew, 1988), was photographed on 12 August on the Teeside Marshes (JD). The individual however seemed to have a less obviously clubbed abdomen than is typical of the adult male of this species, and the identity of the insect is still under review. On the Continent there has been some speculation that *S. striolatum* may on very rare occasions show a moustachial streak (M. Wasscher, pers. comm.). The possibility of a hybrid must also be considered.

Discussion

In summarizing the events of 2000, it was stated (Parr, 2001) that 'Although the total number of migrants observed ... was not as high as in the best of recent years, it is clear that the trend towards the increased occurrence in Britain of what were previously thought of as 'southern' species still continues.' Although the precise details of the year's events were different, this statement also provides a very appropriate summary for 2001. The increasing occurrence of 'southern' species appears to be unprecedented and may well be related to some factor with broad influence, such as climate change. As such, shifts in the British odonate fauna deserve continual close scrutiny. An increasing

number of observers are now aware of migrant dragonflies, but the events with *E. viridulum* have shown that damselflies are also affected by the phenomenon. A similar close scrutiny of damselfly populations might prove enlightening, with species such as *Lestes barbarus* (Fabricius) perhaps a candidate to appear on the British mainland in the near future. These are certainly interesting, if uncertain, times!

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Mate guarding behaviour during intense competition for females in the Common Blue Damselfly *Enallagma cyathigerum* (Charpentier)

STEVE CHAM

24 Bedford Avenue, Silsoe, Bedford MK45 4ER

Introduction

Male guarding of female Odonata during oviposition is well documented over a range of species (Corbet, 1999). Females of the Common Blue Damselfly, *Enallagma cyathigerum* (Charpentier) oviposit underwater in the stalks and leaves of a range of plant species. Males hover over the site where females are ovipositing waiting for them to resurface. Miller (1990) provides a comprehensive account of this process and discusses the rescue service provided by males of *E. cyathigerum*. This paper provides further insight into the need for contact guarding in *E. cyathigerum* during oviposition.

Observation site

Observations of *E. cyathigerum* behaviour were made at a large brick pit complex in west mid-Bedfordshire over a period of 15 years. Large areas of open water with bare margins have formed in these pits. The water is typically deep and cold, inhibiting the lush growth of submerged plants and the open nature of the pits creates allows wind-driven waves to erode the banks and further inhibit the growth of marginal vegetation. Small stands of Common Reed (*Phragmites*) and Bulrush (*Typha*) have developed in more sheltered areas. In these areas submerged fine leaved plants such as the Fennel Pondweed (*Potamogeton pectinatus*) have also gained a foothold in water depths of about 2m. Where it breaks the water surface, this plant provides preferred oviposition sites for *E. cyathigerum*. Under favourable weather conditions, high densities of males can be seen in these 'favoured' areas.

During August 1993, filming of guarding behaviour was undertaken at Rookery Pit using a Canon Ex1 Hi8 video camera. Subsequent analysis of the film sequences revealed some additional details of guarding behaviour during oviposition that were not apparent during the site visits.

Observations

During filming of an area of submerged vegetation (approximately 1m by 2m), an estimated 50–70 males were in view. At such high densities, competition between males is intense. Males either hover over the prime areas searching for resurfacing females, or

perch on any small plant stem above the surface in readiness. Hovering males readily investigate any floating objects that 'look' like females, such as the parachute seeds of flowers of the Compositae.

Tandem pairs approaching the prime ovipositing sites immediately come under harassment from single males. The females in tandem appear from the recordings to be the passive party in site selection. The males 'steer' the tandem in an attempt to avoid the attentions of other males. As the pair approach the water, the female will readily grasp any plant that breaks the surface. Single males repeatedly harass the tandem pair, trying to grasp the female with their legs. This occurs most frequently when the female is on, or close to, the surface of the water. However, several observations were made of single males attempting this whilst the tandem was still in flight.

In one tandem pair, the male remained in tandem whilst the female started ovipositing just below the water surface. He remained attached for 43 seconds before releasing her to continue on her own. This contact guarding behaviour is perhaps understandable in the light of the following observation.

A tandem pair was observed approaching the water with the male steering towards the patch where submerged vegetation just reached the surface. On contact with the water, the female immediately submerged with the male still in tandem. The male released its hold on the female at the point at which his upper thorax was just submerged. At this point a single male flew in and attempted to grasp the almost submerged female with its legs. The first male reattempted tandem with the female, but a struggle followed in which the aggressor was able to displace the first male from the female. At this point the female was below the surface of the waters and held by both males. The first male resurfaced and flew off. The second male then proceeded to climb down the back of the female's abdomen whilst she was fully submerged and attempting to oviposit until he successfully achieved tandem with her. Using jerks of his upper body, the male was able to pull the female free of the plant stem and float to the surface with her. The tandem was initially unable to fly off due to waterlogging of the body and wings, but the male managed to drag her to the nearest emergent stem about 0.3m away. After a few attempts they flew off in tandem.

Discussion

These observations demonstrate that single males of *E. cyathigerum* will harass tandem pairs as they approach the oviposition site and also when oviposition commences. When densities are high it is in the interest of the males to stay in tandem with the female for as long as possible. This increases his chances of guarding the female until she has laid the eggs that he is likely to have fertilized. This guarding behaviour is imperative at high densities as aggressor males appear to go to great lengths to 'win over' a female and are prepared to submerge in order to achieve tandem.

These observations would have been difficult without filming this behaviour. At high densities there is so much happening that it is difficult to discern the detail of underwater activities. Filming provides a useful tool and can reveal many details that go unobserved in the field.

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INSTRUCTIONS TO AUTHORS

Authors are asked to study these instructions with care and to prepare their manuscripts accordingly, in order to avoid unnecessary delay in the editing of their manuscripts.

Word-processed manuscripts may be submitted in electronic format either on disk or by e-mail.

Typewritten manuscripts should be produced using black ribbon, double-spaced, on one side of the page only and with margins at least 25mm at the left, top and bottom. Text pages should be numbered and footnotes avoided.

Words that are to appear in italics (e.g. names of genera and species, though not of families) should be underlined if an italic font is not available.

Use of these terms is acceptable: 'exuvia' for cast skin (plural: 'exuviae'); 'larva' (instead of 'naiad' or 'nymph'); 'prolarva' to designate the first larval instar.

Dates in the text should be expressed in the form: 24 July 1994.

References cited in the text should be in the form '(Longfield, 1949)' or '... as noted by Longfield (1949)'. All references cited in the text (and only these) should be listed alphabetically at the end of the article in this form:

Hammond, C. O. 1983. *The dragonflies of Great Britain and Ireland*. 2nd edition (revised by R. Merritt). Harley Books, Colchester. 116 pp.

Longfield, C. 1949. The dragonflies of the London area. *The London Naturalist* 28: 90--98.

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The legend for each table and illustration should allow its contents to be understood fully without reference to the text. The approximate position of each table and figure should be indicated in the text.

SCIENTIFIC AND ENGLISH NAMES OF BRITISH ODONATA

ZYGOPTERA

Calopteryx virgo
Calopteryx splendens
Lestes sponsa
Lestes dryas
Platycnemis pennipes
Pyrrosoma nymphula
Ceragrion tenellum
Coenagrion mercuriale
Coenagrion scitulum
Coenagrion hastulatum
Coenagrion lunulatum
Coenagrion armatum
Coenagrion puella
Coenagrion pulchellum
Enallagma cyathigerum
Ischnura pumilio
Ischnura elegans
Erythromma najas
Erythromma viridulum

ANISOPTERA

Aeshna caerulea
Aeshna juncea
Aeshna mixta
Aeshna cyanea
Aeshna grandis
Anaeshaesna inaeceles

DAMSELFLIES

Beautiful Demoiselle
Banded Demoiselle
Emerald Damselfly
Scarce Emerald Damselfly
White-legged Damselfly
Large Red Damselfly
Small Red Damselfly
Southern Damselfly
Dainty Damselfly
Northern Damselfly
Irish Damselfly
Norfolk Damselfly
Azure Damselfly
Variable Damselfly
Common Blue Damselfly
Scarce Blue-tailed Damselfly
Blue-tailed Damselfly
Red-eyed Damselfly
Small Red-eyed Damselfly

DRAGONFLIES

Azure Hawker
Common Hawker
Migrant Hawker
Southern Hawker
Brown Hawker
Norfolk Hawker

Anax imperator

Anax parthenope

Anax junius

Hemianax ephippiger

Brachytron pratense

Gomphus vulgatissimus

Cordulegaster boltonii

Cordulia aenea

Somatochlora metallica

Somatochlora arctica

Oxygastra curtisii

Libellula quadrimaculata

Libellula fulva

Libellula depressa

Orthetrum cancellatum

Orthetrum coerulescens

Sympetrum striolatum

Sympetrum nigrescens

Sympetrum fonsolombei

Sympetrum flavolum

Sympetrum sanguineum

Sympetrum danae

Sympetrum pedemontanum

Sympetrum vulgatum

Crocothemis erythraea

Pantala flavescens

Leucorrhinia dubia

Emperor Dragonfly

Lesser Emperor Dragonfly

Green Darner

Vagrant Emperor Dragonfly

Hairy Dragonfly

Club-tailed Dragonfly

Golden-ringed Dragonfly

Downy Emerald

Brilliant Emerald

Northern Emerald

Orange-spotted Emerald

Four-spotted Chaser

Scarce Chaser

Broad-bodied Chaser

Black-tailed Skimmer

Keeled Skimmer

Common Darter

Highland Darter

Red-veined Darter

Yellow-winged Darter

Ruddy Darter

Black Darter

Banded Darter

Vagrant Darter

Scarlet Darter

Globe Skimmer

White-faced Darter

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