

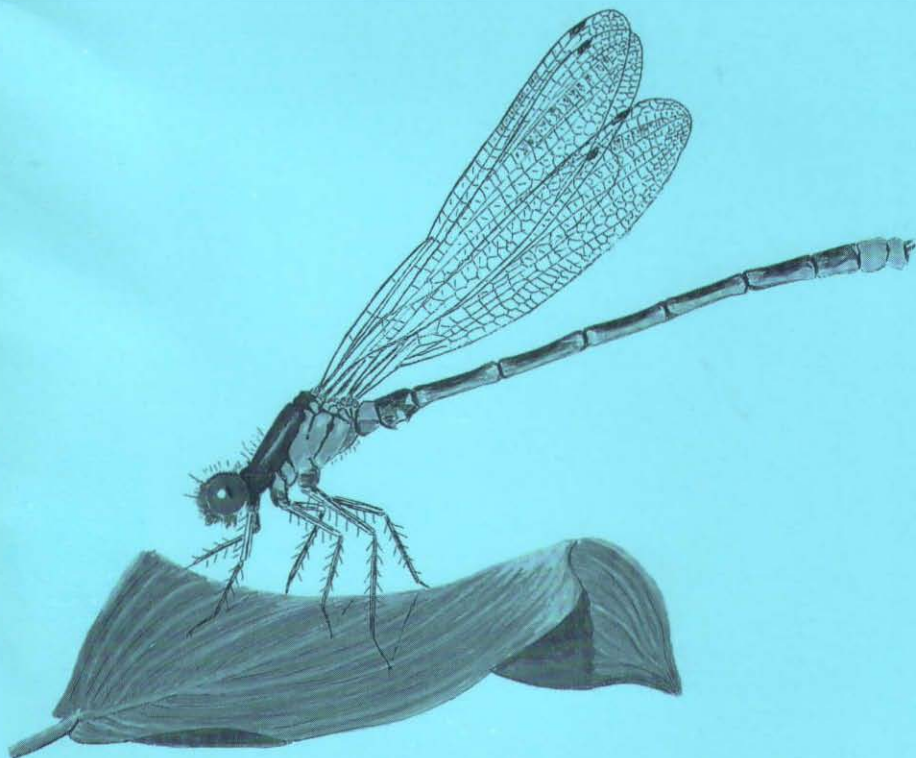


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The Journal of the British Dragonfly Society, published twice a year, contains articles on Odonata that have been recorded from the United Kingdom. The aims of the British Dragonfly Society (B.D.S.) are to promote and encourage the study and conservation of Odonata and their natural habitats, especially in the United Kingdom.

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Front cover illustration of a male Red-eyed Damselfly *Erythromma najas* (Hansemann) by Roderick Dunn.

A comparison of the environmental requirements of larvae of the Banded Demoiselle *Calopteryx splendens* (Harris) and the Beautiful Demoiselle *C. virgo* (L.)

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Introduction

The genus *Calopteryx* is a small one by Odonata standards, with about thirty world species, three of which, represented in a number of sub-species and variable colour forms, occur in Europe. This compares with N. America which has five species.

The two British species, *Calopteryx virgo* (L.) and *C. splendens* (Harris), are both widely distributed through southern England, becoming scarcer further north. Much has been written on their larval requirements, with general agreement on different preferences. *C. virgo* is believed to favour faster flowing water, a greater acidity tolerance, and a higher level of oxygenation. *C. splendens* prefers more open habitats, fewer trees, slower water and has a greater tolerance of alkalinity. However, no work has been undertaken on the precise levels at which each species' requirements differ, or reach mutual acceptance or rejection. The object of this project was to provide a contribution towards rectifying this.

The only previous detailed work on the habitats and ecological requirements of the two British *Calopteryx* species covered the Wey river system of Hampshire and Surrey. Here the author observed that there has been considerable variation in the reported habitat requirements of these species (Prendergast, 1988).

Methods

Ten localities over three counties were chosen for each species (Tables 1–3). Only one of the two species occurs at each site. Although all the sites chosen for *C. virgo* are located in Hampshire and all the sites chosen for *C. splendens* are located in Dorset and Wiltshire, both species are widely distributed throughout the three counties. From March 1989 to February 1990, each site was visited during the first week of each month, with pH, temperature and water flow, depth and volume recorded. Temperature and pH were measured using a B.D.H. Electronic Jenway meter (model 3061). The rate of flow was measured by timing a table-tennis ball floated between two fixed points. Mid-water and basal flow rates may of course differ from the surface flow rate. The composition of the surface of the stream bed (substrate) was noted in January. In July the marginal, emergent and aquatic vegetation was recorded and measured at its peak. Dissolved

oxygen and nitrate concentrations were measured by colorimetry in the first week of July 1990, October 1990, January 1991 and April 1991 to represent summer, autumn, winter and spring levels.

Table 1. *C. virgo* Locations

No.	Grid Ref.	Locality	Geology
1	SZ 347994	West Crockford Stream, New Forest, Hants	Osborne and Headon Beds
2	SU 254048	Blackwater Stream, New Forest, Hants	Alluvium
3	SU 251038	Oberwater Stream, New Forest, Hants	Peat
4	SU 223017	Holmsley Passage, New Forest, Hants	Barton Sands
5	SU 234004	Avonwater Stream, New Forest, Hants	Peat
6	SU 271027	Silver Stream, New Forest, Hants	Peat
7	SU 186076	Linford Brook (tributary), New Forest, Hants	Barton Clay
8	SU 254025	Duckhole Bog, New Forest, Hants	Peat and Barton Sands
9	SU 199058	Ridley Bottom, New Forest, Hants	Barton Clay and Barton Sands
10	SZ 214996	Stony Moors, New Forest, Hants	Headon Beds

Locality 3 contains the highest population density of *C. virgo*.

Table 2. *C. splendens* Locations

No.	Grid Ref.	Locality	Geology
11	SZ 154942	River Avon, Christchurch, Dorset	Alluvium
12	SZ 158931	Mill Stream, Christchurch, Dorset	Alluvium
13	SZ 118958	Leaden Stour, Throop, Dorset	Alluvium
14	SZ 126985	Moors River, Hurn, Dorset	Alluvium
15	SZ 158952	Winkton Stream, Dorset	Alluvium
16	SZ 161943	Burton Stream, Dorset	Alluvium
17	SZ 052939	Alderney Heath, Poole, Dorset	Bagshot Beds
18	SU 175222	Downton, Wiltshire	Alluvium, bordering Valley Gravel on W side
19	SZ 133937	River Stour, Bournemouth, Dorset	Alluvium
20	SU 162277	Britford Canal, Wiltshire	Alluvium, bordering Valley Gravel on E side

Locality 13 contains the highest population density of *C. splendens*.

Conditions in 1989 varied from floods in February to drought in July, providing a comprehensive range. The twenty fixed points used for collection of all data were selected because they supported an actively breeding population of the species concerned and were chosen by numbers of larvae and exuviae found. The survey assumes these points to be of maximum suitability for the *Calopteryx* species present.

Breeding species of Odonata were recorded from each of the sites throughout the study period. Records were collected from a 50m length of the waterway in each direction from the point of study. The record is therefore not a complete record for the named waterway, but applicable to the general data collected.

Physical Factors

It has been observed that *C. virgo* larvae often live amongst the stones on the bottom, as well as in weed, whereas *C. splendens* larvae are usually confined to the weed (Gibbons, 1986). Welstead & Welstead (1984) states sandy or gravelly conditions for *C. virgo*, as does Savan (1977). Muddy beds for *C. splendens* are mentioned by McGeeney (1986) and Askew (1988). Of the 20 localities in this survey, only at location 9 for *C. virgo* was the substrate predominately muddy. *C. splendens* was present at three localities with sands and gravels predominating (locations 14, 15, and 19) and one of pebbles (location 17). The general pattern is a strong preference, but not a necessity, for muddy bottoms for *C. splendens*, with silt and detritus, whilst *C. virgo* favours clean pebble bottoms with little or no accumulation of sediment materials.

Table 3. Nature of Locations

Location No.	Width of Sites at study point	Substrate
1	1.55m	clean pebbles to 50mm diameter, small areas of silt & litter
2	4.85m	clean pebbles to 60mm, minimal patches of Tertiary Clay
3	3.38m	pebbles to 60mm with algae, localized litter & detritus
4	2.80m	extensively vegetated, patches of silt, open pebble areas to 65mm
5	5.25m	pebbles to 40mm with algae
6	1.43m	clean pebbles to 75mm
7	1.17m	clean pebbles to 185mm, patches of Tertiary Clay
8	1.20m	extensively vegetated over pebbles to 95mm with algae
9	0.87m	muddy, patches of gravel, much vegetation
10	1.80m	pebbles to 130mm with algae, extensive areas of Tertiary Clay
11	38.60m	heavy silt, vegetation extensive
12	4.54m	silt with detritus, patches of gravel, pebbles to 70mm
13	10.20m	deep silt, leaf litter, patches of gravel to 35mm
14	11.10m	gravel to 50mm with patches of silt
15	2.55m	sand and gravel, clean pebbles to 80mm
16	2.15m	heavy sediment, vegetation localized
17	0.79m	clean pebbles to 115mm
18	7.80m	silt on chalk, flint nodules
19	40.70m	sand and gravel, pebbles to 100mm
20	6.80m	heavy silt, slight gravel to 30mm, chalk fragments

The width of waterways used by each species showed marked differentiation, sites for *C. virgo* showing a median of 1.67m, and a mean of 2.43m. The range was from 0.87m to 5.25m. *C. splendens* sites showed a median of 7.30m, with a mean of 12.52m. The range was a very extensive 0.79m five metres wide would appear to suit either species equally, but those above that width were colonized only by *C. splendens*.

Water temperature

Despite the wide range of waters inhabited by the two species, no great variation in average temperatures throughout the year was found. At the main period of spring emergence, estimated to be the second week of June for *C. splendens* and the last week of May for *C. virgo*, the temperature range for each species varied by 2°C at the lower end of the range. The upper range was almost identical at this point, with a variation of only 0.3°C. The 240 measurements recorded are summarized in Tables 4 and 5. The more shaded localities favoured by *C. virgo* would suggest colder waters, but this appears to be more a tolerance level than a preference.

Table 4. Water Temperature (°C) *C. virgo*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	7.4	9.1	9.2	12.0	12.5	13.7	17.4	19.4	16.3	13.5	8.4	5.6
Mean	7.4	9.2	9.3	11.9	13.3	13.9	17.1	19.4	15.6	13.6	8.7	5.8
Minimum	6.9	8.7	7.1	7.8	10.5	11.9	13.5	15.0	12.7	12.3	7.5	3.4
Maximum	8.0	9.9	11.7	15.3	17.5	16.1	19.4	22.5	17.2	15.2	10.9	7.6

Table 5. Water Temperature (°C) *C. splendens*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	8.7	7.5	10.1	11.7	13.4	15.4	18.3	19.6	16.8	13.4	8.2	5.3
Mean	8.9	7.6	10.2	11.6	13.9	15.4	18.0	19.5	16.4	13.8	8.1	5.8
Minimum	7.7	6.8	9.4	10.7	11.8	12.6	16.7	18.1	14.5	12.7	6.8	3.9
Maximum	10.8	8.9	11.6	12.5	17.1	17.8	19.9	21.3	17.6	15.9	9.4	9.9

When the streams reach a dangerously low level in summer, larvae retreat to pools up to 0.75m

Such pools are of almost still water, and remain approximately 5°C below the temperature of the running stream, with a much reduced O₂ level. If water levels are low at times of emergence, this takes place from such pools, where pH is frequently as low as

4.0. By this stage the pools may be isolated by drought and have evaporated to an average 0.3m in depth in high summer. As such pools are invariably beneath deeply shaded areas, particularly high temperatures are seldom reached.

The more open streams favoured by *C. splendens* remain a more equable habitat throughout their length and, with flatter bases, most maintain a uniform temperature determined by the depth and flow.

Water flow

An unexpected aspect of the project was that of water flow. It has long been observed that *C. virgo* favours rapidly flowing streams and *C. splendens* quietly flowing ones (Longfield, 1937; Fraser, 1956; Hammond, 1983; Chelmick *et al.*, 1980; McGeeney, 1986; Askew, 1988). Whilst the survey showed this frequently to be the case, a more complex pattern emerged (Tables 6 and 7). Most of the streams frequented by *C. virgo* were subject to extreme variation throughout the year, with rapid flow in winter and high susceptibility to drought in the summer. Some streams completely dried up and others were reduced to a trickle connecting deep, almost still pools on the oxbows and bends by a few centimetres of water through stones. Subsequent seasons have shown this to be a regular pattern. In comparison, some of the streams populated by *C. splendens* were found to have rates of flow during normal rainfall conditions that were similar to most of the streams used by *C. virgo*. The *C. virgo* streams were generally located in deeply eroded or artificially produced cuttings. Therefore, in times of high water levels, particularly in February, most of the water was contained within the streams causing a temporary but considerable increase in flow and little or no flooding. During such times further erosion of the sands and gravels tends to produce further bank collapse, both narrowing the channel and increasing flow. Excessive cutting of drainage streams affects some localities (e.g. location 6).

Table 6. Flow in metres per second *C. virgo*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	0.308	0.474	0.328	0.282	0.293	0.189	0.155	0.135	0.117	0.169	0.239	0.213
Mean	0.291	0.499	0.385	0.354	0.309	0.174	0.150	0.149	0.150	0.171	0.220	0.227
Minimum	0.129	0.230	0.127	0.215	0.030	0.033	0.026	0.060	0.081	0.068	0.092	0.065
Maximum	0.497	0.769	0.826	0.625	0.775	0.364	0.265	0.323	0.307	0.307	0.366	0.353

Table 7. Flow in metres per second *C. splendens*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	0.303	0.428	0.324	0.275	0.261	0.182	0.109	0.106	0.101	0.094	0.138	0.109
Mean	0.261	0.500	0.322	0.263	0.265	0.202	0.159	0.115	0.115	0.118	0.139	0.131
Minimum	0.063	0.118	0.094	0.070	0.111	0.027	0.042	0.022	0.040	0.062	0.031	0.025
Maximum	0.354	1.020	0.520	0.440	0.495	0.497	0.370	0.320	0.316	0.323	0.292	0.383

C. splendens streams under flood conditions generally spilt over adjacent land with comparatively little alteration of flow (locations 13 and 11, February). In circumstances where such increase could still be contained (location 19, February), flow increased markedly.

The speed of flow, even when sufficient water was present, could be very variable in *C. virgo* sites owing to their sometimes small size and the frequent transition from clear open stretches to densely vegetated areas forming a barrier through which water has to drain. Such lengths of stream are frequently followed by erosion steps and plunge pools where there is a more rapid flow (locations 6 and 7).

When *C. splendens* areas were heavily vegetated the aquatic vegetation tended to be trailing in the flow, providing little hindrance to flow. In the larger streams frequently used by this species, pondweeds could trail for several metres (locations 11 and 19).

Depth

Little has been recorded on the preferred depths for the *Calopteryx* species, despite emphasis on sizes of waterways and their flow requirements. Prendergast (1988) found an increasing population of *C. virgo* with a decreasing water depth and suggested O₂ requirement as the principle reason for this.

Table 8. Depth in metres *C. virgo*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	0.27	0.42	0.21	0.19	0.22	0.19	0.21	0.17	0.21	0.21	0.23	0.22
Mean	0.30	0.46	0.26	0.25	0.27	0.24	0.24	0.23	0.24	0.25	0.28	0.25
Minimum	0.17	0.26	0.12	0.12	0.14	0.09	0.09	0.11	0.12	0.12	0.14	0.12
Maximum	0.54	0.76	0.52	0.54	0.51	0.51	0.51	0.43	0.47	0.51	0.52	0.49

Table 9. Depth in metres *C. splendens*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	0.60	1.54	0.59	0.43	0.45	0.48	0.53	0.43	0.44	0.50	0.39	0.48
Mean	0.78	1.51	0.74	0.67	0.65	0.66	0.63	0.65	0.61	0.73	0.75	0.64
Minimum	0.16	0.12	0.14	0.15	0.13	0.14	0.14	0.18	0.24	0.23	0.09	0.11
Maximum	2.23	2.86	2.30	2.37	2.34	2.30	2.35	2.29	2.16	2.34	2.34	2.15

Sites with the largest populations were also the most shallow. The twenty localities in this survey were measured to the nearest centimetre depth on flat bed, at the zones favoured by the larval population present. In small streams this site was frequently at the centre but less often so in larger waterways and very infrequently in rivers. Considering the number of recordings, the mean results throughout the year for both species, excluding the severe floods of February, were remarkably uniform, showing very stable conditions and an ability to restore levels rapidly (Tables 8 and 9).

Despite drought and variable catchments, the midsummer and midwinter mean levels for *C. virgo* streams were consistently around 0.25m, whereas those for *C. splendens* streams were around 0.75m. Only 10 per cent of the recordings for *C. virgo* streams exceeded 0.5m. For *C. splendens* streams, 90 per cent exceeded a depth of 0.25m; 50 per cent were deeper than 0.5m; 23 per cent were deeper than 1m; and 11 per cent were over 2m deep. In the deeper waterways, vegetation of sufficient size for emergence was very scarce, suggesting the *C. splendens* may use the shallows for emergence.

The shallowest water recorded was similar for both species at 0.09m (localities 2 and 17). At locality 2, drought prevailed in July and most of the *C. virgo* larvae were to be found surviving in deep, almost static, pools on bends under conditions that were probably unsuitable for their long-term existence. At locality 17, the shallowest site for *C. splendens*, the water level was exceptionally low in November, feeding into a very shallow pond.

Volume

It has been noted that depth variation from climatic sources generally achieved rapid stabilization, but more extreme variation was indicated in the volume data, measured at m³/s. The condensed data for volume appear in Tables 10 and 11.

Table 10. Volume in cubic metres per second *C. virgo*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	0.131	0.290	0.090	0.076	0.100	0.100	0.052	0.043	0.038	0.062	0.094	0.178
Mean	0.237	0.649	0.285	0.332	0.280	0.153	0.133	0.114	0.097	0.146	0.184	0.187
Minimum	0.036	0.107	0.052	0.048	0.005	0.005	0.003	0.011	0.023	0.014	0.023	0.013
Maximum	0.763	1.641	0.841	1.444	0.961	0.619	0.581	0.423	0.308	0.508	0.694	0.441

Table 11. Volume in cubic metres per second *C. splendens*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	1.196	3.192	1.554	1.207	1.062	0.553	0.479	0.279	0.338	0.485	0.373	0.425
Mean	5.544	20.846	7.072	4.865	3.687	2.758	1.536	1.810	1.286	1.343	2.256	1.776
Minimum	0.030	0.011	0.010	0.008	0.012	0.015	0.010	0.004	0.007	0.016	0.010	0.007
Maximum	26.830	118.730	41.016	26.621	8.787	12.990	6.440	8.751	6.936	6.774	13.285	9.128

The *C. virgo* waterways, during the February floods, produced a maximum increase of 4.0 times the January volume (location 2), and a minimum increase of 1.7 times (location 9). At the former it was not until April that the volume of water returned to the January level, and at the latter it did not do so until June.

Drought conditions in July produced a maximum fall to 22 per cent of the June volume (location 2) with the minimum fall being to 88 per cent of its previous level (location 10), and the losses were not rectified until November at location 2, but by August at location 10. Losses and gains were not excessive despite being largely contained, but sometimes took considerable time to stabilize. Throughout the year the volume of all *C. virgo* streams ranged from 0.003–1.64m³/s.

The February floods at the *C. splendens* sites produced a maximum increase of 5.6 times the January volume (location 18) with a minimum increase of 1.37 times (location 16), with both sites resuming previous levels by March. The July drought produced a maximum fall to 50 per cent of the June volume (location 11) with the minimum fall being to 81 per cent of the previous level (location 19). These losses were subsequently rectified by November and September respectively. Throughout the year the water volume at all of the *C. splendens* waterways ranged from 0.004–1.19m³/s.

Variation in volume at the *C. splendens* localities was considerably greater than at those for *C. virgo*. This is possibly a factor in the wider range of substrates used by *C. splendens* larvae. In addition to basal stones and detritus, dense and trailing masses of aquatic vegetation would offer greater protection from sudden severe change in water volume. Although *C. virgo* was occasionally found in vegetation, this was generally short vertical growth. It may be that *C. virgo* has little difficulty in maintaining position on relatively unprotected substrates in waterways where there is less variation in water volume.

Water Chemistry

Hydrogen-ion concentration (pH)

It is generally supposed that *C. virgo* tolerates greater acidity than *C. splendens* and the former is frequently found in streams flowing through lowland heath. *C. splendens* appears to confirm this by frequenting chalk streams. Gibbons (1986) found most good sites for *C. virgo* to be acid to neutral, and Miller (1987) observed that the pH of the

water may affect the distribution of the larvae. A preference for acid streams was noted by McGeeney (1986) for *C. virgo* larvae, and Welstead & Welstead (1984) observed neutral to moderately acid for *C. virgo*, and neutral to alkaline for *C. splendens*.

Table 12. Hydrogen-ion concentration (pH) *C. virgo*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	6.30	5.91	6.12	6.42	7.30	6.87	6.62	6.20	6.46	6.11	6.54	5.66
Mean	6.04	5.88	6.19	6.52	7.13	6.87	6.43	6.22	6.31	5.82	6.16	5.44
Minimum	4.53	5.09	5.58	5.53	5.99	6.36	5.06	4.54	4.65	4.46	4.66	4.21
Maximum	6.92	6.62	6.91	7.92	8.16	7.42	7.36	8.65	8.69	6.98	7.28	6.41

Table 13. Hydrogen-ion Concentration (pH) *C. splendens*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Median	6.38	6.94	6.86	7.71	7.81	7.60	7.34	7.61	7.41	6.81	7.42	7.12
Mean	6.40	7.03	7.03	7.70	8.22	7.48	7.59	7.55	6.54	6.78	7.38	7.03
Minimum	5.90	6.14	6.29	6.91	7.53	6.60	6.95	6.45	6.34	6.28	6.63	6.23
Maximum	7.54	7.75	8.05	8.27	9.05	8.33	8.54	8.69	8.73	7.38	7.98	7.58

Although many streams in the survey were nutrient-deficient with podzolization contributing to increased acidity, low pH was also frequently associated with extensive catchment areas and streams high in nutrients. In addition, the chalk syncline present through much of the Hampshire area, with Upper Eocene tertiary stratas of sands, gravels, and clays, combine to form a more involved pattern than is immediately apparent from vegetation and topography. The more recent Headen Beds from the Oligocene are also a contributory factor to base enrichment. Conversely, the two large chalkstreams Avon and Stour are fed by a large number of source streams draining from different stratas. The Avon is affected in its lower reaches from acidic New Forest streams in certain areas, although it also carries with it a profuse rich silt over a wide flood-plain.

Despite these various factors, a clear preference for, or tolerance of, acidic conditions was found in *C. virgo*, sometimes to a marked degree, and this species emerges as the more readily able to adapt. Hydrogen-ion concentration data, condensed from the 240 readings taken, are shown in Tables 12 and 13. The comparatively wide range of water conditions tolerated by *C. virgo* became largely and summer drought. Readings showed that pH would rise rapidly during the former

and fall quickly during the latter. The generally larger waterways frequented by *C. splendens* provide more drought protection and should be influenced far less by flood conditions. The overall mean pH for the *C. virgo* sites over the year was 6.25, compared with a figure of 7.22 for the *C. splendens* sites. The pH of the *C. virgo* sites ranged from 4.21 to 8.69 over the year whilst the *C. splendens* sites ranged from 5.90 to 9.05. This supports the general observation that *C. virgo* may be more tolerant of low pH than is *C. splendens*.

Oxygen

A preference for well-oxygenated water has long been noted for *C. virgo*, with *C. splendens* appearing to need less oxygenation (d'Aguilar *et al.*, 1986). The rectal gills of *Calopteryx*, lacking the tracheal gills of the Anisoptera, are not so efficient. The family possess a notable triquetral gill for resting on the stream bed or flat stones, for maximum water exposure (Tillyard, 1917). Summer oxygen produced by the aquatic plants enables the saturation level of dissolved oxygen for a given temperature to be reached and helps to offset the oxygen lost by the temperature increase.

Table 14. Dissolved Oxygen in mg/l

	Locality	Mean	Month	Mean
<i>C. virgo</i> oxygen mg/l				
	1	7.7	Jan	8.6
	2	8.2	April	8.1
	3	8.0	July	6.3
	4	6.2	Oct	7.9
	5	7.5		
	6	8.2		
	7	8.0		
	8	8.0		
	9	7.0		
	10	8.2		
<i>C. splendens</i> oxygen mg/l				
	11	6.5	Jan	7.2
	12	6.7	April	6.3
	13	5.7	July	6.1
	14	6.7	Oct	4.7
	15	7.5		
	16	3.5		
	17	6.7		
	18	4.5		
	19	6.2		
	20	6.5		

The tracheal system is designed to allow the passage of oxygen from water to insect tissue without an increase in the partial pressure of nitrogen and the consequent leakage of this gas from the tracheae (Tillyard, 1917). It is probable that the larvae of *C. splendens*, which spend more time above the stream bed, can make more use of vegetative oxygen than larvae of *C. virgo*. The preference of *C. virgo* for well-oxygenated waters may also be influenced by their more frequent use of the basal stones and debris (Gibbons, 1986). Shallow streams, although rich in oxygen at low temperatures, will warm up much more quickly than larger waterways, and consequently lose oxygen more rapidly.

Oxygen levels at the twenty locations are presented in Table 14. At the ten localities for *C. splendens*, the mean oxygen level of the water in January was 84 per cent of the comparable figure for the *C. virgo* localities. This fell to 77 per cent in April, increased to 97 per cent in July and fell to 59 per cent in October. Over the year, the mean oxygen level in the *C. splendens* streams was 79 per cent of that in the *C. virgo* streams. The mean oxygen level in the *C. virgo* streams in January was 3.1 mg/l below the oxygen saturation level for the mean temperature of that month (Table 4). The oxygen levels ranged from 66–76 per cent of the saturation levels throughout the year. The mean levels of oxygen in the *C. splendens* streams were further below saturation, ranging from 46–65 per cent of the saturation levels throughout the year.

Nitrate

The healthy oxygen levels attained at all the study sites indicated no excessive nitrate enrichment by 'Nitrobacter' activity. Higher nitrate levels would be expected in the *C. splendens* localities, resulting from higher autumnal decay of vegetation carried into the water from the catchment area. The nitrates would then appear in the January water samples, as a result of winter decomposition.

The comparative lack of soft plant decay at most of the *C. virgo* sites produced consistently low nitrate levels. The only slight variation occurred in January when the highest readings for each site were obtained (with the exception of location 4). The nitrate levels in January, April, July and October at the *C. virgo* sites (except location 10) were generally below 5mg/l apart from location 3, which attained 10mg/l in January and July; location 4, which reached 10mg/l in July; and location 5, which reached 25mg/l in January. Location 10, with levels of 35, 10, 25 and 5mg/l for the four samples was exceptional. No cause for these comparatively high levels was ascertained.

Table 15. Nitrate in mg/l – *C. splendens*

Mean NO_3 readings for the four months (January, April, July, October) at each of the ten *C. splendens* locations, are as follows:

Location	Mean NO_3
11	43.7
12	48.7
13	62.5
14	43.7
15	33.7
16	14.5
17	50.0
18	40.0
19	62.5
20	37.5

Mean readings for January *C. splendens* sites were 67.0, with 31.5 for April, 56.0 for July, and 20.3 for October.

Less than 5mg/l was recorded only once at the localities for *C. splendens* (location 16 in October). Far higher nitrate levels were recorded throughout the year at these sites, with 85mg/l at location 12 in January and 100mg/l at locations 13 and 19 in January. Mean nitrate levels at the *C. splendens* sites were 67mg/l in January, 32mg/l in April, 56mg/l in July and 20mg/l in October. The mean nitrate levels for the ten *C. splendens* sites are presented in Table 15.

Ecological Factors

Aquatic Vegetation

Habitat distinctions between the two species became particularly apparent when the aquatic vegetation was looked at. Trophic ranks, as given in Holmes & Newbold (1984), were attributed to the predominant aquatic plant species at each of the twenty studied locations (Table 16). The mean trophic rank for the *C. virgo* sites was 25, excluding localities 6 and 8 where no rank was assigned. This contrasts with a mean of 109 for the *C. splendens* sites. Of the *C. virgo* sites, only at location 3 did the trophic rank indicate mesotrophic to meso-eutrophic conditions that are generally associated with sandstone and limestone, and only at location 5 did the rank indicate eutrophic conditions. No sites were included within the oligo- to mesotrophic range, with the remaining sites strongly oligotrophic, conditions usually attributed to nutrient poor Tertiary sands. Of the *C. splendens* sites, none were oligotrophic, and only locations 13 and 18 were classified as meso- to meso-eutrophic. The remaining *C. splendens* sites were all strongly eutrophic.

Table 16. Predominant aquatic vegetation

Locality	Trophic rank	Species
1	18	<i>Myriophyllum alterniflorum</i>
2	18	<i>M. alterniflorum</i>
3	71	<i>Elodea canadensis</i>
4	4	<i>Potamogeton polygonifolius</i>
5	83	<i>Callitriche obtusangula</i>
6	no rank assigned	<i>Lythrum portula</i>
7	4	<i>P. polygonifolius</i>
8	no rank assigned	<i>L. portula</i>
9	4	<i>P. polygonifolius</i>
10	4	<i>P. polygonifolius</i>
11	124	<i>Potamogeton lucens</i>
12	144	<i>Ceratophyllum demersum</i>
13	71	<i>E. canadensis</i>
14	45	<i>Ranunculus fluitans</i>
15	83	<i>Callitriche obtusangula</i>
16	143	<i>C. stagnalis</i>
17	143	<i>C. stagnalis</i>
18	69	<i>Ranunculus penicillatus</i>
19	148	<i>Myriophyllum spicatum</i>
20	124	<i>P. lucens</i>

Location 5 also contained Curled Pondweed (*Potamogeton crispus*), which has a trophic rank of 137. However, this species spans the entire trophic range and is thus not a good indicator of any specific trophic conditions. Holmes & Newbold (1984) recommend omission of this species for calculating the mean score for an individual habitat. This species, together with Canadian Waterweed (*Elodea canadensis*), may also occur where deposits of Eocene clay result in local areas of enriched sediment, sometimes covering very small areas of the stream bed.

The dominant plant species at any particular site was not necessarily the one favoured by the *Calopteryx* larvae. Bog Pondweed (*P. polygonifolius*), which is very common in many *C. virgo* streams, offered little concealment or protection beyond that of overhead floating leaves. In very shallow water, however, the plants formed mats of dense cover. At such locations (e.g. locations 9 and 10) *P. polygonifolius*, which is generally associated with still or slow-flowing water, thrived in the shallow but more rapid flow. The growth of long, flowing vegetation, as at locations 11, 14 and 20, was possible only in the deeper waters used by *C. splendens*. Water-milfoil (*Myriophyllum* spp.) also offered flimsy cover in small quantity, but when in dense masses it became much used by a range of aquatic and semi-aquatic insect larvae, including *Calopteryx*. The aquatic vegetation at locations 6, 8 and

16 is frequently found in wet mud as well as water, but appeared in considerable quantity indicating the favourable conditions at these sites.

Emergent Vegetation

The peak emergent vegetation, recorded in July, was generally higher and more extensive in the luxuriant, less shaded habitats where *C. splendens* was found (Table 17). The mean height for the *C. splendens* sites was 1.37m (median of 1.45m), compared with 0.59m (median of 0.63m) in the *C. virgo* streams. These heights are not necessarily required for the emergence of the teneral, but *C. splendens* imagines prefer to rest in reeds and herbage, rather than in trees and bushes. Both species are particularly sensitive to vegetation clearance or disturbance (Askew, 1988).

Table 17. Predominant emergent vegetation

Locality	Trophic rank	Species	Emergence Height
1	26	<i>Ranunculus flammula</i>	0.31m
2	77	<i>Mentha aquatica</i>	0.27m
3	103	<i>Sparganium erectum</i>	0.93m
4	77	<i>M. aquatica</i>	0.49m
5	60	<i>Iris pseudacorus</i>	1.05m
6	unassigned	<i>Hypericum elodes</i>	0.14m
7	unassigned	<i>Juncus acutiflorus</i>	0.81m
8	unassigned	<i>Carex pseudocyperus</i>	0.71m
9	unassigned	<i>J. acutiflorus</i>	0.60m
10	97	<i>Rorippa nasturtium-aquaticum</i>	0.67m
11	62	<i>Myosotis scorpioides</i>	0.74m
12	97	<i>R. nasturtium-aquaticum</i>	0.58m
13	103	<i>S. erectum</i>	1.60m
14	142	<i>Schoenoplectus lacustris</i>	2.15m
15	103	<i>S. erectum</i>	1.30m
16	103	<i>S. erectum</i>	0.98m
17	26	<i>R. flammula</i>	0.39m
18	116	<i>Glyceria maxima</i>	2.00m
19	142	<i>S. lacustris</i>	2.10m
20	78	<i>Phalaris arundinacea</i>	1.87m

Welstead & Welstead (1984) observed that *C. splendens* was associated with a good growth of littoral vegetation and that *C. virgo* was associated with abundant floating vegetation. The present study indicates that *C. splendens* is, in addition, associated with extensive floating vegetation and *C. virgo* is associated with low emergent vegetation and frequently with sparse floating vegetation. In inclement conditions, imagines of *C. splendens* usually have an abundance of high emergent vegetation in which they shelter low down the stems, whereas *C. virgo* has frequently to resort to marginal growth further from the water. At sites where *C. virgo* lacks a sheltered marginal belt (e.g. localities 6

and 8), the imagines will use adjacent heathers, grasses and herbs to escape wind, rain and cold.

The emergent vegetation on the *C. virgo* streams showed a mean trophic rank of 73.3, excluding localities 6 to 9 where no trophic rank was allocated. This value indicates a meso-to meso-eutrophic environment. The emergent vegetation indicates considerably more enriched conditions than the aquatic vegetation, suggesting higher nutrient availability at the greater depths reached by their root systems. The ranks for the *C. virgo* sites indicated eutrophic conditions at localities 3 and 10, but oligotrophic conditions only at site 1.

The mean trophic rank for the *C. splendens* sites was 97.2 indicating well-enriched eutrophic conditions. Locality 17 was only site where oligotrophic conditions were indicated and locality 11 was the only oligo- to mesotrophic site.

Marginal Vegetation

In contrast to the emergent vegetation, the marginal growth was generally higher in the more sheltered and shady habitats of *C. virgo* (Table 18), where the mean height was 4.46m (median of 4.35m). However, not all localities were well shaded, and *C. virgo* appear to be as sun loving as most other Odonata, but with the capacity to hunt in more shaded areas.

Table 18. Predominant marginal vegetation

Locality	Species	Height
1	<i>Crataegus monogyna</i>	3.7m
2	<i>C. monogyna</i>	4.9m
3	<i>Prunus spinosa</i>	3.6m
4	<i>Salix caprea</i>	3.8m
5	<i>Alnus glutinosa</i>	7.6m
6	<i>Myrica gale</i>	0.6m
7	<i>S. caprea</i>	5.6m
8	<i>M. gale</i>	1.0m
9	<i>S. caprea</i>	5.3m
10	<i>Betula pendula</i>	8.5m
11	<i>Phragmites australis</i>	2.4m
12	<i>Salix fragilis</i>	7.0m
13	<i>Phalaris arundinacea</i>	2.0m
14	<i>A. glutinosa</i>	10.5m
15	<i>Senecio jacobaea</i>	1.3m
16	<i>Symphytum officinale</i>	1.3m
17	<i>S. caprea</i>	6.4m
18	<i>P. arundinacea</i>	2.3m
19	<i>Conium maculatum</i>	2.7m
20	<i>Glyceria maxima</i>	1.4m

Oviposition and courtship routines, particularly striking in species of *Calopteryx*, were both observed only in open sunny stretches. Chelmick *et al.* (1980) states a preference for tree-lined rivers and streams, and tree-lined edges are specified by Savan (1977). Fraser (1956) describes their habitat as woodland edges, and Longfield (1937) mentions 'areas usually surrounded by trees'. Only *C. virgo* and *Cordulegaster boltonii* (Donovan) in the British dragonfly fauna regularly fly in shade, but this appears to be an ability rather than a preference. Tubbs (1986) states that shaded reaches of streams are frequented only by these two species, but does not say that they are confined to them.

Localities 6 and 8 of this study are very open and windswept, but most of the others have high marginal growth along their northern edge, leaving the southern edges in full sun and shelter. On hot sunny days, adjacent, completely open drainage ditches were much used for hunting, courtship and oviposition. All marginal growth at localities for *C. virgo* was composed of woody shrubs or trees.

The marginal vegetation at the localities of *C. splendens* exhibited several marked differences from the vegetation at the *C. virgo* localities. The sites were more open with generally shorter growth. The mean height for the *C. splendens* localities was 3.73m, with a median of 2.35m, the difference largely explained by seasonal summer growth, which died back in winter to become quite open to the elements. In July, both this growth and the flight period of *C. splendens*, were at their optimum levels. Only at three sites was there permanent cover (localities 12, 14 and 17). Emergent vegetation was classed as marginal when it occurred at the margins in the absence of other vegetation. The barrier formed by this summer growth was in all cases more dense and impenetrable than the often higher but frequently sparse trunks and branches at the *C. virgo* localities. Beyond the marginal growth, many sites for both species were located in open country (e.g. localities 3, 4, 6, 8, 11, 15, 16 and 18).

Odonata Species

Tubbs (1986) gives a maximum of seven species of Odonata breeding in the New Forest streams, but the author has regularly found in excess of this in larval sampling.

Platycnemis pennipes (Pallas) is frequently described as confined to the Oberwater (location 3) (Welstead & Welstead, 1984) but also breeds in the Silver Stream (location 6). Species such as *Coenagrion mercuriale* (Charpentier) and *Ischnura pumilio* (Charpentier) will breed in slower reaches of the streams, particularly when passing through boggy marshland areas. The nine species included are not complete for New Forest streams, but other species have been excluded where they are undoubted wanderers from adjacent ditches and runnels. Some lists would also have been longer if the 50m limits for observations had been extended. The *C. splendens* sites were more attractive to a wider range of species (Table 19).

Table 19. Odonata recorded from each of the twenty sites throughout the study period (■ indicates presence).

Location	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Platycnemis pennipes</i> (Pallas)			■			■							■						■	
<i>Pyrphasoma nymphula</i> (Sulzer)		■	■	■	■	■	■	■	■	■			■	■	■	■	■		■	
<i>Coenagrion mercuriale</i> (Charpentier)	■				■			■		■										
<i>Coenagrion puella</i> (L.)	■		■			■		■	■	■		■	■	■	■	■	■	■	■	
<i>Enallagma cyathigerum</i> Charpentier											■							■	■	
<i>Ischnura elegans</i> (Vander Linden)	■	■		■							■	■	■	■	■	■	■	■	■	■
<i>Aeshna cyanea</i> (Müller)																		■		■
<i>Aeshna grandis</i> (L.)																				■
<i>Aeshna mixta</i> Latreille													■							
<i>Brachytron pratense</i> (Müller)													■	■						
<i>Cordulegaster boltonii</i> (Donovan)	■	■	■	■	■	■	■			■										
<i>Libellula fulva</i> Müller													■	■						
● <i>Orthetrum coerulescens</i> (Fabricius)	■		■	■	■	■	■	■	■	■										
<i>Sympetrum stialatum</i> (Charpentier)			■		■	■		■	■				■				■	■		■

Conclusions

Levels of overlap between the conditions at localities occupied by either *C. splendens* or *C. virgo* were found within every specific comparison made, but in each case preferences emerged. These and related data produced an overall pattern of differing requirements of the two species. The two species are occasionally found together, and where this occurs on the same waterway, the habitat changes rapidly, i.e. from an open sunny area to shaded and sheltered conditions.

The individual characteristics frequently stated as limiting for each species emerge as rarely sufficient on their own, as any stream may vary extensively in physical and ecological characteristics over comparatively short distances. It would appear to require a combination of several of the factors chosen for the study, to produce a general habitat of satisfaction to either species. A notable exception was the variation in nitrate levels between the sites for the two species, which showed great divergence throughout.

Each species will thrive, given a suitable number of the acceptable tolerance levels, and where both meet, the tendency is for one to have an abundance of suitable criteria and the other to be struggling with the minimum possible. Isolated individuals are always liable to make occasional visits to unsuitable localities, and this was observed with the recording of one mature male *C. splendens* on the New Forest Oberwater (location 3) on 25 August, 1990.

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Migrant and dispersive dragonflies in Britain during 1999

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Summary

Compared to some recent years, 1999 was a relatively quiet year for migrant dragonflies, although there were several highlights. Two small influxes of migrants were noted – in early July (*Anax parthenope* in particular) and during August (*Sympetrum* spp., notably *S. flaveolum*). A specimen of the North American *Pachydiplax longipennis* was discovered on an oilrig in the North Sea during early September, although the possibility of its being an accidental introduction to the rig cannot be totally discounted. Several other exciting discoveries were made which probably relate to immigrations in past years. Colonies of the damselfly *Erythromma viridulum*, a species new to Britain, were found in Essex. Small numbers of exuviae also provided confirmation of breeding by *A. parthenope* at two sites in Cornwall and, with oviposition also observed at one of these sites during 1999, further adults will hopefully emerge in this region in years to come.

Account of Species

Significant records reported to the BDS Migrant Dragonfly Project during 1999 are outlined below. See Parr (1999) for a report on the events of 1998.

Culopteryx splendens (Harris) – Banded Demoiselle

1999 – One was recorded at Redmoor, Cornwall, on 7 August (TA). This is at least 40km away from the nearest known breeding population (S. Jones, pers. comm.).

Erythromma viridulum (Charpentier) – Small Red-eyed Damselfly

1999 – Three colonies of this species were found in one small area of Essex (Dewick & Gerussi, 2000), which were the first ever records for the British Isles. On the Continent *E. viridulum* has expanded its range markedly over the last 30 years. In The Netherlands, there were only three records prior to 1970, but the species is now one of the most abundant damselflies in some areas (Wasscher, 1999). Since it has succeeded in colonizing many of the islands off the Dutch and German coasts (Wasscher, 1999; Ketelaar, 2000), the species clearly has strong powers of dispersal, and therefore the British records are perhaps not unexpected. The nature of some or all of the Essex colonies suggests that they may be established and would therefore have originated from an immigration occurring earlier than 1999. It will be interesting to see if other colonies are discovered in south-east England in the near future.

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

1999 – There was little evidence of large-scale immigration of this species during 1999. One adult was observed arriving over the beach at Gibraltar Point, Lincolnshire, on 24 July (KW), and another was attracted to UV light at Bradwell-on-Sea, Essex, on the night of 4 August (SD). Small gatherings were reported from several migration hot spots later in the season. The northwards expansion of this species within Britain continues apace, with records for 1999 received from as far north as County Durham.

***Aeshna affinis* Vander Linden – Southern Migrant Hawker**

1998 – A male was photographed on 17 July 1998 at St. Martin, Jersey, although it was not until 1999 that its true identity was established (Long, 2000). This represents the first record for the Channel Isles. The only other reports are one from Kent on 5 August 1952 (Parr, 1996), and a 'probable' from Avon on 14 August 1992 (Holmes, 1993). Since a significant invasion in 1995, the species has been recorded quite regularly in The Netherlands (Dijkstra *et al.*, 1999; Ketelaar, 2000), and it may well be that *A. affinis* occurs more frequently in Britain than is generally appreciated, but is overlooked.

***Anax imperator* Leach – Emperor Dragonfly**

1999 – One was seen arriving over the beach at Gibraltar Point, Lincolnshire, on 27 July (KW), and another was recorded arriving from off the sea at Bonchurch, Isle of Wight, on 30 August (AB).

***Anax parthenope* Sélys – Lesser Emperor**

1999 – Since its first documented appearance in Britain during 1996 (Phillips, 1997), this species has been reported annually, with records apparently increasing in frequency. During 1999 the following sightings were made:

2–18 July	Up to two males at Bake Farm, near Trerulefoot, Cornwall (KP)
10 July	Male at Dungeness, Kent (DW, IH, GH, OL)
11 July	Male at Marazion, Cornwall (PC)
12 July	Male in the Forest of Dean, Gloucestershire (JP)
12 July	One at Barn Elms, Greater London (RB)
12 July	Female at Bake Farm, Trerulefoot, Cornwall (KP)
18 July	Male at Dungeness RSPB Reserve, Kent (RP), probably different to the individual seen nearby on 10 July.
30 July	Male at Stithians Reservoir, Cornwall (GC)
12 August	Male at Bake Farm, Trerulefoot, Cornwall (KP)
31 August–6 September	Male at Marazion, Cornwall (PF, SJ)
4 September	One at Luccombe Down, Isle of Wight (AB)

The highlight of 1999 was the discovery of Lesser Emperors breeding in Cornwall. The female at Bake Farm was seen ovipositing (Pellow, 2000a) while still in tandem with the male. More dramatic was the discovery, between 31 July and 4 September, of a total of five exuviae from Bake Farm and another site on the Lizard Peninsula further to the west

in Cornwall (Jones, 2000; Pellow, 2000a). The emerging adults probably developed from eggs laid during the influx into the region during 1998. Interestingly, only a male had been observed in 1998 at Bake Farm, and the species was not observed at all during either 1997 or 1998 at the Lizard site, although there was one record from a locality a few miles away. This suggests that ovipositing pairs can be quite elusive, and breeding could thus be easily overlooked unless exuviae are found. Jones (2000) gives useful information on the identification of the exuviae of *A. parthenope*.

***Hemianax ephippiger* (Burmeister) – Vagrant Emperor**

1999 – There were no confirmed records, though a large brown dragonfly seen at Luccombe Beach, Isle of Wight, on 27 January (PJ) could have been of this species, since there are precedents for winter records of *H. ephippiger* in Britain (Parr, 1998a).

***Libellula depressa* L. – Broad-bodied Chaser**

1999 – Craine (2000) briefly mentions the first record of *L. depressa* from the Isle of Man during mid-July 1999. An individual near Darlington, County Durham, on 26 September (via DC) was both unusually far north and unusually late. Like *Aeshna mixta*, *Anax imperator* and some other species, *L. depressa* appears to be expanding its range in Britain.

***Orthetrum coerulescens* (Fabricius) – Keeled Skimmer**

1999 – Single individuals were reported from the Epping Forest and Lea Valley areas of Essex on 8 and 28 July respectively (AM, BW). The origins of these individuals are unknown as the nearest known breeding site is some 40–50km away (S. Cham, pers. comm.).

***Pachydiplax longipennis* (Burmeister) – Blue Dasher**

1999 – A female of this North American libellulid was found dead on the Sedco 706 oil rig in the North Sea off Shetland (60°38'N, 1°39'E) during the first few days of September (Parr, 2000). This is the first record of the species from Europe. The rig is known to receive supplies direct from the Houston area of the USA, so the possibility of an accidental introduction cannot be discounted. However, there is some suggestion that the insect could have been a genuine vagrant. The weather at the time was appropriate for Nearctic vagrancy (P. Davey, pers. comm.) and the largest arrivals of American wading birds (Charadriiformes) ever seen in Scotland started in earnest during the same general time period (Parr, 2000). Unlike *Anax junius*, the other Nearctic species that recently appeared in Europe (Parr, 1999), *P. longipennis* is not regarded as a strong migrant. There is, however, a suggestion that the abundance of this species in many areas of the USA may make it difficult for migratory movements to be picked up, and the species may be more mobile than is generally appreciated (R. Barber, pers. comm.).

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

1999 – Low numbers of this species apparently accompanied the influx of the various

species of *Sympetrum* seen during late summer/early autumn (see below for further details). No less than 19 were attracted to UV moth traps at Bradwell-on-Sea, Essex, during the period 17 July to 9 October. The maximum single catches were of three individuals on the nights of 6 August and 19 September (SD). Few large aggregations were reported during 1999, a count of 100 away from water at Kingsgate, Kent, on 6 September was one of the most notable.

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

1999 – By recent standards (e.g. Parr, 1997 & 1999), 1999 was a relatively quiet year for the species, though several records were still received. Emergence in spring and early summer (starting on 15 May, but timing varied from site to site) was noted at several localities, with records of teneral adults and/or exuviae from sites in Cornwall (the Lizard and Bake Farm), Kent (near Dover) and on the Spurn Peninsula, East Yorkshire. However, sightings of mature adults later in the season were erratic at these sites, and elsewhere, with the exception of Dungeness, Kent. This is another known breeding site where a few individuals were seen fairly regularly during June and July. The reason for the scarcity of summer records following good emergence in the spring is not completely clear. It may be that, like the generation emerging in autumn (Parr, 1999; Pellow, 1999), the generation emerging in spring is also highly dispersive, with most individuals leaving the area before sexual maturation is complete. This raises the possibility that the continuity of *S. fonscolombei* at sites in Cornwall (e.g. Pellow, 1999 & 2000b) and Kent during recent years could have resulted from the breeding of fresh immigrants, rather than the presence of established resident populations. More detailed studies of the breeding biology and dispersal of this species are required.

The timing of reports of mature adults from some Cornish sites suggests that a proportion of records from these localities could have related to migrants. On more than one occasion these reports coincided with periods of known or suspected immigration, as did a peak in the counts at Dungeness, where a maximum of 12 were present on 8 July. Away from known breeding sites there were also records of one individual at Bellcrag Flow, Northumberland on 10 July (via DC); a female at Staveley NR, Yorkshire on 21 August (PT); and a mature male near Horstead Keynes, Sussex, on 12 October (DD). Records suggest that fresh immigrations of *S. fonscolombei* took place during 1999, but on a relatively small scale. Immigration was also detected in The Netherlands, but interestingly here it seemed somewhat more substantial (Ketelaar, 2000).

Despite the relatively poor year for *S. fonscolombei* in Britain, a small-scale autumn emergence was noted from the site at Bake Farm, Cornwall, during mid-September. This adds further complexities to thoughts on the possible breeding strategies that the species may employ (Pellow, 2000b). Irrespective of whether British-bred or immigrant individuals were involved, some obvious breeding activity was also noted in southern England during the second half of 1999. Mating was observed at Dungeness on 8 July,

and oviposition at a site on the Lizard on 4 September (SJ). It therefore seems likely that *S. fonscolombei* will again emerge in Britain during the year 2000.

***Sympetrum flaveolum* (L.) – Yellow-winged Darter**

1999 – A small influx took place in the last days of July and during August, with individuals reported from localities in Kent (1 site), Essex (1), Suffolk (2), Norfolk (5), Cheshire (1) and Merseyside/South Lancashire (2). Records spanned the period from 31 July to 4 September, which closely coincides with the timing of a similar immigration of *S. flaveolum* detected in The Netherlands (Ketelaar, 2000). Typically, British records were of groups of one to five individuals, though up to 20 were recorded at Kingsgate, Kent, on 6 August (FS). In total, nearly 60 individuals were reported. The East-West split of records is intriguing, and shows some similarities to previous immigrations (Parr, 1996). It is possible that the westerly individuals seen in 1999 could have originated from breeding colonies established following the 1995 influx (Silsby & Ward-Smith, 1997), although these were believed to have become extinct. Alternatively, they may represent new immigrants. One explanation for a disjunctive distribution of records could be that a proportion of immigrants arriving from the Continent stop-off when they first reach land at the east coast, but others continue onwards only to stop once they reach the west coast. A good showing at North Warren NR, Suffolk, with a maximum of 16 males on 6 August (RM), may possibly reflect a contribution from locally-bred individuals. The species has been recorded on the reserve each year since 1995, but the timing of records does coincide with the presence of individuals elsewhere in the region that are more obviously immigrants.

An immature with a slightly damaged wing seen at Swinley Brick Pits, Berkshire, on 30 June (JWS) may have been locally bred. Although *S. flaveolum* had not been seen at this site since the big influx of 1995, it is possible that a small breeding population had been overlooked. There was circumstantial evidence following the influx of 1995 that the species may sometimes require more than one year to complete a generation, so that adults may not necessarily emerge at a site every year, particularly when the site has only recently been colonized (Parr, 1998b). On the other hand a full four-year development period seems unlikely, unless eggs may remain dormant for some years before hatching, e.g. in a dry area that is not flooded each year.

***Sympetrum sanguineum* (Müller) – Ruddy Darter**

1999 – At Bradwell-on-Sea, Essex, a total of nine were attracted to UV moth traps between 15 July and 9 August, with a maximum of two on the night of 6 August (SD). One was noted away from water near Kingsgate, Kent, on 6 August, when obviously migrant *S. flaveolum* and *S. danae* were also present in the area (FS).

***Sympetrum danae* (Sulzer) – Black Darter**

1999 – A few *S. danae* accompanied the late summer influx of *S. flaveolum* and other *Sympetrum* spp., with records being received during August and early September from

unexpected localities near the coasts of Kent (1 site), Suffolk (1; Cornish, 1999), Norfolk (3), Lincolnshire (2), and East Yorkshire (1). Records were typically of single males, with occasional groups of up to five. This movement of *S. danae* was also detected in The Netherlands (Ketelaar, 2000). High numbers of *S. danae* were reported during 1999 from several localities in the west of England that are some distance away from known breeding sites, presumably as a result of dispersal from sites with strong populations. It is also possible that a few immigrants from the Continent may also have penetrated inland. Records from Birkdale Sandhills LNR, S. Lancashire, are about 30km from the nearest known breeding site (P. Smith, pers. comm.).

Discussion

The year had a number of highlights. New species continued to be recorded in Britain in 1999, and while this may simply reflect an increase in the numbers and awareness of observers, it also seems that several European species are currently undergoing genuine range expansions. This may be a result of regional or global climate change, changes in the ecological requirements of the species, or a combination of these and other factors. It will be interesting to see if, or more likely when, further species turn up in Britain. Perhaps the major feature of 1999 was the large number of immigrant species which were found breeding. The breeding biology of many of these species is poorly understood, especially in a northern European context, and it will be interesting to see if any species succeeds in establishing a permanent breeding base in Britain. It will be important to understand the breeding requirements of many of these migrant species if we are to explain the current changes in their distributions.

Acknowledgements

I would like to sincerely thank all those individuals who submitted records and made this analysis possible. The following have been identified in the text by their initials: T. Askem (TA), R. Bullock (RB), A. Butler (AB), D. Clarke (DC), P. Clarke (PC), G. Cockill (GC), S. Dewick (SD), D. Dey (DD), P. Fraser (PF), I. Henshaw (IH), G. Hollamby (GH), P. Johnson (PJ), S. Jones (SJ), O. Leyshon (OL), R. Macklin (RM), A. Middleton (AM), K. Pellow (KP), J. Phillips (JP), R. Price (RP), F. Solly (FS), P. Treolar (PT), D. Walker (DW), J. Ward-Smith (JWS), K. Wilson (KW) and B. Wurzell (BW). In addition, I would like to acknowledge my fellow members of the Odonata Records Committee (J. & G. Brook, S. Jones, J. Phillips and M. Tunmore) who provided invaluable help with the documentation and verification of reports of rare species.

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Larvae of the Downy Emerald *Cordulia aenea* (L.) examine the space for eclosion with their hind-legs

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Introduction

Emergence in dragonflies is a hazardous process that entails increased predation risk and sometimes an unsuccessful ecdysis. Therefore, natural selection may have forced the larvae to choose carefully the time and space for the last moult. Individuals of Anisoptera that emerge in dense vegetation need ample space around the body for expansion of the adult organs. Plant stems or leaves may be physical obstacles preventing normal spreading of the wings. Many anisopteran species belong to the 'hanging type' of emergence (Eda, 1959) in which the larvae, having reached a suitable position, make conspicuous movements before eclosion starts. Aeshnidae wriggle the abdomen convulsively from side to side (e.g. Corbet, 1962 & 1999). Similar behaviour has been reported in *Gomphus vulgatissimus* (L.) (Robert, 1958). *Sympetrum fonscolombei* (Sélys) may make several sharp kicks with one or other of the hind-legs (Robert, 1958), and some corduliids are reported to describe circling movements with their hind-legs at this time (Bilek, 1961; Grand, 1997; Knaus, 1999). In *Cordulia aenea* (L.) it has been observed that circling movements of the hind-legs shortly before definite anchoring and eclosion is an obligatory element of the behaviour in emerging larvae (Wildermuth, 1998).

The abdominal and leg movements immediately preceding eclosion are interpreted as indicating a need: (1) to test the grip of the tarsal claws; or (2) to ensure that adequate space exists for unhindered expansion of the wings; or (3) to reduce the likelihood of physical contact with adjacent individuals competing for the same emergence support (Corbet, 1962 & 1999). Authors agree that pre-eclosion hind-leg circling in corduliids is probably undertaken to ascertain that ample space is available for completion of ecdysis (e.g. Bilek, 1961; Grand, 1997; Wildermuth, 1998). However, none of these possibilities has so far been experimentally tested. The difficulty is that only a few seconds are available for the test, and the right moment is not precisely predictable. An indoor study of the larval behaviour of *C. aenea* in May 1998 offered a good opportunity to test hypothesis (2). As a great number of final-instar larvae were kept in aquaria, there was a good opportunity to perform the necessary experiment, the results of which are presented here.

Materials and methods

Over 100 final instar of *C. aenea* were collected in early May from two small lakes that hold large populations of this species. Five to eight larvae were kept together in each of several plastic boxes ($19 \times 14 \times 9$ cm), containing 2 cm of water. Each box was equipped with suitable supports for eclosion. These consisted of three unbranched sticks with rough surfaces, 25 cm in length and 4 mm in diameter, fixed in a vertical position about 7 cm apart on a small piece of wood. The air temperature ranged between 19° and 21 °C. Emergence took place mainly in the morning, and the earliest individuals left the water shortly before sunrise. Although the larvae were monitored periodically, the right moment for the experiment was missed in most cases. When an emerging larva was noticed climbing up a stick, it was observed until it had reached a possible moulting site and had started circling its hind-legs. A natural obstacle was then simulated by holding a pencil behind or beside the larva (Fig. 1). As soon as one of the hind femora or tarsi had come into physical contact with the experimental obstacle, the pencil was withdrawn. The procedure was repeated once. This experiment was carried out with four individuals.

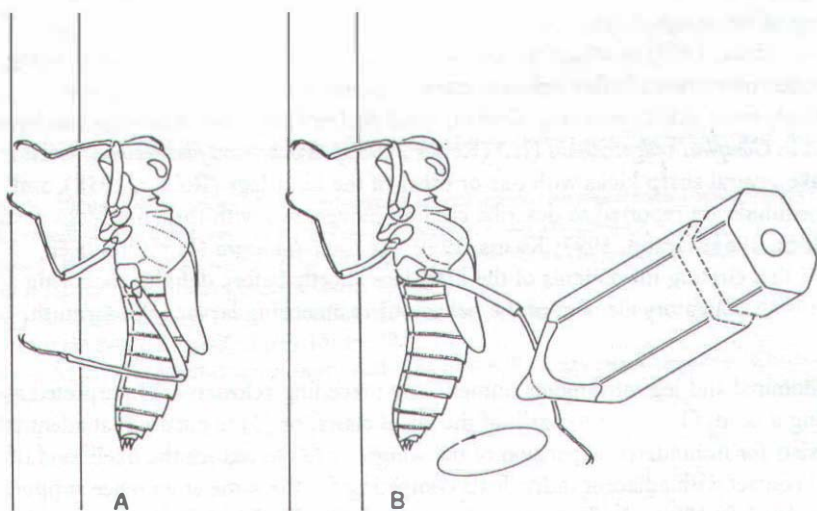


Figure 1. Larva of *Cordulia aenea* shortly before emergence. (A) posture of larva immediately before finally clinging to the support. (B) experiment for testing the function of hind-leg circling. The movement is briefly interrupted by physical contact with a pencil.

Results and discussion

Larvae of *C. aenea* that were allowed to perform emergence unhindered, climbed up a stem rather rapidly and stopped briefly from time to time, making 'searching movements' mainly by waving their fore and middle legs in the air. Sometimes they descended and

again climbed the same support before they decided on a moulting site. Finally, while immobile, they started circling their spider-like hind-legs slowly a few times, describing wide lateral and dorsal movements. The legs were almost stretched out and acted alternately, rarely synchronously, the abdomen being slightly curved (Fig. 1). After a pause of up to 10 minutes, a larva clung tightly with its thorax and abdomen pressed against the support, securely anchored, and soon started eclosion. In most cases eclosion took place on the upper half of the stick offered to the larvae, often at the top.

The reactions to contact with the experimental obstacle during hind-leg circling were the same in all four larvae tested. None remained at the site but all descended and tried to find a new place. However, they did not return to the water but climbed up the same stick and repeated the procedure as before. Having found a new site for emergence, definite clinging and ecdysis ensued. No reaction was found when the pencil was held close to the larvae without physical contact.

From the reactions of the larvae it is concluded that only physical contact of the circling hind-legs with the obstacle causes a larva to leave the site and search for a new one for ecdysis. Responses of larvae showed that visual cues were not dictating the behaviour observed. The findings support the hypothesis that an important function of the circling leg movements in emerging *C. aenea* larvae is to test the space around them for unhindered eclosion. Clearly, in natural situations, impinging vegetation or simultaneously emerging larvae can constitute obstacles to the successful completion of stage 3 of the moult. During this stage the abdomen is withdrawn from the exuvia and the wings and the abdomen attain full size (cf. Corbet, 1962 & 1999). The circling of the hind-legs in *C. aenea* does not appear to serve to test the grip of the tarsal claws because the movements are sluggish and not violent, as are the abdominal wriggles of Aeshnidae.

Hind-leg circling in emerging larvae also occurs in *Epitheca bimaculata* (Charpentier) (Bilek, 1961; B. Trockur in litt.; own observations) and in *Somatochlora meridionalis* Nielsen (Grand, 1997), both of which have relatively long legs like *C. aenea*. On the other hand, *S. alpestris* (Sélys), the legs of which are comparatively short, exhibits the same behaviour (Knaus, 1999). This behaviour may be characteristic for all corduliids, which typically have a short and relatively inflexible abdomen, unlike Aeshnidae and some Gomphidae. The adaptive value of hind-leg circling before eclosion is evident. One would wish to know whether such behaviour also occurs in libellulids other than *Sympetrum fonscolombei* (Robert, 1958) and in the macromiids with their extremely long hind-legs.

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Predation of a bumblebee (*Bombus* sp.) by the Four-spotted Chaser *Libellula quadrimaculata* L.

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At c. 1130h GMT on 24 June 2000, at the Waldegrave Pool, near Priddy, Somerset, a *Libellula quadrimaculata* L. was observed in flight holding a small, probably male, bumble-bee of the genus *Bombus* in its mouth. The *L. quadrimaculata* was observed at a distance of c. 2.5m in good light and, although followed in flight through binoculars, it was eventually lost from sight and so, unfortunately, it is not known whether the prey was eventually eaten.

It is known that larger dragonflies will, at times, prey upon bees, although it is probably unusual for bumblebees to be taken. Askew (1988: 30) states that Anisoptera will occasionally feed on Hymenoptera, although bumblebees are not specifically mentioned. Corbet (1999) discusses Odonata attacking bees (*Apis mellifera*) as they fly from a hive and mentions Wright (1944) who recorded *Coryphaeschna ingens* (Rambur) and *Anax junius* (Drury) feeding extensively on hive-bees in Louisiana, USA. Moore (in Corbet *et al.*, 1960) also confirms that dragonflies can be important predators of hive bees in the USA where they may weaken colonies severely. Corbet (1999) also mentions Alford (1975) who observed *Cordulegaster boltonii* (Donovan) rejecting all but the abdomen of a large bumblebee (*Bombus*). However, I think it is doubtful that dragonflies in Britain commonly seize hive-bees and the predation of bumblebees is probably an even more rare occurrence.

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Predation of Four-spotted Chaser *Libellula quadrimaculata* L. by Otter *Lutra lutra* L.

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During June 2000, a collection of dragonfly wings was observed clustered on wet sphagnum moss beside a shallow drainage channel on the coastal raised bog of Cors Fochno (Borth Bog), Ceredigion. Closer inspection revealed a total of sixteen wings. The wings were identified from their distinctive markings as belonging to the Four-spotted Chaser, *Libellula quadrimaculata* L., a common breeder at the location.

The cluster of wings was found on a route regularly used by Otter *Lutra lutra* L. This route follows a clearly marked trail through the floating carpet of sphagnum moss covering much of this ditch. The Otter run was followed beyond the ditch into an area of tall vegetation, dominated by Purple Moor-grass (*Molinia caerulea*), where a second, smaller cluster of wings was found close by an Otter spraint. Analysis of the spraint revealed fragments of glossy brown and black carapace matching the thoracic markings of *L. quadrimaculata*. This confirmed the suspicion that an Otter was responsible for the predation. It seems likely that the Otter had been reaping a harvest of dragonflies plucked from roosting sites located beside a regular foraging route.

A few weeks later, at the western-most edge of the Cors Fochno peatland, a further collection of *L. quadrimaculata* wings was observed in a similar situation. The distance between the sites of the two observations is about 2.5km. Whilst it is possible that the same individual could have been responsible on both occasions, it would seem more likely that another Otter was involved, suggesting that the feeding habit may be widespread amongst the local Otter population.

The diet of Eurasian Otter has been investigated in some detail but this appears to be the first recorded instance of predation on adult Odonata (Chanin, 1985; Mason & Macdonald, 1986). Corbet (1999) states that 'it is expected that small opportunistic Carnivora, such as Felidae and Mustelidae, will sometimes take large Anisoptera in numbers', but does not quote any published observations of this phenomenon.

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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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Figures should be prepared in black ink, and scaled to allow a reduction of 1.5 to 3 times.

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
Platyneomis pennipes
Pyrhosoma nymphula
Ceriagrion tenellum
Coenagrion mercuriale
Coenagrion scitulum
Coenagrion hastulatum
Coenagrion lunulatum
Coenagrion armatum
Coenagrion puella
Coenagrion pulchellum
Enallagma cyathigerum
Ischnura pumilio
Ischnura elegans
Erythromma najas

ANISOPTERA

Aeshna caerulea
Aeshna juncea
Aeshna mixta
Aeshna cyanea
Aeshna grandis
Anaciaeschna tsacaeles

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

DRAGONFLIES

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

Anax imperator
Anax parthenope
Anax junius
Hemianax ephippiger
Brachytroch praenese
Gomphus vulgatissimus
Cordulegaster boltonii
Cordulia aenea
Somatoclora metallica
Somatoclora arctica
Oxygastra curtisii
Libellula quadrimaculata
Libellula fulva
Libellula depressa
Orthetrum cancellatum
Orthetrum coerulescens
Sympetrum striolatum
Sympetrum nigrescens
Sympetrum fonscolombei
Sympetrum flavescens
Sympetrum sanguineum
Sympetrum daniae
Sympetrum pedemontanum
Sympetrum vulgatum
Crocothemis erythraea
Pantala flavescens
Leucorrhinia dubia

Emperor Dragonfly
Lesser Emperor Dragonfly
Green Darer
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
Keel 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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