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BDS

The aims of the **British Dragonfly Society** (BDS) are to promote and encourage the study and conservation of Odonata and their natural habitats, especially in the United Kingdom.

The Journal of the British Dragonfly Society, published twice a year, contains articles on Odonata that have been recorded from the United Kingdom and articles on European Odonata written by members of the Society.

Articles for publication should be sent to the Editor. Instructions for authors appear inside the back cover.

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Species Reviews: Various species reviews are in the process of being written so if anyone is considering writing a review of their favourite species, please contact the Editor first.

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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 form either on disk or by e-mail.
- Manuscripts should be one and a half spaced, on one side of the page only and with margins at least 25mm on both sides and top and bottom. Footnotes should be avoided.
- 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 2010.
- 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 the following forms:
  Hammond, C.O. 1983. *The Dragonflies of Great Britain and Ireland* 2nd Edition (revised by R. Merritt), Harley Books, Colchester, 116pp.
  Longfield, C. 1949. The Dragonflies of the London area. *The London Naturalist* **28**: 90-98.
- Titles of journals should be written out in full.
- Figures, plates and tables should be presented on separate, unnumbered pages.
- Legends for figures, plates and tables should be presented together in sequence on separate, unnumbered pages.
- The legend for each table and illustration should allow its contents to be understood fully without reference to the text.

Please refer to a recent issue of the journal for further style details.

SCIENTIFIC AND ENGLISH NAMES OF BRITISH ODONATA

ZYGOPTERA	DAMSELFLIES
Calopteryx splendens	Banded Demoiselle
Calopteryx virgo	Beautiful Demoiselle
Ceriagrion tenellum	Small Red Damselfly
Chalcolestes viridis	Winter Emerald Damselfly
Coenagrion armatum	Norfolk Damselfly
Coenagrion hastulatum	Northern Damselfly
Coenagrion lunulatum	Irish Damselfly
Coenagrion mercuriale	Southern Damselfly
Coenagrion puella	Azure Damselfly
Coenagrion pulchellum	Variable Damselfly
Coenagrion scitulum	Dainty Damselfly
Enallagma cyathigerum	Common Blue Damselfly
Erythromma najas	Red-eyed Damselfly
Erythromma viridulum	Small Red-eyed Damselfly
Ischnura elegans	Blue-tailed Damselfly
Ischnura pumilio	Scarce Blue-tailed Damselfly
Lestes barbarus	Southern Emerald Damselfly
Lestes dryas	Scarce Emerald Damselfly
Lestes sponsa	Emerald Damselfly
Platycnemis pennipes	White-legged Damselfly
Pyrrhosoma nymphula	Large Red Damselfly
Sympecma fusca	Winter Damselfly
ANISOPTERA	DRAGONFLIES
Aeshna affinis	Southern Migrant Hawker
Aeshna caerulea	Azure Hawker
Aeshna cyanea	Southern Hawker
Aeshna grandis	Brown Hawker
Aeshna juncea	Common Hawker
Aeshna mixta	Migrant Hawker
Anaciaeshna isoceles	Norfolk Hawker
Anax ephippiger	Vagrant Emperor
Anax imperator	Emperor Dragonfly
Anax junius	Green Darner
Anax parthenope	Lesser Emperor
Brachytron pratense	Hairy Dragonfly
Cordulegaster boltonii	Golden-ringed Dragonfly
Cordulia aenea	Downy Emerald
Crocothemis erythraea	Scarlet Darter
Gomphus flavipes	Yellow-legged Club-tail
Gomphus vulgatissimus	Common Club-tail
Leucorrhinia dubia	White-faced Darter
Leucorrhinia pectoralis	Large White-faced Darter
Libellula depressa	Broad-bodied Chaser
Libellula fulva	Scarce Chaser
Libellula quadrimaculata	Four-spotted Chaser
Orthetrum cancellatum	Black-tailed Skimmer
Orthetrum coerulescens	Keeled Skimmer
Oxygastra curtisii	Orange-spotted Emerald
Pantala flavescens	Wandering Glider
Somatochlora arctica	Northern Emerald
Somatochlora metallica	Brilliant Emerald
Sympetrum danae	Black Darter
Sympetrum flaveolum	Yellow-winged Darter
Sympetrum fonscolombii	Red-veined Darter
Sympetrum pedemontanum	Banded Darter
Sympetrum sanguineum	Ruddy Darter
Sympetrum striolatum *	Common. Darter *
Sympetrum vulgatum	Vagrant Darter

* Includes dark specimens in the north-west formerly treated as a separate species, *Sympetrum nigrescens* Highland Darter

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Timothy ‘Tim’ Beynon (1939 – 2016)

David Goddard

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It was with a great sense of sadness that I learnt from Bill Furse that Tim Beynon had passed away on Saturday 18th June 2016.

Tim Beynon was born on 13 January 1939 in Mumbles on the Gower Peninsula. He grew up in idyllic surroundings and, not being allowed to have pets at home, he developed a love of the natural world: butterflies, birds, plants and of course his favourite - dragonflies. He went to the local grammar school where he excelled at sport and most subjects. He played rugby for Wales as a schoolboy and, later on, club rugby for Swansea but after winning a place at Kings College, Cambridge to read Pure Maths (later transferring to Mechanical Engineering) he focused on rowing. He stayed on an extra year at Kings because he had a trial for the Goldie boat and during that year decided to train as a teacher.

His first post was at the City of London School for Boys where he taught maths and rugby after which he spent fourteen years at Merchant Taylors’ School in Northwood. While at Taylors’ he was able to spend plenty of time teaching maths and rugby but, more importantly, on his favourite extra-curricular activities ringing birds and sharing his ornithological passion with the boys.

He moved from Merchant Taylors’ to Denstone College in Staffordshire, where he was headmaster from 1978-1986. At Denstone he became the first head to make a girl head of school and supported the first expedition to Inaccessible Island, part of the archipelago of Tristan da Cuhna in the South Atlantic, in 1982, following which he was made a Fellow of the Royal Geographical Society. He left Denstone to return to Cambridge as headmaster of The Leys School from 1986-1990. Unfortunately much of his time as a head was spent on administration and school politics but he soon moved back to the outdoors as Head Warden of Saltwells Nature Reserve in Dudley. As the UK’s largest urban reserve (247 acres), Saltwells had its fair share of urban crime (burning cars and fly tipping in particular) which Tim enjoyed dealing with almost as much as the flora and fauna.

Tim retired from Saltwells at 65 and, when he was made President of the BDS, it was very clear that this was his favourite job. He was able to spend all of his time and energy focusing on Odonata: in the field (especially in his spiritual home at Chartley Moss) and hours of reading and reviewing books and photographs. He was President from 2000 to 2004 and, in recognition of his outstanding service to the Society, was made an Honorary Member in 2004. During this period we appointed our first conservation officer, Charlotte Murray and we also had to deal with a thorny issue regarding a migrant dragonfly from North America - *Anax junius* Green Darner. It was a pleasure to serve alongside Tim as a trustee during this period. His profound knowledge and calm common sense were inspirational. His excellent good manners allowed everyone to express their opinions whilst keeping them on topic. He had the ability to draw everything together, succinctly sum up the discussion, and then propose a resolution to be voted upon.

Tim also spent time working with the BDS Dragonfly Conservation Committee and latterly (since 2006) as a reviewer of papers for the BDS Journal. Tim was also responsible for the BDS's continued presence at the British Birdfair held at Rutland Water every year. He recognised the value of our presence at such an event in raising the profile of the society, making contacts within the conservation world and in the publicity and sales at this prestigious event. Throughout our friendship I was constantly surprised by his continued interest in research in Odonata, his profound knowledge, his excellent identification skills and his generosity in sharing his knowledge and experiences. Whether working together on the BDS stand at the Birdfair, travelling to Bulgaria or in pottering around Chartley Moss searching for dragonflies with Tim and his dog, he was unfailingly kind and courteous, warm and highly intelligent.

Please permit me to give some personal insights from my time working with and holidaying at home and abroad with Tim. The BDS had won a contract with English Nature to write a paper outlining the methods to survey and monitor all Sites of Species Scientific Interest (SSSI) within England, along with cost estimates for the then 4,112 sites. As I was at that time between jobs, Tim contacted me and I, along with Caroline Daguet, the then BDS conservation officer, set about writing the paper with guidance and input from Tim. After several meetings this document was completed and accepted by English Nature. It was at this time that I decided I would switch careers so I asked Tim to write a letter supporting my application to undertake an environmental degree at Nottingham Trent University. Tim was very happy to do so and I was accepted onto the course and, as they say, the rest is history.

I have had the pleasure to be on site with Tim at such places as Chartley Moss SSSI, where Tim not only knew and could speak with great authority about the dragonflies but also the birds and plants at this special site. I would draw the reader's attention to the numerous papers Tim wrote about *Leucorrhinia dubia*

Plate 1. Tim enjoying a holiday in Chamonix in 1965.

Plate 2. Tim at Chartley Moss in 2004. From Dragonfly News 47 (2005). Photograph by Mike Averill.

Plate 3. Tim in Bulgaria in 2006.

Plate 4. Tim (second from right) in Bulgaria in 2009.

White-faced Darter at Chartley Moss SSSI for further information.

Having spent many happy hours out in the field with Tim I decided that I would organise a holiday to Scotland so that Tim would be able to finally get to grips with the Scottish dragonfly specialities, namely *Aeshna caerulea* Azure Hawker, *Coenagrion hastulatum* Northern Damselfly and *Somatochlora arctica* Northern Emerald, along with the many other species of dragonflies, birds and plants that can be found. So four of us set off with high hopes and indeed, with Tim's good humour, knowledge and identifications skills, all the Scottish dragonfly specialities were seen along with many of the Scottish bird specialities and a surprising ten species of orchid. Indeed the holiday was such a success that it was repeated the following year.

When Tim suggested to me that I go with him on a holiday to Bulgaria with 'A Quest for Nature' led by Dan and Rosie Powell, having previously been on the same holiday and given me such a glowing report of the dragonfly, butterfly and bird species recorded, I could not resist. Tim was a great joy to be with on the holiday and was happy to freely share his knowledge and expertise of the natural world with those he came into contact with and it has been my privilege to be able to call him a great friend.

Tim's time and efforts representing the BDS in whatever he was doing were always carried out with great tact and diplomacy and he will be missed by his many friends and colleagues within the BDS.

Acknowledgement: *I should like to thank Tim's daughters Sorrel and Polly for providing me with background information.*

Migrant and dispersive dragonflies in Britain during 2015

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Summary

Like many of its immediate predecessors, the year 2015 was an eventful one for migrant dragonflies in Britain. During June/July there were large-scale immigrations of *Sympetrum fonscolombii* (Red-veined Darter), with records as far north as east Lothian in Scotland. Later in the summer, four *Aeshna affinis* (Southern Migrant Hawker) were unexpectedly recorded away from the recently-established breeding population around the greater Thames Estuary, presumably as a result of fresh immigration. These sightings mostly involved southern counties (Cornwall, Sussex and Suffolk) but included a female in Lancashire. In addition to these highlights, other notable events included the first sightings of *Sympetrum flaveolum* (Yellow-winged Darter) for several years and further autumn appearances of *Anax ephippiger* (Vagrant Emperor). An intriguing series of dragonfly sightings over the Christmas period (unfortunately not all well-documented) probably also refer to migrants.

In addition to this news relating to primary immigration, significant developments also affected several of our recent colonist species. Both *Erythromma viridulum* (Small Red-eyed Damselfly) and, more especially, *Chalcolestes viridis* (Willow Emerald Damselfly) thus showed continuing range expansion. While *Lestes barbarus* (Southern Emerald Damselfly) and *Coenagrion scitulum* (Dainty Damselfly) seem not to be spreading at present, their recently-established populations do appear stable. Continued monitoring of all of our recent colonist species would seem desirable.

Account of species

Notable sightings reported to the BDS Migrant Dragonfly Project during 2015 are detailed below; for information on events during 2014, see Parr (2015).

Calopteryx virgo (L.) – Beautiful Demoiselle

A record from Brockadale, south-west Yorkshire, during the course of the year

(DA) represents the first vice-county record for at least 50 years (per AMc).

Chalcolestes viridis (Vander Linden) – Willow Emerald Damselfly

Chalcolestes viridis has been steadily increasing its range in southeast England since its appearance in Suffolk during 2007 (Brame, 2008), and the current reporting period saw continued expansion. There were thus several new site records from both Surrey and Cambridgeshire, where the species had been noted for the first time only during 2014 (Parr, 2015). There was also a significant new sighting of an individual at Woods Mill, West Sussex, on 29 September (DS), this being the current most south-westerly record in England and almost 30km away from any previously-known site.

Lestes barbarus (Fab.) – Southern Emerald Damselfly

This recent colonist continues to do well at its breeding site at Cliffe in Kent, with many adults being seen during the summer and several exuviae also being found in mid-June (JGB). Elsewhere, fortunes were apparently more mixed, though the species is easily overlooked and it is believed that a degree of under-reporting may also take place due to the sensitive nature of some sites with suitable habitat. Records from the species' other well-known site at Winterton Dunes, Norfolk, were thus restricted to just a single sub-mature female noted on 1 August (PH), and the only other report received was of a single male at Gunners Park, Essex, on 21 & 27 July (AA *et al*.).

Sightings at Winterton have been regular, if not quite annual, since the species' discovery there, new to Britain, during 2002 (Nobes, 2003). Numbers seen are, however, typically low and successful breeding has never been proven. Perhaps the species does indeed breed there. However, it is also possible that a few immigrant individuals now regularly arrive on the coast of southeast England each year, but that it is only at sites with favourable habitat such as at Winterton where they remain around long enough to be noted by odonatologists. Further long-term scrutiny of a variety of coastal localities from (roughly) west Sussex through to north Norfolk may ultimately determine whether this is indeed the case. The possibility that the species is more strongly established around the greater Thames Estuary than is currently appreciated also seems worthy of investigation.

Lestes dryas Kirby – Scarce Emerald Damselfly

The first records from Hertfordshire for 50 years were made when several individuals were noted at Hertford Heath during early July (BR). The species is known to be univoltine (Brooks *et al*., 2014) and, since exuviae were later found, the site must clearly have been colonised not in 2015, but in 2014 at the very latest. Recent range expansion by this quite rare and local species (Cham *et al*., 2014) would clearly seem to be continuing.

Coenagrion scitulum (Rambur) – Dainty Damselfly

Although exuviae of this recent colonist species were discovered at two known sites on the Isle of Sheppey, Kent, during 2014, no flying adults were noted that year (Parr, 2015). It is thus pleasing to report that nearly 20 individuals were seen at these sites during early summer 2015 (JGB). Brook & Brook (2015) summarized the fortunes of this Kent population in greater detail. The species continues to do well on the near Continent, so it is possible that new sites in England may perhaps also become established in the short–medium term future.

Erythromma viridulum (Charp.) – Small Red-eyed Damselfly

This species first appeared in Britain during 1999, and by 2006 had spread across much of England south of a line from east Devon through to southeast Yorkshire. Since then, range expansion has slowed considerably (Cham *et al*., 2014). A significant further increase was, however, noted during 2015, when several individuals were seen at Warmingham Flash, Cheshire, over 18–27 August (AG *et al*.).

As has become regular, signs of continuing dispersal/immigration were noted on the East Anglian coast. Some 40 individuals were thus observed at Winterton Dunes in Norfolk on 1 August, whereas only 3–4 were present on the preceding or following days (PH). Singletons were also attracted to UV light at Bawdsey on the Suffolk coast during the nights of 19 & 20 July (MD).

Aeshna affinis (Vander Linden) – Southern Migrant Hawker

In many ways, this species provided the highlights of the 2015 season. There were thus numerous sightings from its recently-established breeding sites around the greater Thames Estuary. In Kent, *A. affinis* was seen regularly near Cliffe, and a number of exuviae were found during mid July (JGB). In Essex, the well-known site at Wat Tyler Country Park saw many reports during late July–mid-August (NP *et al*.), with an unusual blue-phase female even being photographed there on 15 August (SBu). Elsewhere in southern Essex, there were further records from West Canvey Marshes (2 August; TC), Canvey Wick (2 August; TC), Hadleigh Country Park (7 August; DC), Rainham Marshes (15 August; KB) and Hockley Woods (18 July; SJ).

In addition to records relating to Britain's newly-established breeding population, a further influx of migrants clearly also took place. The following records have been accepted by the national Odonata Records Committee:

10 July	Female photographed at Ainsdale, Lancashire (C. Storey)
22 August	Male photographed at Southease, East Sussex (R. Mundy)
29 August	Male seen at Bawdsey, Suffolk (B. Buffery)
18–19 September	Male photographed at Marazion Marsh, Cornwall (C. Moore)

The wide spread of these sightings, both in terms of geography and timing, would suggest several distinct waves of immigration, and it is possible that further individuals were also present but went unnoticed due to their close similarly to the more familiar and expected *A. mixta*. The record from Lancashire is of considerable interest, being well to the north. The Cornish record is also notably, though not unprecedentedly, late in the accepted flight period for this species. It will be interesting to determine whether new breeding colonies may have become established in Britain as a result of the 2015 immigrations.

Aeshna mixta Latreille – Migrant Hawker

During late summer and autumn there were signs of significant movement by this species in parts of eastern Britain. Some 500 individuals were thus seen at Chambers Farm Wood, Lincolnshire, on 25 August (GH), while later in the season an 'influx' was noted at Spurn, East Yorkshire, with 100 present from 27 September to 1 October (BS). Around that time, a male was also noted at Winnyfold Plantation, Aberdeenshire, on 25 September (IB). This is the current most northerly British record and one of very few sightings north of the Scottish Borders.

In addition to the above records, a male was found dead on the Hewett 48/29B oil platform in the southern North Sea some 25 miles off Cromer (per ATh) during the course of 2015. Unfortunately the exact date of its arrival could not be determined, and how this event fits into the bigger picture thus remains unclear. Records made at sea, however, clearly provide valuable insight into dragonfly migration.

Aeshna isoceles (Müller) – Norfolk Hawker

The first records for Hertfordshire were made during late June 2015, a single being seen at Amwell on 25 June and three, including a mating pair, being noted there the following day (GC). It would seem that the recent range expansion being shown by this species in Britain (Cham *et al*., 2014) is continuing apace.

Anax ephippiger (Burmeister) – Vagrant Emperor

There have been several significant influxes of this well-known Afro-tropical migrant species in recent years (Cham *et al*., 2014) and 2015 continued in similar vein, with significant arrivals being noted during October and November. Single females were seen and/or photographed at Hessle in East Yorkshire on 11 October (BW), near Torrington, Devon, on 14 October (JC) and at Hayling Island, Hampshire, on 10 November (JW). Males were similarly noted on Bardsey Island, Gwynedd, and at Marazion Marsh, Cornwall, on 1 November (SS and CM, respectively), with another at Plymouth, Devon, on 5 November (PF). An unsexed individual was present on Lundy Island, Devon, on 13 October (IL & KR).

In addition to these confirmed records, sightings of 2–3 unidentified 'hawker' dragonflies in southern England during mid April, co-incident with the arrival of Saharan dust, and later in the year over the Christmas period, may perhaps also refer, at least in part, to *A. ephippiger*. This must, however, remain speculative.

Anax parthenope Sélys – Lesser Emperor

It was a fairly average year for the species, with confirmed reports from some 17 sites. These were predominantly in southern England (involving counties such as Cornwall, Kent, Hertfordshire, Buckinghamshire, Greater London, Essex, Norfolk and Gloucestershire), though more northerly records came from Wintersett Reservoirs in South Yorkshire (per PS) and from Messingham Sand Quarries, Lincolnshire (SR).

Records spanned the period 18 June–7 September, peaking in mid July. Although, as usual, it seems that many sightings referred to fresh immigrants, there was circumstantial evidence that a significant number of locally-bred individuals were also involved during 2015. There were thus reports from Hilfield Park Reservoir in Hertfordshire (SM) and New Hythe Lakes in Kent (per JGB), where there have been many sightings in recent years, and where exuviae of *A. parthenope* were found at the latter site during 2011 (Parr, 2012). Numerous individuals, perhaps up to half a dozen, were also reported from the Trinity Broads complex in Norfolk over the period 2–11 July (RF, PH, SR, DW *et al*.), this being an area where equality impressive numbers had been reported in 2014, and where oviposition had also been observed (Parr, 2015). The most clear-cut evidence for local breeding was, however, an immature male with one un-inflated hindwing seen in Buckinghamshire, just west of the village of Wilstone, on 10 July (RW). Although this individual could still fly, it seems unlikely that it could have travelled long distances.

Libellula fulva Müller – Scarce Chaser

Libellula fulva has been steadily expanding its range in southern England over recent years (Cham *et al*., 2014), and further evidence of the species' dispersive potential was seen in 2015. An immature female reported from Amwell, Hertfordshire, on 5 June (BR) was either the first or second county record. Similarly, the second record for Cornwall was made near Bude, in the north of the county, on 10 June (SG); the first record, perhaps an immigrant from the Continent, had been some distance away at Marazion Marsh on 17 July 2013 (Parr, 2014).

Orthetrum cancellatum (L.) – Black-tailed Skimmer

A male seen at Millars Moss, Berwickshire, on 5 July (DG) is unusually far to the north for this species. Several *S. fonscolombii* were noted at the same time, and a possible *A. parthenope* had been seen the previous day. Whether this implies that the skimmer was a long distance migrant, as opposed to just being a wanderer of English origin is, however, unclear.

Orthetrum coerulescens (Fab.) – Keeled Skimmer

A male seen at Ainsdale dunes, Lancashire, on 3 July (PK) represents only the second county record, the nearest significant populations being in Cumbria and northwest Wales. Wandering *O. coerulescens* also turned up unexpectedly during July at Winterton Dunes and Upton Fen in Norfolk (per PT), though in this instance the species does breed elsewhere in the county.

Sympetrum danae (Sulzer) – Black Darter

One was noted at Gibraltar Point, Lincolnshire, on 10 September (per KW). The species is not established in the area, and the record potentially relates to an immigrant from the Continent.

Sympetrum flaveolum (L.) – Yellow-winged Darter

Two individuals were reported from Winterton Dunes, Norfolk, during the year – a male on 1 August and a female on 7 August (PH). These are the first confirmed British records for several years, and arrivals of this well-known migrant species clearly continue to be highly erratic in nature. This contrasts with the situation for *S. fonscolombii*, which historically used to be an even more rare and erratic visitor, but which has in recent decades become a regular immigrant, often in some numbers.

Sympetrum fonscolombii (Sélys) – Red-veined Darter

With several distinct waves of immigration being seen during the season, 2015 turned out to be a very productive year for *S. fonscolombii*. The first records were in May, with a "red dragonfly" likely to have been a male of this species reported from the Cotswold Water Park, Wiltshire, on 4 May (SBi) and a female reported from the Isle of Wight on 16 May (AB). Large-scale arrivals then began on 5 June, with records from no less than 24 sites being made in the subsequent ten days. These involved areas as widespread as Cornwall, Devon, Dorset, Hampshire, the Isle of Wight, Kent, Greater London, Suffolk, Norfolk, Hertfordshire, Gloucestershire and Pembrokeshire. Subsequent to this, another major wave of arrivals then took place in the last days of June and first few days of July. Apart from inland sightings in Nottinghamshire and Staffordshire, and a record in the west from Lancashire, the bulk of records during this particular immigration event came from eastern coastal areas. Reports were thus received from Suffolk, Norfolk (several sites), Lincolnshire, East Yorkshire (Flamborough Head, CT), North Yorkshire (Filey, JH & MP), Cleveland (Brotton, 6 July), Berwickshire (Millars Moss, 4–11 July; DG) and East Lothian (Aberlady Bay, 7 July; AMa). Records of *S. fonscolombii* in Scotland are still quite unusual, so to have reports from two separate sites in July 2015 is of some significance, and serves to demonstrate the extent of this particular influx. Remarkably, no less than 24 individuals were present at Millars Moss on 5 July (DG).

While there was little conclusive evidence for (m)any locally-bred individuals being seen in spring/early summer, most sightings clearly referring to immigrants, the autumn was to provide a marked contrast. The first locally-bred (second generation) progeny resulting from the spring arrivals were thus found at Badminston, Hampshire, on 22 August, with 'several' tenerals being discovered. Sightings of tenerals and/or immatures were to continue at this site for at least two months (PW, PR). Further successful local breeding was also noted during the autumn at Felbrigg in Norfolk (SC), Windmill Farm in west Cornwall (CM) and near Reculver in Kent (MH). Given the magnitude of the spring arrivals, it seems likely that successful breeding may also have occurred at other sites, but passed unnoticed.

In addition to the locally-bred individuals, there was also a series of mainly coastal sightings made during the late summer/autumn that probably refer to new migrants. Some dragonflies may have been dispersing second-generation individuals from breeding sites in England or elsewhere in northwest Europe but, since several were fully mature when seen rather than the immatures more normally encountered in autumn, it also seems likely that further invasions from southern Europe took place. Records included individuals at Filey in North Yorkshire (DL, MP) and Tynemouth Castle in Northumberland (TS) around

24/25 August, with at least one individual seen arriving in off the sea (DL). Three were noted at Spurn, East Yorkshire on 6 & 10 September (BS) and there were several records during the period 12 September–2 October from the Portland Bill area of Dorset (per MC), with a male also seen nearby at Weymouth on 12 September (per PW). Finally, a male was noted on St Agnes, Isles of Scilly, on 13 September (BD), with a female at Cold East Cross, Dartmoor, Devon, on 25 September (DT).

Sympetrum striolatum **(Charp.) – Common Darter**

There were few signs of any large-scale movements by this species during the year, though smaller-scale migration can be hard to detect due to the simultaneous presence of numerous resident individuals. Records of dragonflies caught overnight in UV moth-traps may perhaps refer to migrants (Parr, 2006) and, during the current reporting year, individuals of *S. striolatum* were noted in such a manner from Bawdsey, Suffolk, on 21 August and 25 October (MD), and from Portland Bill, Dorset, on 7 & 13 August (MC).

Remarkably, and unprecedentedly, three dragonflies thought to be female *S. striolatum* were observed in Britain over the 2015 Christmas period. Individuals were thus noted from the Southampton area of Hampshire (per PW) and at Dawlish Warren in Devon (per KR) on 26 December, and at Idle Valley NR, Nottinghamshire, on 27 December (per AH). Although December had been remarkably mild (Met Office, 2016), it seems unlikely that these dragonflies were exceptionally late residents, and possibly they were immigrants from North Africa, Spain or southern France, where late December records of *S. striolatum* are well-known (Boudot & Kalkman, 2015; Curd, 2016). However, sadly none of the sightings were rigorously documented and the possibility of some mis-identifications cannot therefore be totally excluded. *Anax ephippiger* is one species already known to sometimes occur in Britain during mid winter (Cham *et al*., 2014).

Other Species

i) **Exotics**

At least three individuals of the Afro-Asian species *Ischnura senegalensis* (Rambur) emerged from an indoor aquarium in Tilbury, Essex, during early March (RC). The species is clearly now being accidentally imported into Britain (typically in association with tropical waterweed for use in aquaria) on quite a regular basis; Parr (2010) and Laister *et al*. (2014) provide further background to the issue of accidentally-imported dragonflies in Britain and Europe.

ii) **Un-verified records**

On 12 May, a possible *Pantala flavescens* (Fab.) was seen by a very experienced observer near Otterton on the south Devon coast (AS). While common in many parts of the world, this species is still extremely rare in Europe. It is, however, an outstanding migrant and has recently turned up in unexpected localities such as the Courish Spit, Kaliningrad Oblast, western Russia (Buczyński *et al*., 2014). The report is thus credible, but unfortunately must be considered unsubstantiated.

Conclusions

The 2015 reporting year was quite an eventful one for migrant and dispersive dragonflies in Britain. *Anax ephippiger* continued its recent run of appearances and there were major arrivals of *Sympetrum fonscolombii*, with at least two distinct waves of immigration in spring/early summer and further influxes during the autumn. From once being considered a very scarce and erratic immigrant, within the last 20 years this species has become a regular visitor and the large-scale arrivals seen during 2015 are thus perhaps no longer particularly unexpected. By contrast, *Aeshna affinis* is still seemingly not a very regular visitor to the UK (though maybe it goes overlooked due to its similarity to *A. mixta*?), and the appearance of several geographically well-scattered individuals during July–September 2015 is thus of some note. Perhaps new breeding populations may even become established to supplement the one that has developed over the last few years in the greater Thames Estuary area. Finally, significant immigrations of *Anax parthenope* were again reported during the year, with growing evidence that resident populations of this species might now also be becoming established.

The major events of 2015 can be summarised as continued consolidation by our new colonist species, the continued arrival of good numbers of migrants whose main strongholds lie in more southerly regions of Europe (though a few migrants of more easterly origin also appeared during the year), and the successful local breeding by some of these incoming migrants. These events clearly continue the trends that have developed in northern Europe over the last two to three decades, which no doubt are largely being driven by climatic warming. Within this broader context, three issues stand out as worthy of further study: (i) how far will the ranges of our new colonist species expand, and why are some species expanding more rapidly than others, (ii) what is the interplay between local breeding and migration in populations of highly dispersive species such as *S. fonscolombii* (and others?), and (iii) are there new species for Britain soon to arrive on our shores, and if so, what might they likely be? Clearly these remain exiting times for odonatologists.

Acknowledgements

I would like to thank all those people who submitted records during the year. The following observers have been identified in the text by their initials: D. Andrew (DA), A. Armstrong (AA), K. Bentley (KB), S. Birt (SBi), I. Broadbent (IB), S. Burch (SBu), J. & G. Brook (JGB), A. Butler (AB), M. Cade (MC), G. Canny (GC), T. Caroen (TC), D. Chelmick (DC), S. Chidwick (SC), R. Chowdhury (RC), J. Cullen (JC), B. Dawson (BD), M. Deans (MD), R. Fairhead (RF), P. Fenn (PF), A. Goodwin (AG), D. Graham (DG), S. Green (SG), J. Harwood (JH), M. Heath (MH), P. Heath (PH), G. Hopwood (GH), A. Horsley (AH), S. Jellett (SJ), P. Kinsella (PK), I. Lakin (IL), D. Lombard (DL), A. McLean (AMc), A. Marland (AMa), C. Moore (CM), S. Murray (SM), M. Pearson (MP), N. Phillips (NP), B. Reed (BR), P. Ritchie (PR), S. Routledge (SR), K. Rylands (KR), P. Smith (PS), D. Sadler (DS), T. Sexton (TS), B. Spence (BS), S. Stansfield (SS), A. Swash (AS), C. Thomas (CT), A. Thorpe (ATh), D. Turrell (DT), J. Walters (JW), B. Warrington (BW), D. Weaver (DW), K. Wilson (KW), P. Winter (PW), R. Woodward (RW).

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Flight periods of dragonflies and damselflies in Orkney

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Summary

There are eight breeding species of odonate in Orkney, four zygopterans and four anisopterans. Using data from records for Orkney, the flight times of these species have been established to provide an Orcadian flight season table.

Introduction

National (UK) and regional (County) atlases for Odonata usually contain details of the flight period for each species (e.g. Cham *et al.* 2014). Several leaflets produced for mainland Scotland also have this feature but, as is so often the case, things are different in Orkney. To address this phenological shortfall, the Orkney records for dragonflies and damselflies which breed in the county were analysed to provide a more accurate set of flight periods for these species.

Orkney (a label that encompasses all the islands of the archipelago) is situated across the Pentland Firth from the north of mainland Scotland, where the Atlantic Ocean meets the North Sea. It lies around 59°N and comprises about 70 islands of which 18 are inhabited (Fig. 1). It covers an area in the region of 990 km^2. Never too hot, nor too cold, the prevailing weather is wind and, with few trees or hedges to provide shelter, it is a harsh environment for a winged insect.

The majority of the inhabited islands within the Orcadian archipelago have a recorded odonate presence, with only Stronsay and Wyre seemingly bereft of Odonata (Table 1). However, on the island of Hoy, in the south-west, with its moorland hills, bogs, pools and burns, it is possible to find all of Orkney's dragonfly and damselfly species. Two of the better sites, offering the opportunity to witness the majority of these species, are to be found on Wee Fea (Plate 1) and near Lyness (Plate 2).

Records

Records were obtained for the years 1992 to 2015. Whilst these records have

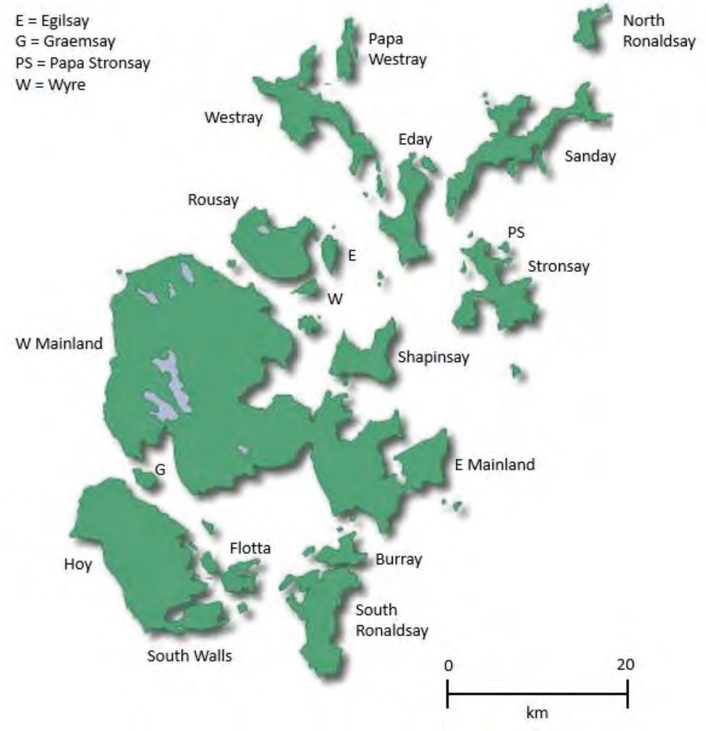

Figure 1. The Orkney archipelago. The named islands are the 18 that are inhabited. Reproduced with the kind permission of Sigurd Towrie and Orkneyjar.

primarily been used to map the geographical spread of the Orcadian odonate assemblage, they also provide information which offers an opportunity to attempt the construction of a flight period table. All of the records are within the window of May to October. However, it is entirely possible, if somewhat improbable, that benign weather could cause earlier emergences. Conversely, a prolonged spell of bad weather could have the reverse effect.

None of the species has a continuous set of records covering all the years between 1992 and 2015, although seven of the eight breeding species have been present for most of that time. The eighth species, *Lestes sponsa*, Emerald Damselfly, was first recorded in Orkney during 2010. Additionally, a number of records do not contain sufficient information to allow an accurate assessment of date, either due to a lack of date, too vague a date or technical problems within Excel. These records had to be ignored, reducing the data set and hence somewhat decreasing the accuracy of the results. However, since the omitted

Table 1. Recorded species distribution across Orkney

Island	**Species**							
	Lestes sponsa	***Pyrrhosoma nymphula***	***Enallagma cyathigerum***	***Ischnura elegans***	***Aeshna juncea***	***Cordulegaster boltonii***	***Libellula quadrimaculata***	***Sympetrum danae***
Hoy	✓	✓	✓	✓	✓	✓	✓	✓
East Mainland		✓	✓	✓	✓	✓		✓
West Mainland		✓	✓	✓	✓	✓		✓
South Ronaldsay		✓	✓	✓	✓			✓
Rousay		✓	✓		✓			✓
Sanday			✓	✓	✓			
Burray		✓		✓				
Eday				✓				✓
Egilsay			✓	✓				
Westray			✓	✓				
Flotta					✓			
Graemsay				✓				
North Ronaldsay				✓				
Papa Stronsay				✓				
Papa Westray			✓					
Shapinsay					✓			
South Walls				✓				
Stronsay								
Wyre								

records were mainly from the earlier years of the dataset, the impact will be minimal. The percentage of useable records for each species is shown below in the relevant species account. It is hoped that the final table of flight periods will better reflect the current situation in the Orcadian archipelago than the information currently available.

Several other factors were taken into account when analysing the records:

- The few records of vagrant individuals were ignored.

Plate 1. Small bog pools on Wee Fea, Hoy

Plate 2. Larger pool near Lyness, Hoy

- If numbers were not recorded, then the number of a species seen was assumed to be 1, as any less would not have generated a record in the first place.

- If the number recorded was merely denoted by '+', then the number of a species seen was assumed to be 2.

- If a letter was used to denote the number, as per standardised categories (A = 1, B = 2-5, C = 6-20, D = 21-100, E = 101-500, F > 500), then the lowest number in the category was assumed.

The flight period of each species is illustrated by a bar chart showing the number of flying adults which were recorded per half month throughout the flight season in Orkney, for the years 1992 to 2015 (Figs 2-9).

Damselflies

Lestes sponsa **(Hansemann) - Emerald Damselfly**

The newest member of our odonate assemblage, *Lestes sponsa* was first recorded in Orkney in 2010. The species has been seen in each subsequent year, with 2015 providing the most data. There are 18 records in the database, 100% of which were useable. Altogether 143 flying individuals have been recorded during 2010-2015. The flight season begins in late July, peaks in late August and ends in early September (Fig. 2).

Pyrrhosoma nymphula **(Sulzer) - Large Red Damselfly**

Pyrrhosoma nymphula is usually the first species to emerge in Spring. With some records from 1994 and 1996, there is a continuous set of data from 2007 until the present time. There are 293 records in the database, 69% of which were useable. Altogether, 618 flying individuals have been recorded between 1994 and 2015. The flight season begins in early May, peaks in early July and ends in late August (Fig. 3).

Enallagma cyathigerum **(Charpentier) - Common Blue Damselfly**

Enallagma cyathigerum is another early emerger. With some records from 1994, there is a continuous set of data from 2007 until the present time. There are 111 records in the database, 56% of which were useable. Altogether, 354 flying individuals have been recorded between 1994 and 2015.

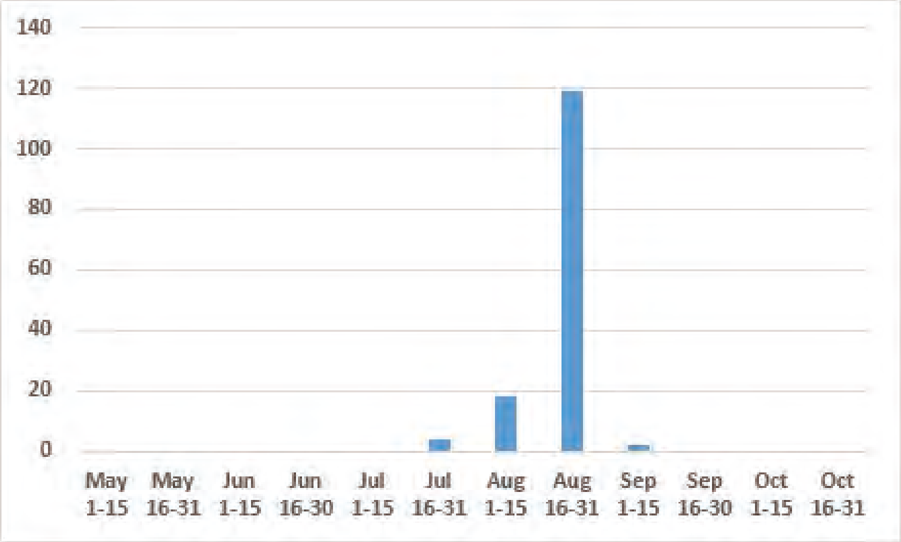

Figure 2. Flight period of *Lestes sponsa* Emerald Damselfly. Number of individuals recorded in each half month.

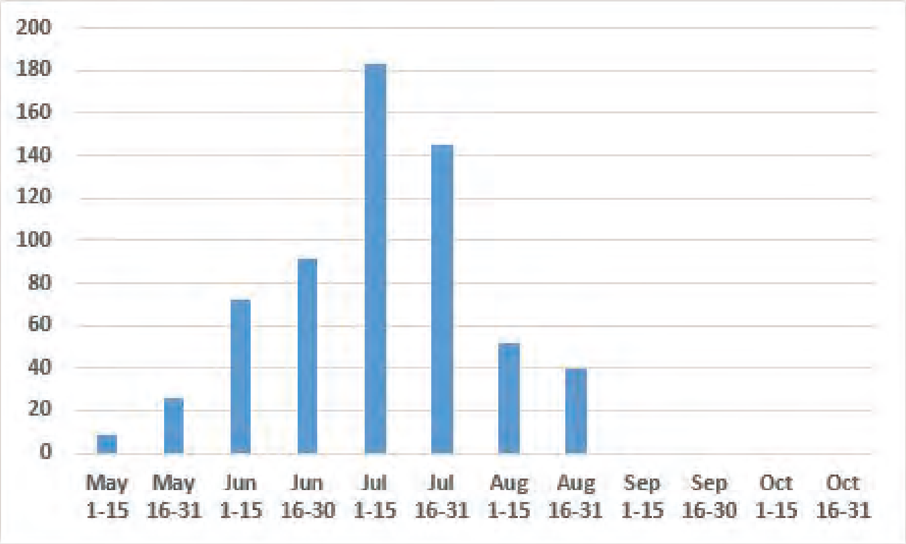

Figure 3. Flight period of *Pyrrhosoma nymphula* Large Red Damselfly. Number of individuals recorded in each half month.

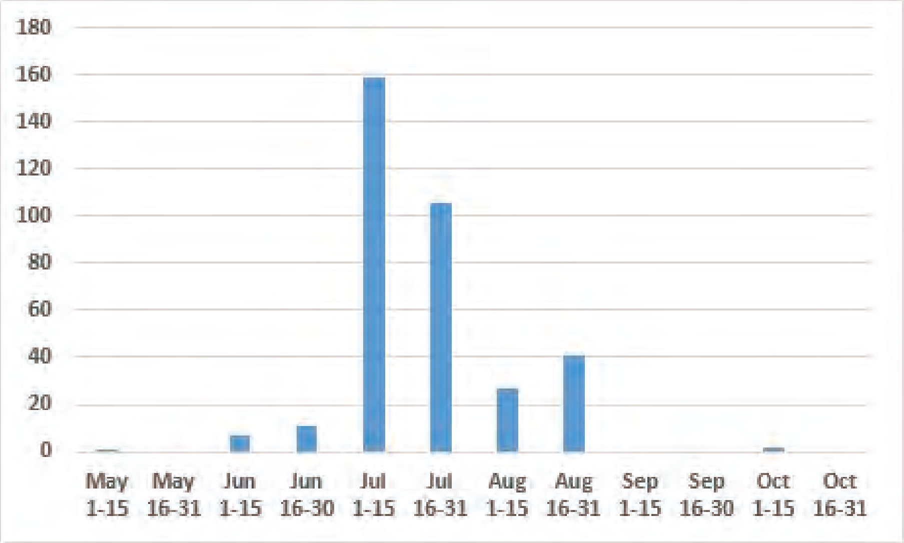

Figure 4. Flight period of *Enallagma cyathigerum* Common Blue Damselfly. Number of individuals recorded in each half month.

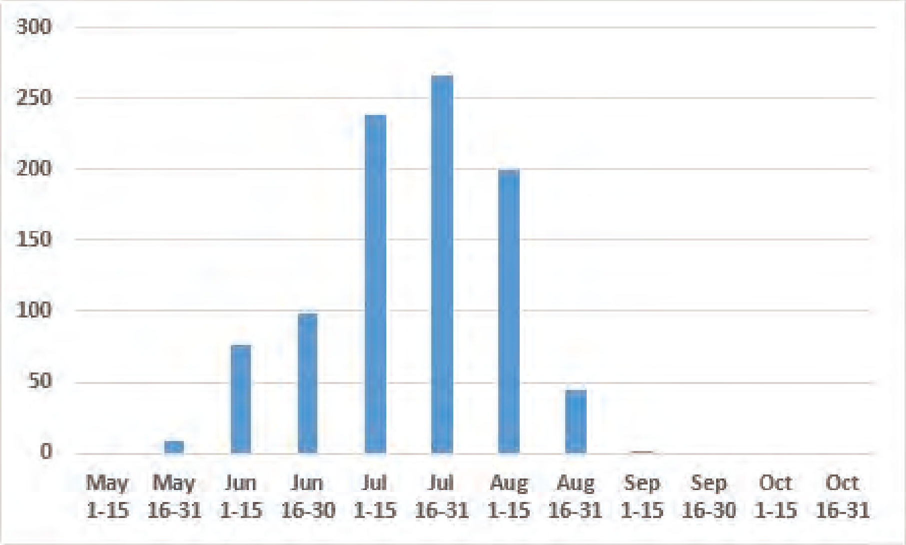

Figure 5. Flight period of *Ischnura elegans* Blue-tailed Damselfly. Number of individuals recorded in each half month.

The dataset for the Common Blue Damselfly contains a very early May record and a very late October record. It is possible that the former was a previous year's final instar larva that chose to enter diapause rather than emerge late in that year. Conversely, the latter may have been a larva that elected to emerge sooner rather than overwinter, perhaps due to a spell of good weather. The flight season begins in early June, peaks through July and ends in late August (Fig. 4).

Ischnura elegans **(Vander Linden) - Blue-tailed Damselfly**

Ischnura elegans is our most widespread species. With some records from 1992 and 1996, there is a continuous set of data from 2007 onwards. There are 196 records in the database, 83% of which were useable. Altogether, 934 flying individuals have been recorded between 1992 and 2015. The flight season begins in late May, peaks in late July and ends in early September (Fig. 5).

Dragonflies

Aeshna juncea **(Linnaeus) - Common Hawker**

Aeshna juncea is a dragonfly with a flight period that is rather late in the year. There is a continuous set of data from 2007 onwards. There are 137 records in the database, 62% of which were useable. Altogether, 154 flying individuals have been recorded between 2007 and 2015. The flight season begins in late June, peaks in late July and can extend all the way into October (Fig. 6).

Cordulegaster boltonii **(Donovan) - Golden-ringed Dragonfly**

Cordulegaster boltonii is our largest species and is strikingly marked in yellow and black, with green eyes. Its preferred habitat is moorland streams, which aren't as accessible as ponds or pools, so there is a paucity of records for this species. Thus there are only 31 records in the database, 55% of which were useable. Altogether, 18 flying individuals have been recorded between 2007 and 2015. The flight season begins in late June, peaks in late July and ends in late August (Fig. 7).

Libellula quadrimaculata **(Linnaeus) - Four-spotted Chaser**

Libellula quadrimaculata is another poorly recorded dragonfly. However, this may well be because it has a less accessible, very limited habitat in Orkney and consequently is more difficult to find. It is the earliest of our dragonflies on the wing. It is hoped that increased recorder effort will be deployed in 2016, in an

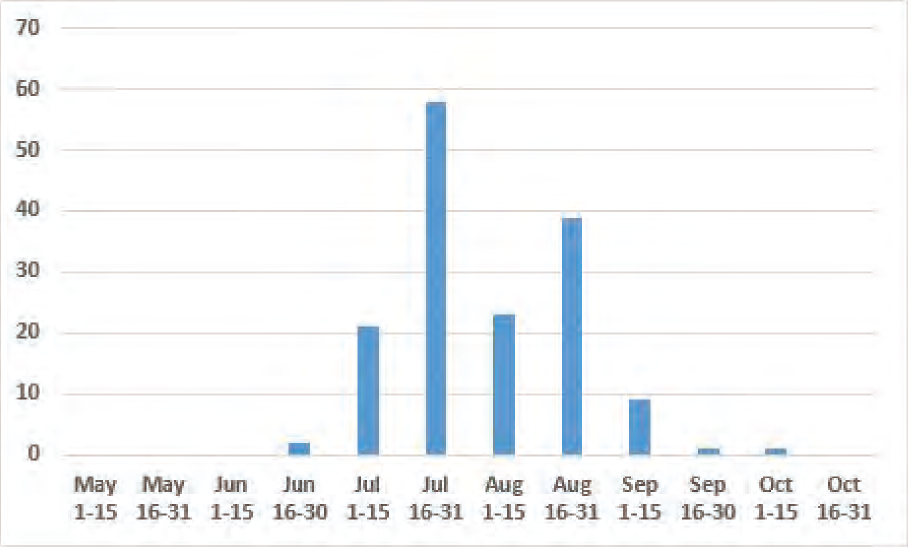

Figure 6. Flight period of *Aeshna juncea* Common Hawker. Number of individuals recorded in each half month.

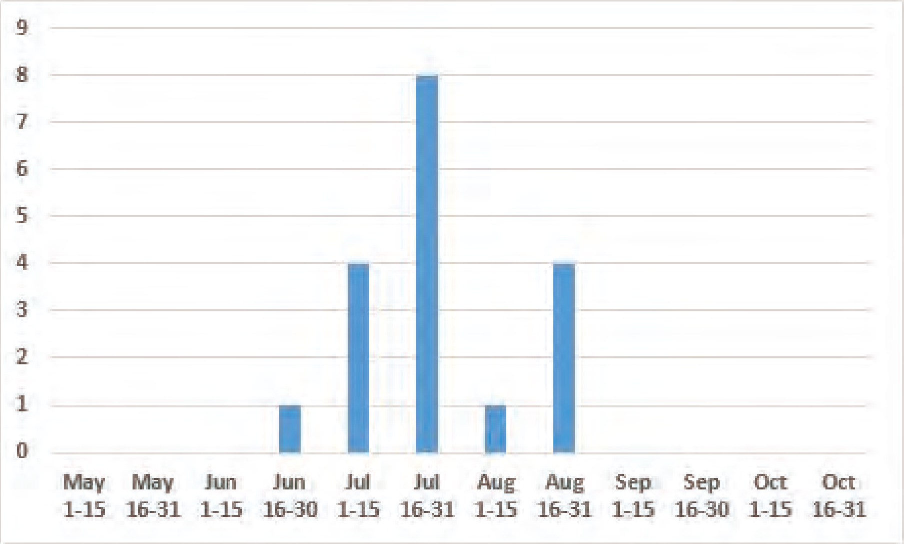

Figure 7. Flight period of *Cordulegaster boltonii* Golden-ringed Dragonfly. Number of individuals recorded in each half month.

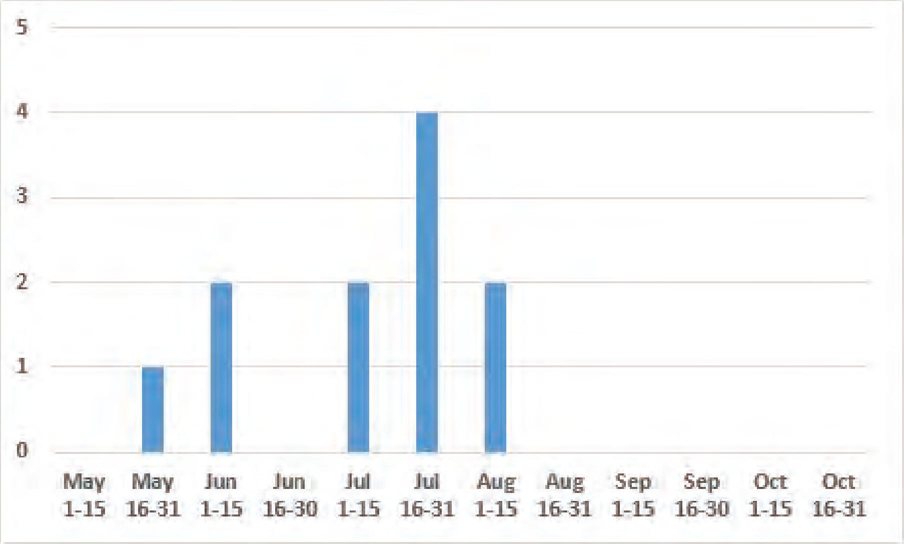

Figure 8. Flight period of *Libellula quadrimaculata* Four-spotted Chaser. Number of individuals recorded in each half month.

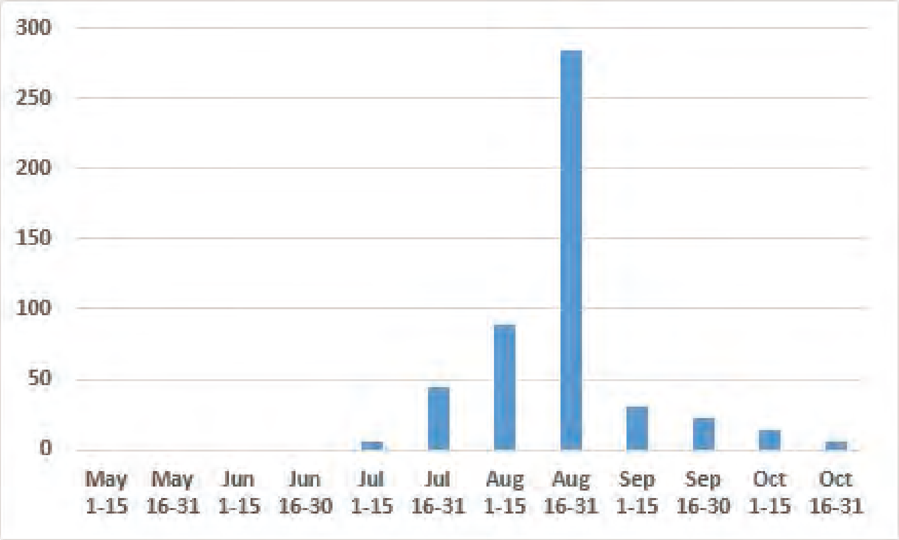

Figure 9. Flight period of *Sympetrum danae* Black Darter. Number of individuals recorded in each half month.

attempt to prove its continued presence in Orkney.

There are only 12 records in the database, 58% of which were useable. Altogether, 11 flying individuals have been recorded in 2008, 2011, 2012 and 2015. With so few records, it is probably inappropriate to draw too many conclusions about the flight period. However, from the available data, the flight season begins in late May, peaks in late July and ends in early August (Fig. 8). Anecdotal evidence would suggest that the peak of the flight period is in early July but more records would be needed to confirm this.

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

Our smallest dragonfly, *Sympetrum danae*, has a flight period later in the year. It is also our most abundant dragonfly and there is a continuous set of data from 2006 onwards. There are 144 records in the database, 72% of which were useable. Altogether, 494 flying individuals have been recorded between 2006 and 2015. The flight season begins in early July, peaks in late August and ends in late October (Fig. 9).

Conclusions

The peak of the flight season corresponds to the period in which most adults are seen and offers the best opportunities to see flying adults at their breeding sites.

Table 2. Flight season for all eight Orkney species

Species	**May**		**Jun**		**Jul**		**Aug**		**Sep**		**Oct**	
Lestes sponsa						▨	🟩	🟩	▨			
Pyrrhosoma nymphula	▨	▨	▨	🟩	🟩	🟩	▨	▨				
Enallagma cyathigerum			▨	▨	🟩	🟩	▨	▨				
Ischnura elegans		▨	▨	▨	🟩	🟩	🟩	▨	▨			
Aeshna juncea				▨	▨	🟩	🟩	🟩	▨	▨	▨	
Cordulegaster boltonii				▨	🟩	🟩	🟩	▨				
Libellula quadrimaculata		▨	▨	🟩	🟩	🟩	▨					
Sympetrum danae					▨	▨	🟩	🟩	▨	▨	▨	▨

Late July and early August are the few weeks when all of the eight breeding species present in Orkney might possibly be on the wing at the same time.

The data sets for *Cordulegaster boltonii* and *Libellula quadrimaculata* are very small, so there could well be inaccuracies in the interpretation of the records. Continued recording and future assessment of new data will help to refine the accuracy of the flight periods.

It should be noted that the bar charts are only an indication of past trends. Both climate change and local weather will have impacts on the phenology of these species, as will any changes to their habitat. Also local circumstances will influence the emergence times and life span of the adults. Nevertheless, the summary of the bar chart for each species (Table 2) will be a useful addition to any future identification guide for the Orkney dragonflies and damselflies.

Acknowledgements

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A review of the role of the abdomen of aeshnid larvae in respiration, jet-propulsive locomotion and prey capture. 1. The digestive, tracheal, muscular and nervous systems.

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Abstract

The structure of the digestive, tracheal, muscular and nervous systems in the abdomen of aeshnid larvae is reviewed, with particular regard to the rôle of the abdomen in producing pressure changes that elicit respiration, jet-propulsive swimming and labial mask extension. The musculature of the labial mask is also described.

Introduction

Ventilation, jet-propulsive swimming and labial mask extension (prey capture) all involve dorso-ventral movements of the floor of the abdomen which produce pressure changes in the abdominal cavity. To understand these functions, a knowledge of the morphology of the digestive, tracheal, nervous and muscular systems of the abdomen is required. The digestive system is important in the context of respiration since a modified region of the hind-gut or rectum (the branchial chamber) contains the gills (Fig. 1) and water is pumped in and out of the branchial chamber through the anus. Tillyard (1916) summarised the early literature on this and, according to him, it was probably Poupart (1700) who first realised that the branchial chamber was involved in respiration. Dufour (1852) was the first to describe the tracheae penetrating the projecting folds in the branchial chamber and thus establish that they are tracheal gills, while Leydig (1866) and Oustalet (1869) demonstrated that the tracheoles do not end blindly in the gills but form loops. Mill (1972, 1977, 1982, 1985, 1997, 1998a,b) has reviewed various aspects of abdominal structure and function. Most of the available information derives from studies on aeshnids. The mechanics and physiology will be described in part 2 of this review (Mill, in prep.).

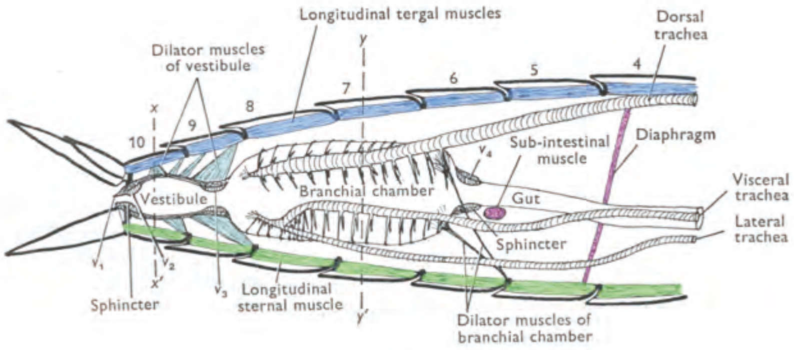
Techniques

A brief outline of the techniques used to study the different systems follows. The general layout of the muscles involved staining with Bouin's fluid (Mill, 1965), while the course of the nerves has been studied using staining with methylene blue (Zawarzin, 1912; Finlayson & Lowenstein, 1958; Mill, 1965). A variety of staining techniques have been used to study the neural pathways within the central nervous system, including methylene blue vital staining (Zawarzin, 1924b), Heidenhain's iron-haematoxylin (Mill, 1964), Ehrlich's haematoxylin (Mill, 1964), Palmgren's silver technique (Mill, 1964 [Palmgren, 1955]), the rapid Golgi technique (Mill, 1964 [Carleton & Leach, 1938]), injection of the fluorecent dye Lucifer Yellow into the axons of individual nerve cells (Komatsu, 1984) and using an antiserotonin antibody to reveal nerve cells exhibiting serotonin-like immunoreactivity (Longley & Longley, 1986). Methylene blue vital staining and back-filling with cobalt chloride have been used to identify the axons of large neurons in the nerves and follow their pathways (Mill, 1965) but both of these techniques are capricious, not necessarily staining all of the larger neurons. Using electron microscopy enables the smaller sensory axons as well as the large sensory and motor axons in the nerves to be counted reasonably accurately (Mill & Whittle, unpub. obs.). However, the axons of the motor neurons divide to innervate the various muscles. Thus, to obtain an accurate count, sectioning at different levels would be necessary but very time-consuming. Recently developed techniques, such as micro-CT scanning, may prove useful in the future (S. Brooks, pers. com.)

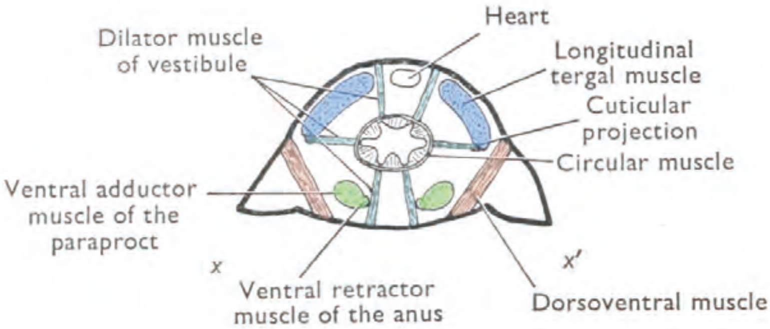
Abdomen

Gills

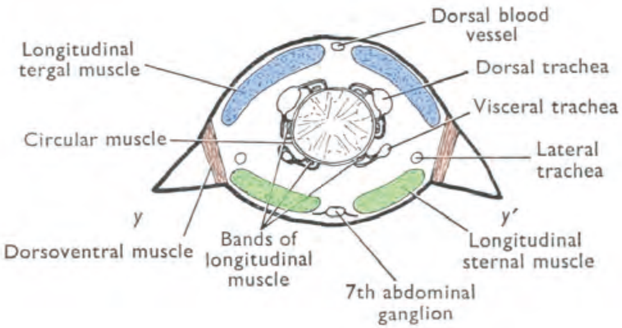
The gills are arranged in six rows within the branchial chamber of anisopteran dragonfly larvae but vary in form in different groups (Ris, 1911; Tillyard, 1916, 1917; Rich, 1918). Tillyard (1916, 1917) described two main types of gill, Simplex and Duplex. In the Simplex System there are six longitudinal gill folds running the length of the branchial chamber, on each side of which are cross folds, and both the longitudinal and cross folds are involved in oxygen uptake from the water. The Simplex System is further divided into two types: a) Undulate. In this type, which is found in cordulegastrids, the longitudinal folds undulate along their length. b) Papillate. This type occurs in most gomphids; the edges of both the main and the cross folds are divided into papillae. In the Duplex System the main folds, when present, do not function as gills and the cross folds (gills) are enlarged. There are three types. a) Implicate. This occurs in *Brachytron*, the gills being in the form of concave plates, each plate slightly overlapping the


Longitudinal tergal muscles
Dorsal trachea
Dilator muscles of vestibule
y
x
10
9
8
7
6
5
4
Diaphragm
Sub-intestinal muscle
v_4
Branchial chamber
Vestibule
Gut
Visceral trachea
Lateral trachea
Sphincter
v_1
v_2
x′
v_3
Sphincter
Longitudinal sternal muscle
y′
Dilator muscles of branchial chamber

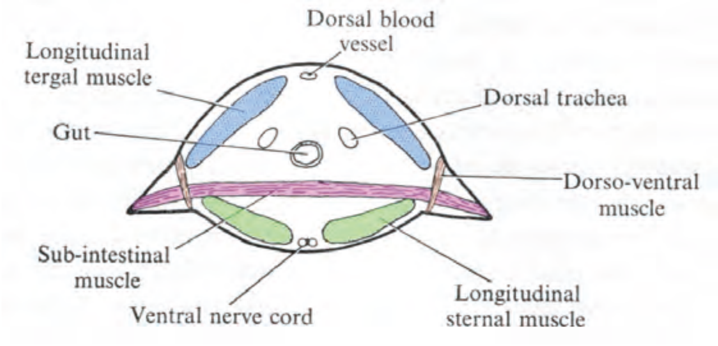
A


Heart
Dilator muscle of vestibule
Longitudinal tergal muscle
Cuticular projection
Circular muscle
Ventral adductor muscle of the paraproct
x
x′
Ventral retractor muscle of the anus
Dorsoventral muscle

B


Dorsal blood vessel
Longitudinal tergal muscle
Dorsal trachea
Visceral trachea
Circular muscle
Lateral trachea
y
y′
Dorsoventral muscle
Bands of longitudinal muscle
Longitudinal sternal muscle
7th abdominal ganglion

C



D

Fig. 1. Sections through the abdomen of a larval *Aeshna* sp. to show some of the main morphological features of the respiratory system. A. Longitudinal section. B. Transverse section through x----x'. C. Transverse section through y----y'. D. Transverse section in the region of the sub-intestinal muscle. v_1-v_4, valves; x----x', plane of figure 1B; y----y', plane of figure 1C. 🟩, longitudinal sternal muscles; 🟦, longitudinal tergal muscles; 🟪, diaphragm and subintestinal muscles; ▨, dorso-ventral muscles; ▨, dilator muscles of the vestibule. A-C after Hughes & Mill (1966); D after Mill & Pickard (1972).

one behind it. b) Foliate. This type is found in *Aeshna* and *Anax* and the base of each gill is constricted. In *Aeshna* the gills are leaf-like and slightly crinkled (normal foliate), whereas in *Anax* each gill bears numerous minute papillae (papillo-foliate). c) Lamellate. In this type each gill consists of a flat plate, each one partially overlapping the one behind it. There are four sub-groups with minor variations: Archi-lamellate, Neo-lamellate, Corduline (e.g. *Cordulia* and *Macromia*) and Libelluline (libellulids) (Tillyard, 1917).

Tillyard (1916) estimated that there are at least 100,000 tracheoles in the gill system of *Anax*. Komnick (1982) counted 84 gills in a 5 mm long larva of *Aeshna cyanea* and 240 in a 25 mm long larva. However, further increase in larval size did not result in any further increase in the number of gills, although their size increased (Komnick, 1982). Gill structure has been described by Greven & Rudolph (1973), Wichard & Komnick (1974) and Komnick (1982) and has been reviewed by Mill (1998b).

Digestive Tract

The pre-branchial valve separates the mid-gut from the branchial chamber. Posterior to the branchial chamber is a muscular anal vestibule, separated from the former by the post-branchial valve and separated from the exterior by the anal valve (Fig. 1A).

In the mid-gut, the gut contents become enclosed in a peritrophic membrane, produced by the cells lining this region (Voinov, 1898; Wigglesworth, 1930) to form a faecal pellet. Thus, as the faecal pellets pass through the rectum, the gills are not in contact with any waste products.

Tracheal system

The tracheal system in aeshnid larvae is ‘closed’, i.e. there are no spiracles and oxygen is taken up directly from the water by diffusion into the dense array of intracellular tracheoles many of which, in *Aeshna* and *Libellula* at least, lie within 1.0 – 1.5 µm of the surface (Greven & Rudolph, 1973; Wichard & Komnick, 1974; Komnick, 1982). Kohnert *et al*. (2004) estimated that, in larvae of *Aeshna cyanea* with a body mass of 271 mg, the total surface area of the gills was about 12 cm^2, 6% of the epithelial volume of the gills consisted of tracheoles and that the mean water-tracheolar diffusion barrier was 0.27 µm.

There are three pairs of longitudinal tracheae, dorsal, visceral and lateral, that run the length of the abdomen. The tracheoles in the gills connect with the dorsal and visceral longitudinal tracheae (Fig. 1A). The visceral longitudinal tracheae connect with the lateral ones near the posterior end of the branchial chamber. Branches from all of the longitudinal tracheae lead into intracellular tracheoles, carrying the oxygen supply to the muscles and other organs (Tillyard, 1917; Mill, 1972). The structure of the tracheae and tracheoles has been reviewed by Mill (1998a).

Muscular system

Insects possess an exoskeleton to which the muscles are attached. Typically, each abdominal segment consists of four rigid plates, a dorsal tergum, a ventral sternum and two lateral pleurites (Fig. 2). The plates within a segment and those of adjacent segments are joined by flexible membranes.

The musculature has been described in *Aeshna grandis* (Wallengren, 1914) and *Anax junius* (Whedon, 1918; Steiner, 1929; Snodgrass, 1954b) but there is little information on muscle innervation (Rogosina, 1928). More recently (Mill, 1965) has studied the muscles and their innervation in *Aeshna juncea*. The following account is based on these species and describes the musculature on one side of a typical abdominal segment (segments 2-8). In each of the first eight abdominal segments there are three functional sets of muscles: longitudinal, dorso-ventral and oblique.

- Longitudinal muscles. There are six longitudinal muscles spanning the full length of the segment. Three of these are ventral or sternal (ls_1, ls_2, IIsp$_1$) and three are dorsal or tergal (It$_1$, It$_2$, IIt$_2$). In addition there are three short sternal muscles (Is$_3$, iIs$_3$, Is$_4$) and four short tergal ones (It$_3$ – It$_6$) (Figs 3-5). When these muscles contract the abdomen is shortened in length.

- <u>Dorso-ventral muscles.</u> There are five vertical, dorso-ventral muscles (atp, adv, rdv, pdv, ptp) (Figs 3B, 6). When they contraction the sternum (i.e. the floor of the abdomen) is raised. One of the dorso-ventral muscles, the respiratory dorso-ventral muscle (rdv), is innervated by numerous tracheoles, implying a high level of activity (Mill & Lowe, 1971).

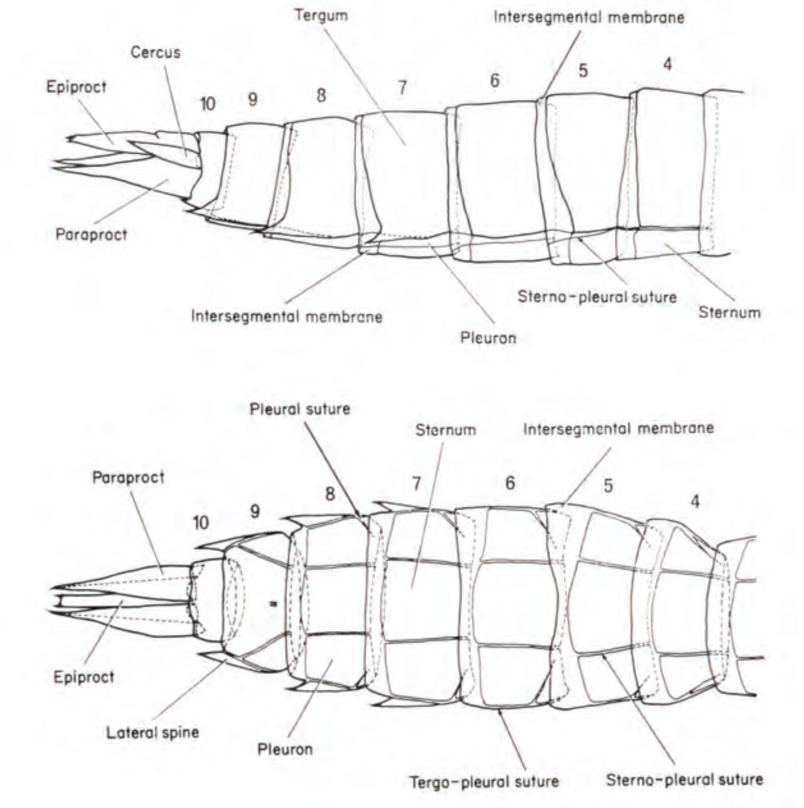


Fig. 2. Abdomen of a final instar larva of a male *Aeshna sp*. (A) lateral aspect, (B) ventral aspect. 4-10, abdominal segments 4-10. From Pickard & Mill (1974).

- Oblique muscles. There are two oblique muscles (otp, dvo) (Figs 3, 6), the contraction of which causes sideways bending of the abdomen.

This gives a total of 20 muscles on each side of the segment (Mill, 1965). In the first three segments and in the ninth and tenth segments there are modifications associated with the abdominal-thoracic junction and the anal appendages respectively (Mill, 1965).

There are also two transverse (unpaired) muscles in the abdomen, one in segment 5 (the diaphragm); the other in segment 6 (the sub-intestinal muscle), each running across the anterior end of its segment (Figs 1, 3, 7).

The branchial chamber has six bands of longitudinal muscles running along its length and there are paired dilator muscles running from the body wall to the branchial chamber (Fig. 1) (Mill, 1965). The vestibule also has a number of paired dilator muscles running to it from the body wall. Thus, at the anterior end of segments 8 and 9 there are ventral (vdv) and dorsal (ddv) dilators; also lateral dilators at the anterior end of segment 8 (ldv) (Fig. 8) (Mill & Pickard, 1975).

The anal valve is controlled by four pairs of retractor muscles, two ventral (vavr), one lateral (lavr) and one dorsal (davr). Each paraproct has a primary ($labp_1$) and a secondary ($labp_2$) lateral abductor muscle, a ventral adductor muscle (vadp) and a dorsal adductor muscle (dad), which is also an adductor muscle for the epiproct. The epiproct has a pair of dorsal abductor muscles (dabe) (Fig. 8) (Mill & Pickard, 1975).

Structure The muscles are cross-striated and, although the arrangement of the actin/myosin array differs from that in vertebrate cross-striated muscle, they operate in basically the same way, i.e. contraction is elicited by the actin and myosin protein filaments sliding over each other to reduce the length of each sarcomere (muscle cell). Tracheoles penetrate the muscles to provide oxygen, the respiratory dorso-ventral muscles receiving a particularly rich supply (Mill & Lowe, 1971; Mill, 1972).

Central Nervous System

The basic insect central nervous system comprises a ‘brain’ and a sub-oesophageal ganglion in the head and a ventral ganglion in each of the three thoracic and 10 abdominal segments, all interconnected by a paired ventral nerve cord. However, in all insects there has been some ‘condensation’ (fusing together) of at least some of the abdominal ganglia. Thus, in aeshnid larvae there are only eight abdominal ganglia, the first of which is partly fused with the

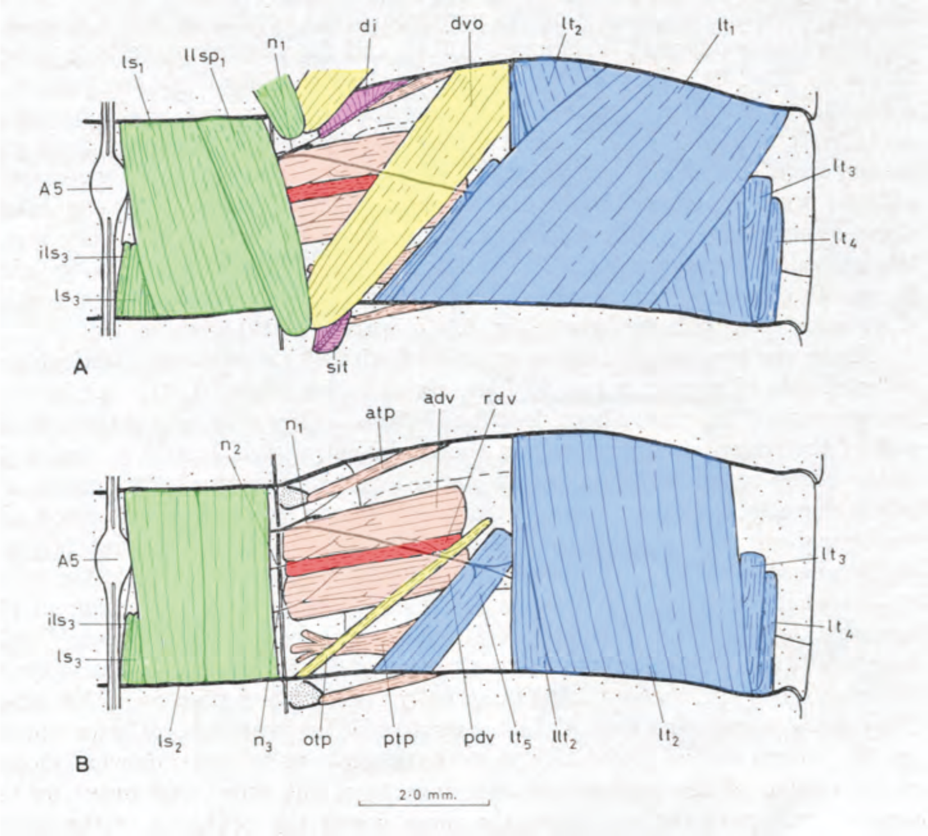


Fig. 3. The right side of the fifth abdominal segment of *Aeshna* sp. viewed internally. Ventral mid-line on the left; dorsal mid-line on the right. (A) with all the muscles present and (B) with some of the inner muscles removed. A5, fifth abdominal ganglion; n1 – n3, the three segmental nerves; 🟩 , longitudinal sternal muscles (ls$_1$- ls$_3$, llsp$_1$, ils$_3$); 🟦 , longitudinal tergal muscles (lt$_1$-lt$_5$); 🟧 , dorso-ventral muscles (atp, adv, pdv, ptp); 🟥, respiratory dorso-ventral muscle (rdv); 🟨 , oblique muscles (dvo, otp) 🟪 , diaphragm (di) and subintestinal muscle (sit). After Mill (1965).

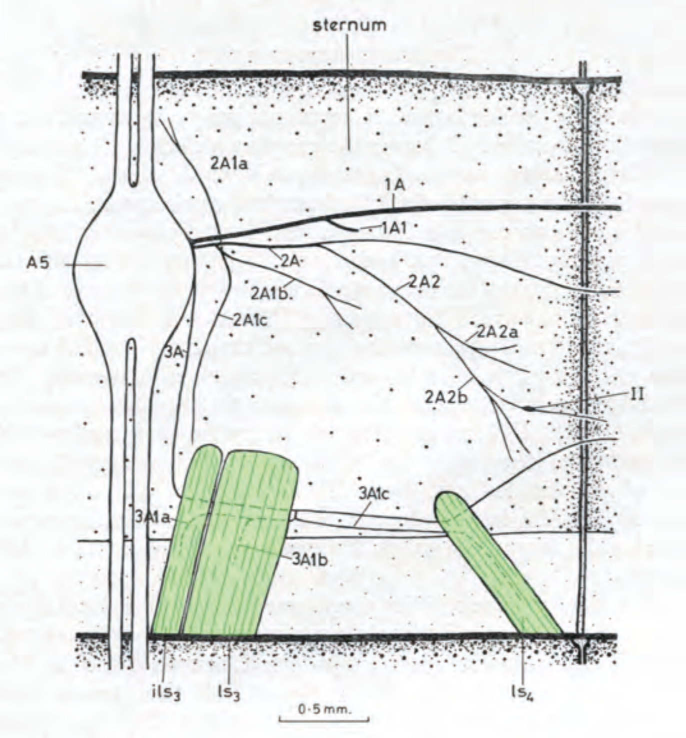


Fig. 4. The sternal region of the right side of the fifth abdominal segment of *Aeshna* sp., viewed internally, with the inner longitudinal sternal muscles removed. A5, fifth abdominal ganglion; 1A, etc. are the numbering of the nerve branches; II, type II sensory neuron; 🟩 , longitudinal sternal muscles (ls$_3$, ls$_4$, ils$_3$. From Mill (1965).

third thoracic one, while the eighth is a fusion of the last three (8-10). The first seven ganglia innervate the first seven abdominal segments respectively, while the eighth innervates the eighth abdominal segment and those posterior to it (i.e. segments nine and ten) (Mill, 1965).

The cell bodies of the motor neurons lie within the ganglia of the central nervous system. In many cases the axon enters a segmental nerve on the same side as its cell body (ipsilateral). However, in the case of the first segmental nerve at least, some axons cross over the ganglion and exit on the opposite side to their cell bodies (contralateral) (Zawarzin, 1924b; Mill, 1964). Zawarzin (1924b) also described some of the interneurons in the abdominal central nervous system while Komatsu (1984) identified interneurons that are associated with ventilation. One of these is an Ascending Expiratory (AE) interneuron with its cell body in the last (8th) abdominal ganglion. Its axon runs forwards (hence 'ascending'), giving

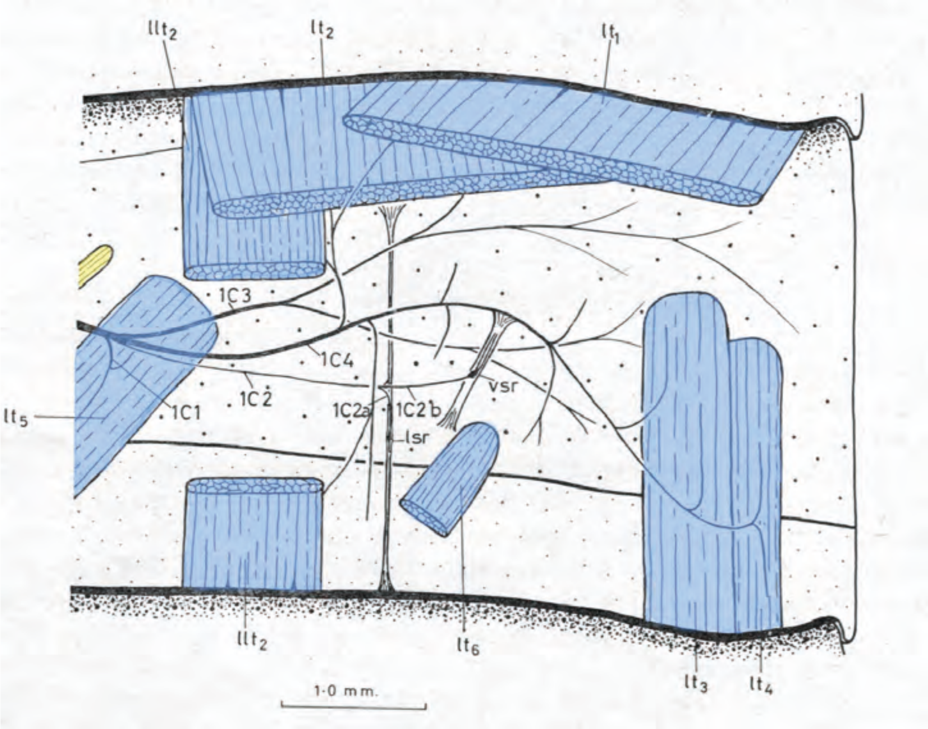


Fig. 5. The tergal region of the right side of the fifth abdominal segment of *Aeshna* sp., viewed internally, to show branches of the first segmental nerve and the innervation of the two stretch receptors (lsr and vsr). 1C3, etc. are the numbering of the nerve branches; 🟦 , longitudinal tergal muscles (lt$_1$-lt$_6$, llt$_2$); 🟨 , oblique muscle. From Mill (1965).

off branches in each abdominal ganglion. A second is an Ascending Inspiratory (AI) interneuron. Again its axon runs through the abdominal ganglia but its cell body has not yet been located.

The motor axons of the median nerves have an unusual configuration. The cell body of each of the two motor neurons concerned lies postero-laterally either side of the ganglion in front of where the nerve leaves the nerve cord. The axons run down the nerve cord to the next posterior ganglion and then loop back anteriorly to enter the median nerve. Each of these motor neurons divides to send one branch to each side (Zawarzin, 1924b; Mill, 1964). Apparently homologous cell bodies in *Epitheca* sp. (Corduliidae) and *Pachydiplax longipennis* (Libellulidae) show serotonin-like immunoreactivity (Longley & Longley, 1986). The sensory axons in the median nerves run forwards to the next anterior ganglion.

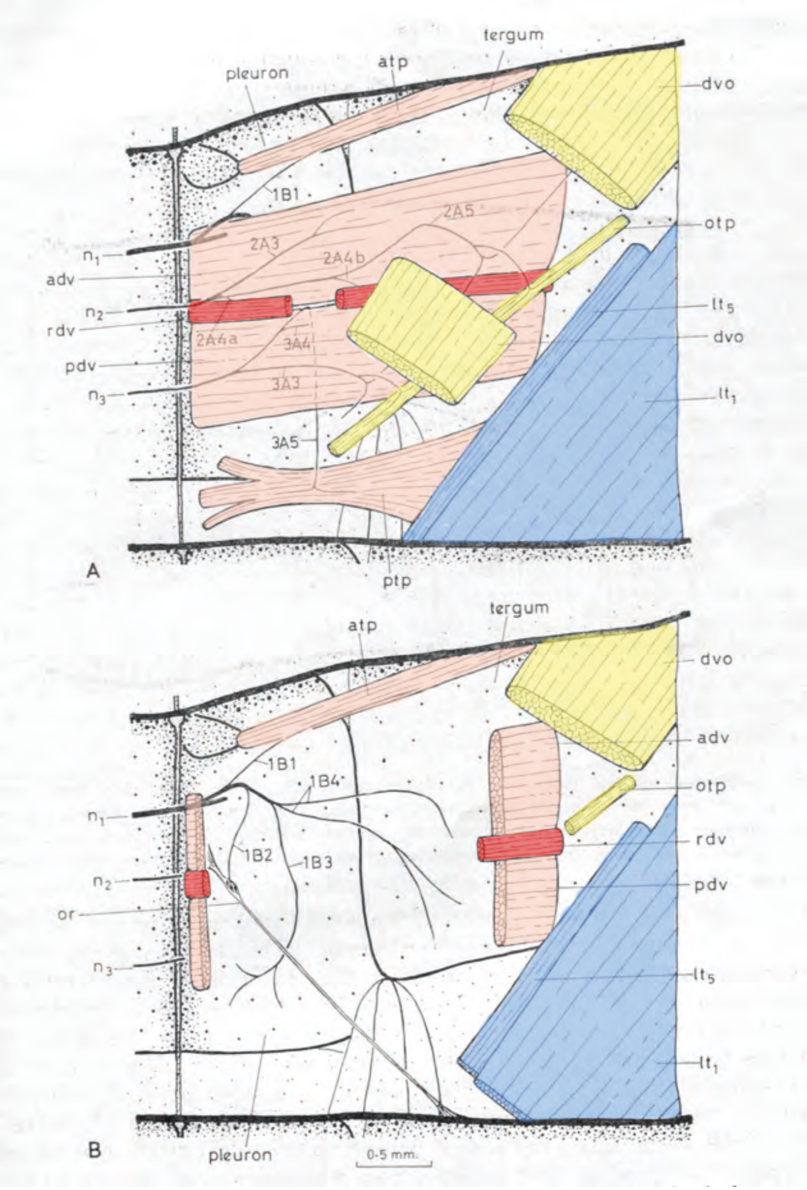


Fig. 6. The pleural region of the right side of the fifth abdominal segment of *Aeshna* sp., viewed internally, with some of the more interior muscles removed. (A) to show branches of the segmental nerves. (B) to show branches of the first segmental nerve and the innervation of the chordotonal organ (or). n1 – n3, the three segmental nerves; 1B1, etc. are the numbering of the nerve branches; 🟦 , longitudinal tergal muscles (lt1, lt5); ◻ , dorso-ventral muscles (atp, adv, pdv, ptp); 🟥 , respiratory dorso-ventral muscle (rdv); 🟨 , oblique muscles (dvo, otp). From Mill (1965).

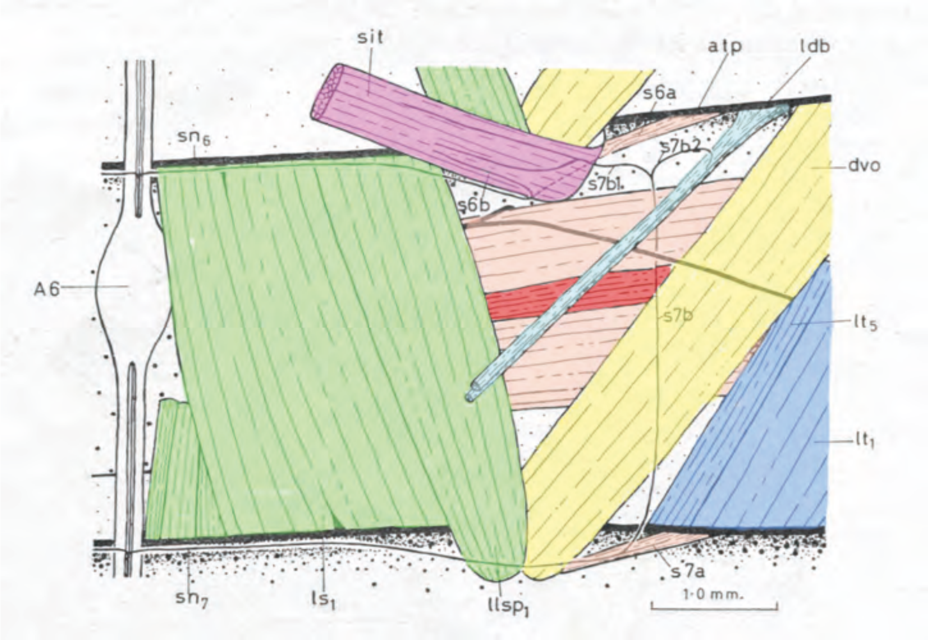


Fig. 7. The right side of the sixth abdominal segment of *Aeshna* sp., viewed internally, to show the median nervous system (sn_6, sn_7). A6, sixth abdominal ganglion; sn_6 and sn_7 the sixth and seventh median nerves; 🟩, longitudinal sternal muscles (ls_1, $llsp_1$); 🟦 , longitudinal tergal muscles (lt_1, lt_5); ▨, dorso-ventral muscles (atp); 🟥 , respiratory dorso-ventral muscle; 🟨 , oblique muscle (dvo); 🟪, sub-intestinal muscle (sit). From Mill (1965).

Peripheral nervous system

The account given below is based on late instar aeshnid larvae. The number of peripheral sense organs and hence the number of sensory neurons almost certainly increases with larval size.

Sense organs On each side of a typical mid-abdominal segment in a penultimate or final stage larva there are in the region of 3,200 sense organs (sensilla). There are two types, spines and hairs, the former being by far the more numerous in aeshnids. Each sensillum is innervated by a single neuron, the cell body of which is located near the hair base, the dendrite ending at the base of the hair shaft. The axons of these neurons are about 1 µm in diameter or smaller. These sensilla are almost certainly tactile in function. In addition there are three internal receptors. Two of these are dorsally located stretch receptors, one oriented longitudinally (lsr), the other vertically (vsr) (Fig. 5). Each is innervated by a single sensory neuron. The third is an oblique chordotonal organ (Fig. 6), innervated by three sensory neurons. Each of these three sense

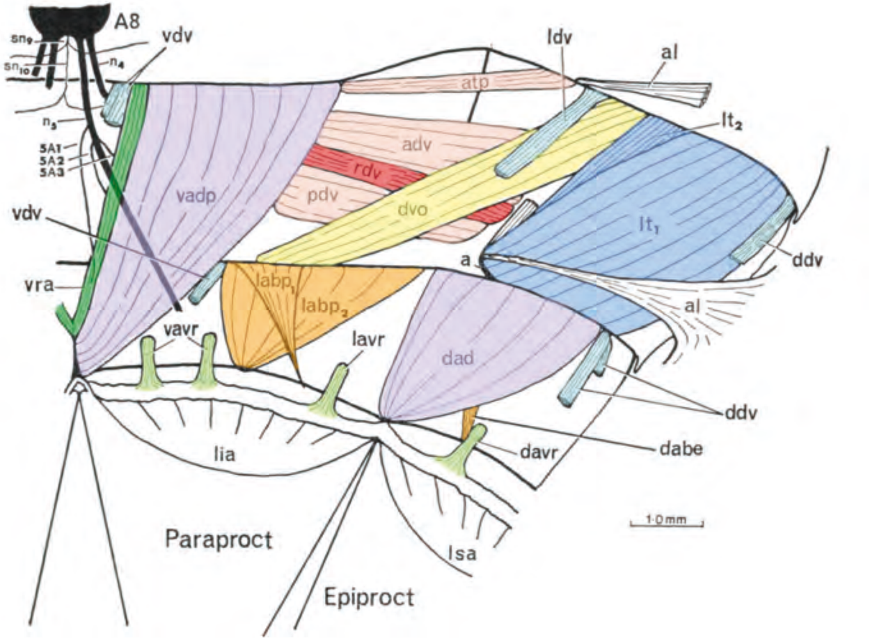


Fig. 8. The musculature of the right side of the ninth and tenth abdominal segments of *Aeshna* sp., viewed internally. A8, eighth abdominal ganglion; n$_4$ and n$_5$, fourth and fifth lateral nerves; 5A1, etc., branches of fifth lateral nerve; sn$_9$ and sn$_{10}$, ninth and tenth median nerves. 🟦 , longitudinal tergal muscles (lt$_1$, lt$_2$); ▨ , dorso-ventral muscles (atp, adv, pdv); 🟥 , respiratory dorso-ventral muscle (rdv); 🟨, oblique muscle (dvo); ⬜, dilator muscles of the vestibule (ddv, ldv, vdv); 🟩, anal valve retractor muscles (davr, lavr, vavr); 🟪, adductor muscles of the epiproct and paraproct (dad, vadb); 🟧, abductor muscles of the epiproct and paraproct (dabe, labp$_1$, labp$_2$); 🟩, retractor muscle of the anus (vra). After Mil & Pickard (1972).

organs consists of a strand of connective tissue in which the cell bodies and their dendrites are embedded and they are all sensitive to stretching of their connective tissue strand (Finlayson & Lowenstein, 1958). The five neurons innervating them are of greater diameter (>5µm) than those innervating the tactile sensilla. The two stretch receptors monitor changes in length of the segment while the chordotonal organ monitors changes in the angle of the segment in relation to the adjacent one (i.e. sideways bending of the abdomen). Another sensory neuron (Type II) is found near the sterno-pleural junction (Fig. 4) (Zawarzin, 1912) and this may possibly, like the chordotonal organ, monitor sideways bending of the abdomen.

Paired lateral segmental nerves. Each of the first seven abdominal ganglia bears three pairs of lateral nerves that innervate, respectively, each of the first seven abdominal segments; the eighth bears five pairs, the first three of which correspond to those of the other abdominal ganglia and innervate the eighth abdominal segment, while the fourth and fifth innervate the abdominal segments behind the eighth (i.e. 9th and 10th). The following is a description of the nerves in a mid-abdominal segment of an aeshnid larva (Mill, 1965). The number of motor neurons (cells) is difficult to determine exactly as some innervate more than one muscle and branching occurs. The figures given below for the number of motor axons (the long processes of nerve cells) are best estimates of the maximum number based on vital staining with methylene blue, cobalt back-staining and electronmicroscopy (Fig. 9, Table 1) (Whittle & Mill, unpub. obs.). It should be noted that, in the first and second segmental nerves, methylene blue staining gives lower numbers than the other techniques (Table 2).

The first segmental nerve (Figs 4-6, Table 1) contains the axons of around 1,950 neurons, most of which are sensory, innervating the tactile sense organs of the pleuron and tergum. About 31 of the axons are of large diameter (>5 µm), the largest having a diameter in the region of 14 -16 µm. Five of these are sensory, innervating the two dorsal stretch receptors and the chordotonal organ. The other 26 are motor neurons innervating the primary (ls_1), lateral primary ($llsp_1$) and secondary (ls_2) longitudinal sternal muscles, all seven of the longitudinal tergal muscles and the anterior tergo-pleural muscle (atp). In at least this nerve the sensory and motor components are separate where they enter the central nervous system.

The second segmental nerve (Figs 4, 6, Table 1) contains the axons of about 1,250 neurons, again most of which are sensory, innervating the sense organs of the sternum, including the type II neuron. There are about seven large diameter motor neurons, the largest of which is about 6.5 µm in diameter. Four of these innervate the anterior (adv) and respiratory (rdv) dorso-ventral muscles, the dorso-ventral oblique muscle (dvo) and the oblique tergo-pleural muscle (otp). The role of the other three is uncertain. One could be the axon of the Type II sensory neuron; the other two could possibly be, as yet unidentified, motor neurons.

The third segmental nerve (Figs 4, 6, Table 1) has only eight or nine axons, all of which are motor neurons, the largest being about 7.5 µm in diameter. They innervate the inner tertiary (ils_3), tertiary (ls_3) and quaternary (ls_4) longitudinal sternal muscles, the posterior dorso-ventral muscle (pdv), the posterior tergo-pleural muscle (ptp), the dorso-ventral oblique muscle (dvo) and the oblique tergo-pleural muscle otp). Hence the two oblique muscles (dvo and otp) are innervated by motor neurons in both the second and third segmental nerves.

Median (unpaired) nerves. In addition to the lateral segmental nerves there

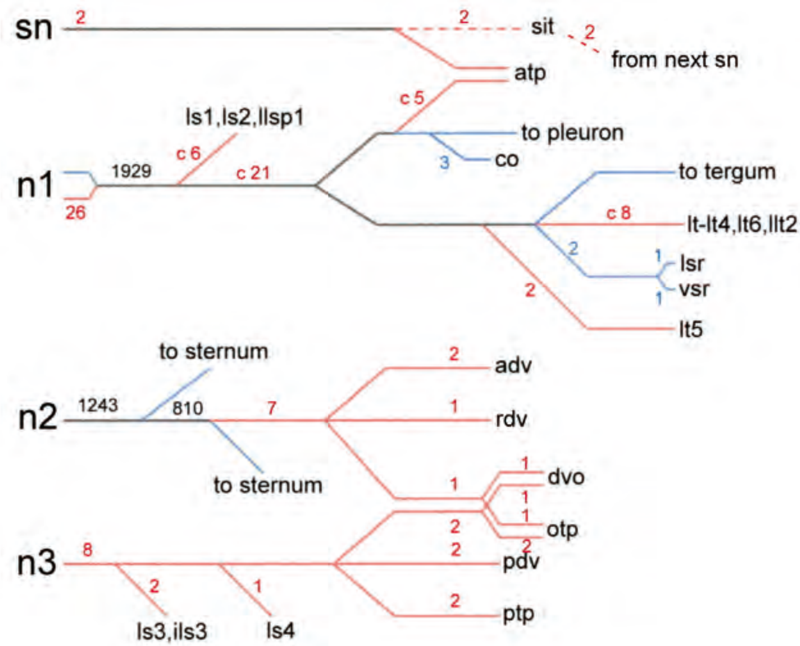


Fig. 9. The numbers of neurons in different branches of the nerves. n1 – n3, first to third lateral nerves; sn, median nerve; —— contains only sensory neurons; —— contains only motor neurons. blue numbers refer to sensory neurons, red numbers refer to motor neurons. sit, sub-intestinal muscle; co, chordotonal organ; ls, longitudinal sternal muscles; lt, longitudinal tergal muscles; lsr, vsr, stretch receptors; atp, adv, pdv, ptp, dorso-ventral muscles; rdv, respiratory dorso-ventral muscle; dvo, otp, oblique muscles. (Whittles & Mill, unpublished observations).

are 10 median, unpaired abdominal nerves (sn$_1$ – sn$_{10}$) which innervate the corresponding first ten abdominal segments. They are both sensory and motor. As noted above, they contain the axons of two motor neurons. sn$_1$ arises between the junction of the third thoracic and first abdominal ganglia, sn$_2$ – sn$_8$ arise from the ventral nerve cord between successive abdominal ganglia while sn$_9$ and sn$_{10}$ arise from near the posterior end of the eighth abdominal ganglion. sn$_1$ – sn$_9$ each divide and run along the posterior edge of the intersegmental fold on each side to innervate the anterior tergo-pleural muscles (atp) of the segment posterior to it (Fig. 7); as noted above, this muscle is also innervated by a branch of the first segmental nerve. The diaphragm (dia) and the sub-intestinal muscle (sit) are both innervated by the median nerves, the former by a branch from sn$_{5,}$ the latter by branches from both sn$_6$ and sn$_7$. The lateral dilator muscles of the branchial chamber (ldb) and the ventral dilator muscles

Table 1. Numbers of motor and sensory neurons in the lateral segmental nerves on one side of a mid-abdominal segment. *The total numbers are based on actual counts from electron micrographs (Whittle & Mill, unpub. obs.)

Segmental nerve	Motor neurons	Sensory neurons				*Total neurons
		Stretch receptors	Chordotonal organ	Type II neuron	Other (small diameter)	
n_1	26	2	3	0	1,898	1,929
n_2	7	0	0	1	1,235	1,243
n_3	8	0	0	0	0	8
Total	41	2	3	1	3,133	3,180

Table 2. The maximum number of motor neurons identified in the lateral segmental nerves on one side of a mid-abdominal segment using methylene blue, cobalt chloride and electron microscopy (Whittles & Mill, unpub. obs.).

	Methylene blue	Cobalt chloride	Electron microscopy
n_1	21	-	26
n_2	4	7	7
n_3	9	-	8

of the vestibule are innervated by branches of sn_9 and sn_{10} respectively (Fig. 7) (Zawarzin, 1924a; Mill, 1965).

Thus the 20 segmental muscles on each side of each mid-abdominal segment are innervated by a total of at most 41 motor neurons in the segmental nerves and one pair in the median nerves. Unlike in vertebrates, most individual muscles are innervated by only one or two motor neurons, with the total number innervating all of the longitudinal tergal and sternal muscles being about eight and six respectively. The anterior tergo-pleural muscle is unusual in that it is innervated by about five motor neurons from the first segmental nerve as well one from the unpaired nerve (Whittle & Mill, unpub. obs.).

Labial Mask

The labial mask comprises a prementum and a postmentum which are hinged so that the resulting ‘labial mask’ is held folded under the head. At the end of the prementum there are two large, spiked labial palps which engage the prey. There are two types of mask: flat, found, e.g., in aeshnids, and concave (spoon-shaped), found in, e.g., libellulids (Tillyard, 1917). The movement and muscles of the labium have been studied a number of times over the last century or so (Amans, 1881; Whedon, 1927; Pritchard, 1965; Tanaka & Hisada, 1980).

The joint between the prementum and the postmentum is controlled by a pair of long extensor muscles, a pair of long primary flexor muscles and two pairs of short (secondary and tertiary) flexor muscles (Fig. 10). At the proximal (head) end of the labial mask the primary flexor muscles in *Aeshna interrupta* and *Libellula quadrimaculata,* at least, are attached to a T-shaped apodeme. There is a pair of grooves at the base of the prementum and a corresponding pair of chitinous knobs on the end of the postmentum (Fig. 10A,C). At rest the knobs are engaged with the grooves, holding the labium in its fully flexed position. The labial palps are controlled by a pair of abductor muscles that extend the palps and a pair of adductor muscles which close them to hold the prey (Fig. 10A) (Pritchard, 1976; Tanaka & Hisada, 1980).

Metamorphosis

The adult breathes air directly into its tracheae via spiracles (three in the thorax and one per segment in the first eight abdominal segments), each of which is controlled by a closer muscle. In the second thoracic spiracle this is innervated by the median nervous system (Miller, 1962) and this is also the case for the closer muscles of the abdominal spiracles (Mill, unpub. obs.). The hind gut is considerably smaller in the adult and no longer plays any role in respiration

Details of the metamorphosis from larva to adult require clarification, particularly with regard to the innervation of the muscles that remain in the adult. Most of the larval muscles degenerate after the final ecdysis to an adult. Thus the primary and secondary longitudinal tergal and sternal muscles, two each of the short longitudinal tergal and sternal muscles, the anterior and respiratory dorso-ventral muscles and the dorso-ventral oblique muscle are all lost. Thus the only functional muscles in the adult are two of the short longitunal tergal muscles (lt_3 and lt_5, - the superior and inferior longitudinal tergal muscles respectively of the adult), one of the short longitudinal sternal muscles (probably ls_3 - the longitudinal sternal muscle of the adult), the anterior tergo-pleural muscle (atp), the posterior dorso-ventral muscle (pdv) and the oblique tergo-pleural muscle

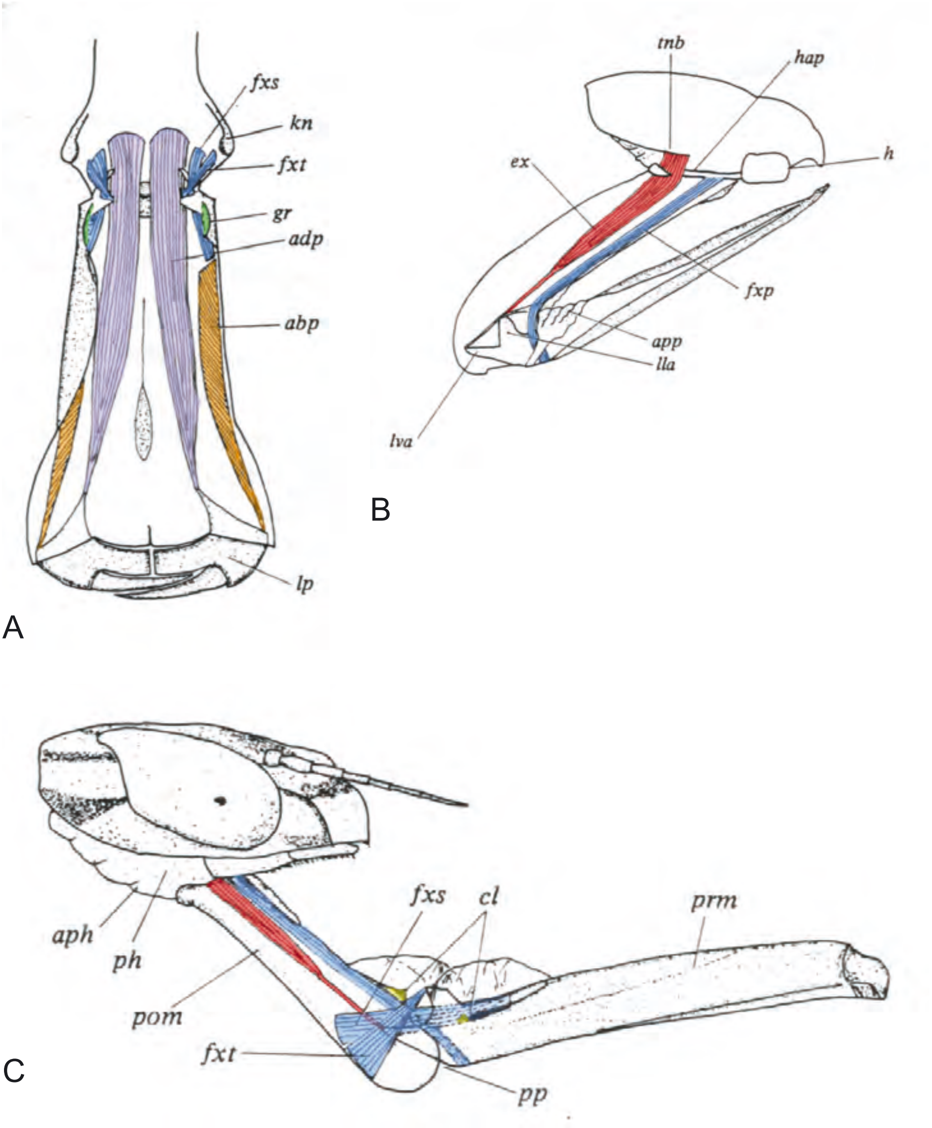


Fig. 10. The structure of the labial mask (postmentum and prementum) of a larval aeshnid. (A) dorsal view of the prementum, (B) longitudinal section through the prementum and postmentum, (C) lateral view of the prementum and postmentum. aph, app, articular membranes off the postmentum-head and postmentum-prementum joints; h, hap, hypopharynx and the hypopharyngeal apodeme; lva, lla, lever arm of the prementum and its lobe; ph, pp, postmentum-head and postmentum-prementum joints; lp, labial palp; pom, postmentum; prm, prementum; tnb, tentorial bar; 🟦 , flexor muscles of the prementum (fxp, fxs, fxt); 🟥, extensor muscle of the prementum (ex); 🟪 , adductor muscle of the labial palp (adp); 🟧, abductor muscle of the labial palp (abp); 🟩 gr, groove of the click mechanism; 🟨 , knobs of the click mechanism (cl). After Tanaka & Hisada (1980).

(otp) (Whedon, 1929; Snodgrass, 1954a; Mill unpub. obs.). The loss of the large dorso-ventral oblique muscles (dvo) means that the abdomen of the adult has lost the ability to bend sideways but is able to bend dorso-ventrally (Mill, unpub. obs.). Muscle degeneration starts after the final ecdysis to an adult and Whedon (1929) noted that it is completed within about three days in *Anax*.

There is no labial mask in the adult, all of the muscles involved presumably degenerating during metamorphosis, except for those controlling the opening and closing of the labial palps.

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Species Review 10:

Chalcolestes viridis (Vander Linden), the Willow Emerald Damselfly

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Summary

Chalcolestes viridis is a recent colonist to southeast England, having appeared within the last decade. This damselfly is seemingly flourishing and is steadily expanding its breeding range in the UK. The background to its colonisation of Britain is discussed, along with details of the species' biology, behaviour and current distribution.

Introduction

Chalcolestes viridis (Vander Linden), the Willow Emerald Damselfly (also sometimes known as the Western Willow Spreadwing), is a damselfly of the family Lestidae. It is of Western Palearctic distribution and broadly resembles the many European species within the genus *Lestes*, though it has some small differences in venation and in the structure of the penis (Kennedy, 1920), is somewhat larger, shows little pruinescence even in mature males, and has a larval mask that has a differently structured prementum to the 'petiolate' form characteristic of many other lestids. Although in the past frequently placed in the genus *Lestes*, there has thus always been a suspicion that the species merited a separate genus of its own. This separation has recently been confirmed and clarified by DNA analysis (Dumont *et al*., 2009; Gyulavári *et al*., 2011), which showed *C. viridis* to have a closer affinity to *Sympecma* than to *Lestes*.

Although once treated as possessing two distinct subspecies, the nominate *C. v. viridis* and a southeast European form *C. v. parvidens*, the species is now considered monotypic. As a result of modern behavioural and genetic studies (Gyulavári *et al*., 2011), the southeast European taxon has thus now been elevated to full species status, namely *Chalcolestes parvidens* (Artobolevskij). *C. viridis* and *C. parvidens* can be separated on the basis of the male abdominal appendages and female ovipositor (Dijkstra & Lewington, 2006), but the differences are slight and require individuals to be in the hand.

Description

Egg

Chalcolestes viridis inserts its eggs directly into woody plant tissue, as outlined in greater detail below. As is typical of endophytically-laid eggs, they are spindle-shaped in form; they have a length of 1.4–1.5 mm (Münchberg, 1933).

Larva

The final stadium F-0 larvae of *Chalcolestes viridis* are typically 17–20 mm in length, excluding the caudal lamellae which add approximately another 7–9 mm; the head width averages 3.95 mm (Cham, 2009; Brochard & van der Ploeg, 2014; Schiel & Buchwald, 2015).

The larva varies in colour from light brown to black, and is of typical lestid structure, having a slender body, relatively broad head and long lamellae (Cham, 2009; Brochard & van der Ploeg, 2014). It somewhat resembles the larva of *Lestes sponsa*, having parallel-sided lamellae with rounded tips usually showing three prominent dark bands, though unlike the case for *L. sponsa*, the central band is often widest and the terminal band somewhat reduced (Brochard & van der Ploeg, 2014). Importantly, the labium, or 'mask', has a prementum that is roughly triangular in shape (Plate 1), rather than the petiolate ('spoon-shaped') form shown by *Lestes* spp. The movable tooth of the labial palp has two to four setae (Askew, 2004; Brochard & van der Ploeg, 2014).

Amongst lestids, the larvae of *Sympecma* spp. (the winter damselflies, not presently found in the UK) also show a non-petiolate prementum. The larva of *C. viridis* can be distinguished from those of *Sympecma* spp. by its larger size, often darker colour (Brochard & van der Ploeg, 2014) and more definitively by the apical margin of the labial palp being finely crenate as opposed to noticeably dentate (Askew, 2004; Brochard & van der Ploeg, 2014).

Adult

Adults (Plates 2, 3) are relatively large, the males being 42-47 mm in length and the females about 3 mm shorter (Askew, 2004). Both sexes are dark metallic green (sometimes with a bronze tinge) above and a very pale yellow below. Pruinescence is essentially absent, though a very slight blue tinge to the thorax may develop, and mature males can show a blue face. There are thin, pale,

Plate 1. Front view of an exuvia of *Chalcolestes viridis*, showing the triangular-shaped prementum. Photograph by Marc Heath (www.marcheathwildlifephotography.zenfolio.com).

thoracic stripes in young individuals, though these tend to become rather less conspicuous in more mature damselflies. The side of the thorax has a distinctive pattern (Plate 4). The metapleural suture (towards the ventral side of the thorax) is thus strongly outlined in black, and there is a short but obvious green 'spur' pushing obliquely downwards from the dark metallic green dorsal section of the thorax into the pale ventral section. A similar but smaller pale spur also pushes up into the dark dorsal section. This overall pattern is characteristic of the species (and *Chalcolestes parvidens*), though very slight 'spur' markings may sometimes also be seen in *Lestes dryas* and *L. sponsa*.

In addition to the thoracic markings, there are a number of other key features shown by *Chalcolestes viridis*. The pterostigmata remain quite pale even in fully mature individuals, typically being off-white to mid-brown in colour, frequently with a diffuse paler central area. The ovipositor of females is differently-coloured to that of other British lestids, being extensively dark with a small pale lateral border rather than showing the more familiar pale dorsal and dark ventral patterning. The anal appendages of male *C. viridis* are also very distinctive, with the superior appendages being pale with a dark tip, and the inferior appendages

Plate 2. Male *Chalcolestes viridis*. Note the pale superior anal appendages. Photograph by Marc Heath.

Plate 3. Female *Chalcolestes viridis*. Note the dark upper (dorsal) surface to the tip of the ovipositor. Photograph by Marc Heath.

Plate 4. Lateral view of the thorax of *Chalcolestes viridis*. Photograph by Marc Heath.

being very short and typically only 1/3 the length of the superior appendages.

Habitat

The typical breeding habitat of *Chalcolestes viridis* includes ponds, lakes and rather slow-flowing rivers with bordering trees or shrubs. Slightly faster-flowing streams may also be frequented where there are quiet backwaters for breeding. On the Continent, *C. viridis* is known to additionally utilize temporary seasonal ponds with trees/shrubs – the damselflies usually emerging before the water completely dries up during the summer, though in very dry years this is not always successful (De Block *et al*., 2005a). It is likely that similar habitat will be occupied in Britain, but as yet there are no reported instances. The species seems able to tolerate a degree of pollution (De Vlinderstichting, 2013).

As discussed in more detail below, bordering trees or shrubby growth that overhangs the water is necessary for oviposition – eggs being inserted directly below the bark of suitable branches. Although willows *Salix* spp. are frequently chosen, hence the species' vernacular name, a very wide range of other soft-barked species may also be utilized.

In addition to its occurrence in its breeding habitat, *C. viridis* can wander quite some distance, and individuals may be encountered well away from water. Here they are typically seen high up in trees, though they may also occur quite low down in open woodland clearings.

The species seems well able to tolerate human influence. Indeed in some areas it may possibly even benefit from a degree of urbanisation, for many man-made habitats such as ponds and flooded gravel pits can go on to develop very suitable breeding habitat.

Distribution

Chalcolestes viridis is restricted to the western Palearctic; its range covers the northern part of the Maghreb and much of western, southern and central Europe north to roughly 53^{o} 30'N. In southeast Europe it is largely replaced by the closely similar *C. parvidens*, with an area of overlap in countries such as Italy, Croatia and Hungary (Olias *et al*., 2007; Boudot & Kalkman, 2015). The range of *C. viridis* has been expanding to the north in recent decades, with the first records for Denmark and Belarus coming in 2005 (Boudot & Kalkman, 2015).

In the Channel Islands, the species has been known from Jersey since the early 1940s. After a period in the 1980s when it went unrecorded – perhaps having been overlooked – it has now become widespread and common once more (Parr & Long, 2015). In Britain, the species was mentioned by some early authors, but McLachlan (1884) considered the species to be of doubtful status. A specimen (now apparently lost) labelled as having been taken by E.R. Speyer at "Shenley, Hertfordshire" on 11 August 1899 was once in the Natural History Museum, London (Gladwin, 1997), but it is quite likely that this was mislabelled, as Speyer also collected on the Continent that summer (Gladwin, 1997). The first confirmed British record was not until as recently as 1979, when a possible vagrant individual was found at Hankham Clay Pit near Pevensey, East Sussex (Belden *et al*., 2004). Over a decade later, a single exuvia was then discovered at Cliffe Marshes, Kent, during 1992 (Brook & Brook, 2003), though no adults were noted either at the time or during subsequent years.

In more recent times, an adult female was discovered close to the Suffolk coast at Trimley, near Felixstowe, on 17 August 2007 (Brame, 2008). No more confirmed sightings are known to have been made here, or indeed elsewhere in Britain, either later that year or during 2008, though it has recently come to light that there was a plausible sighting some 20 km away at Flatford during the latter year. It would seem that, despite the paucity of sightings, this 2007 arrival – of which the Trimley individual was perhaps only the tip of the iceberg – was, however, the forerunner of successful colonisation. In 2009 many hundred individuals were thus to be reported from southeast Suffolk and nearby parts of northeast Essex, centred once more on the Felixstowe area. These records included reports of tenerals (Parr, 2010; Mason & Parr, 2016), and it would seem that a thriving population was already present in the region. The lack of records during 2008 was probably the result simply of the species being overlooked, as a consequence of its habit of spending much time high up in the trees, and thus requiring a rather different search strategy than that normally used for Odonata. During 2009 there was also a record from Strumpshaw Fen in east Norfolk (Parr, 2010), and in the years that have followed, the species' range has continued to expand. It was recorded from the Reculver area of Kent in 2010 (Parr, 2011), and has now reached as far as Cambridgeshire, Hertfordshire, Surrey and very recently even West Sussex (Fig 1). Yet further range expansion is clearly to be expected and, within its established range, populations are likely to increase. In Suffolk, for instance, it is already probably the commonest lestid in the county;

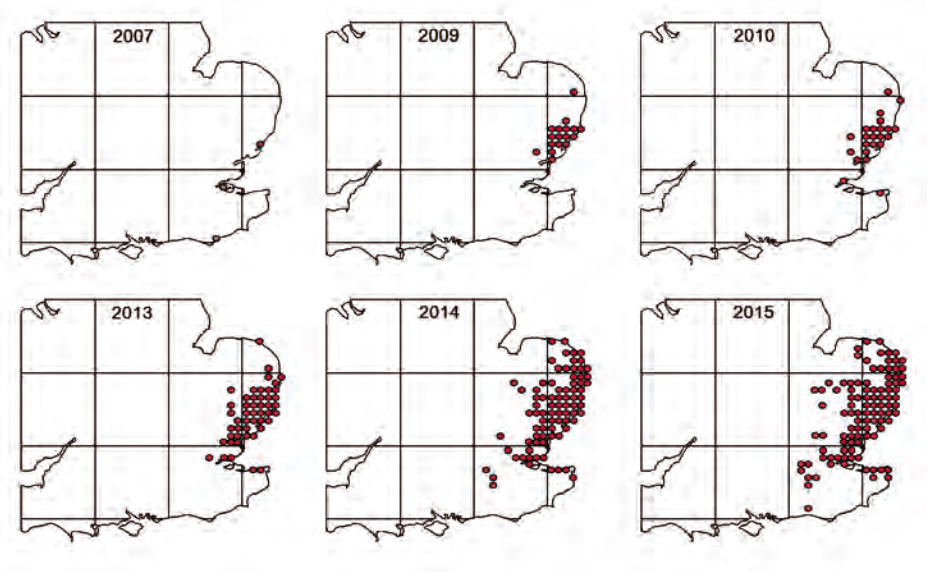

Figure 1. The range expansion of *Chalcolestes viridis* in southeast England. Red dots indicate modern (post 2000) records from individual 10 km x 10 km squares. The grey dots in the first map indicate historic records.

it is certainly the most frequently reported.

The current British population is now thought likely to have largely originated from individuals carried over from the Ostend region of Belgium during early August 2007 (Brame, 2008; Parr, 2009) on a warm air plume that also brought midges *Culicoides* spp. infected with the Bluetongue virus, an animal virus then new to Britain that was similarly discovered in southeast Suffolk in late summer 2007 (Gloster *et al*., 2008). This air plume also reached eastern Norfolk (Gloster *et al*., 2008), which would explain the early discovery of individuals in this county. The early arrival, during 2010, of individuals in north Kent might perhaps be due to a further immigration event, as could the coastal record from Cromer during 2013, some way from other Norfolk sites known at that time. Studies looking for differences in the genetic background of populations from different areas of southeast England have not, however, so far been carried out.

Life Cycle

Egg

Eggs are laid directly into the younger, thinner, branches of soft-barked trees and shrubs overhanging water. Westermann (2000) suggests an optimal branch diameter of 0.4–1 cm, though occasionally slightly larger branches are also used (e.g. Reeve & Reeve, 2011). Although willows *Salix* spp. are commonly employed for oviposition, a very wide range of other species may also be utilised. In Britain, these are known to include Ash *Fraxinus excelsior*, Alder *Alnus glutinosa*, Hawthorn *Crataegus monogyna* and Elder *Sambucus nigra* (A. Parr, unpub. obs.; Chelmick, 2012), while on the Continent additional species include Dogwood *Cornus sanguinea*, Guelder-rose *Viburnum opulus*, Privet *Ligustrum vulgare*, Bird Cherry *Prunus padus* and, more rarely, Elm *Ulmus campestris*, Blackthorn *Prunus spinosa*, Fly Honeysuckle *Lonicera xylosteum* and various Poplars *Populus* spp. (Westermann, 2000). Even this extensive list is known not to be complete.

Eggs are laid directly under the bark in pairs, either side of a central incision, and the eggs of a batch are laid in rapid succession. The size of the eggs, plus the formation of gall tissue around them (Kirby, 1908), ultimately results in the development of a highly characteristic ‘ladder-like’ pattern on the surface of the twig (Plate 5). Particularly during winter, when the leaves have dropped, these egg tracts can be quite noticeable, and can be reliably used to record the occurrence of the species. Signs of such tracts, or oviposition scars, may remain visible for several years, though old tracts become distorted by growth of the underlying branch.

Plate 5. Oviposition tracts of *Chalcolestes viridis* on willow *Salix* sp.

In *Chalcolestes viridis*, the egg is the over-wintering stage, and it is not until winter has passed that the eggs will hatch. In a ‘semi-natural’ study in southwest Germany, the first eggs were found to start hatching at the very end of March, while some only hatched at the end of May; the median date for hatching was 15 April (Schiel & Buchwald, 2015). Rather similar dates have also been reported in the literature for other central/north-western European localities (e.g. Münchberg, 1933; De Block & Stoks, 2005; De Block *et al*., 2005b; Schiel & Buchwald, 2015). Little is currently known of hatching times in Britain, though they are likely to be little-different to those on the near Continent. Certainly egg tracts at Alton Water, Suffolk, examined on 16 April 2012 showed signs of significant hatching having begun (A. Parr, unpub. obs.).

Larva

Following egg hatching, the non-feeding prolarva exits the plant tissue and drops into the water below, where it may then moult into the next larval stage within minutes (Pierre, 1904). If the prolarva instead falls on dry land, it is able to flip about on the surface, providing some chance to reach water before it perishes; in this case moult is postponed (Pierre, 1904).

Counting the prolarva as stadium 1, there are typically 10 stadia (or instars) during larval development (Schiel & Buchwald, 2015), though Münchberg (1933) reported as many as 13 stadia. In southwest Germany, in a detailed laboratory study at ambient temperatures, Schiel & Buchwald (2015) found full larval development to take on average 59 days, with a range of 53–62 days; quite how this relates to the situation in the wild is of course uncertain. Reports of a roughly 60–70 day developmental period are widely mentioned elsewhere in the literature (e.g. Münchberg, 1933; De Block & Stocks, 2005), though Robert (1959) reported a value of just over 100 days.

Larvae live amongst submerged vegetation, and may also rest on or in plant debris lying on the water-bottom. They are excellent swimmers, and disappear from sight at the least sign of danger (d'Aguilar *et al*., 1986; Brochard & van der Ploeg, 2014).

Emergence

The species is univoltine (Corbet *et al*., 2006) and, as implied above, adults appear only some two to three months after the eggs hatch in spring. Emergence (Plate 6) takes place on marginal vegetation such as reeds *Phragmites australis*, on branches hanging in the water and on other similar vertical supports, often within 40 cm of the water surface (d'Aguilar *et al*., 1986; Westermann, 2006; M. Heath, unpub. obs.). Larvae can, however, travel up to 1.8 m from the waters' edge, and/or reach a height of up to 1.3 m (Cordero, 1995). Larvae of *Chalcolestes viridis* show a number of interesting adaptations to reduce mortality during emergence in inclement weather. These include the ability of larvae to delay emergence by up to 14 hours after leaving the water should conditions become sub-optimal, and the ability, if necessary, to select emergence supports that offer some protection from the rain, or else are further from the water-surface so that accidental drowning of the newly-emerged adults becomes less of a threat (Westermann, 2006).

Emergence dates vary between sites, partly reflecting the different environmental regimes but probably also in part as a result of genetic differences between populations (Westermann, 2002; De Block *et al*., 2005b). In southern Germany emergence can begin on or before 23 June and extends until late September (Westermann, 2002). Females on average emerge earlier than males, with the median emergence date differing by four days in one detailed study from Germany (Westermann, 2008). There is currently no published data on emergence times in Britain but these seem likely to be broadly similar to those on the Continent; an observation of a teneral individual in Essex on 22 June

Plate 6. Recently emerged teneral *Chalcolestes viridis* with exuvia. Photograph by Marc Heath.

2016 (A. Shearring, unpub. obs.) implies that emergence in Britain may not necessarily lag much behind that observed in southern Germany.

Adult Behaviour

Adults are unique amongst British damselflies, spending most of their time high up in trees, rather than at the water's edge. Individuals frequently perch in exposed sunny areas, often on bare twig ends, and may then chase prey in a rather 'darter-like' fashion. The damselflies may also withdraw into foliage when ovipositing, or when conditions become unfavourable. Observing the species clearly often requires a rather different search strategy to that normally employed for Odonata. Individuals may, however, also descend to settle on tall vegetation, where they may then be encountered in more normal fashion.

Adults typically rest with wings part-open (as with most lestids), hanging off vegetation at an angle of 45^{o}. When coupled with their large size, this gives the species quite a characteristic ‘jizz’.

Capture-recapture studies have shown mature adults to be quite strongly site-faithful. However, the presence of low genetic differentiation between populations, at least in northern Belgium (Geenen *et al*., 2000; De Block *et al*., 2005a), rather suggests there is significant dispersal of teneral individuals. Curiously, though, most new site records in the UK currently seem to be made during September. Maybe it is at this time that dispersing adults return to sites where they are more readily observable.

Reproduction

In the far south of its range, e.g. in southern Spain, *Chalcolestes viridis* shows a very long pre-reproductive period of up to three or four months – i.e. it essentially aestivates (Agüero-Pelegrin *et al*., 1999). In central and more northerly areas, this pre-reproductive period, however, shortens significantly; in Germany it is roughly one month in length (Agüero-Pelegrin *et al*., 1999).

Once mature, males are territorial and defend vertical territories in trees slightly back from the water’s edge (Dreyer, 1978), or at the water’s edge itself (De Block & Stoks, 2007). Here they await the arrival of females flying in from woodland further way. After mating, oviposition subsequently takes place in branches of trees/shrubs overhanging water, with egg tracts having been noted from 0.5–10+ metres above the water level; the lower branches are, however, seemingly preferred (Westermann, 2000). Egg-laying is usually carried out while still in tandem, the female strongly arching her abdomen to get the correct angle for insertion of the eggs. The species is not territorial when egg-laying and pairs may oviposit very close together. Reeve & Reeve (2011) described some observations of reproductive behaviour made in Britain.

Once the female has laid one batch of eggs, it may be up to 12 days before a subsequent round of oviposition (Dreyer, 1978).

Flight Season

Over much of its range on the Continent, away from the far south, *Chalcolestes viridis* has been reported on the wing mainly between early June and the end of October/beginning of November, though it may persist until late November in southern France (Boudot & Kalkman, 2015). Adults of *C. viridis*, like several other lestids, are known to be quite long-lived (Corbet, 1999). The peak flight period is around August-time, slightly earlier in the south of its range and later in the north (Boudot & Kalkman, 2015). In Britain, flight data is based on fewer observations than elsewhere, but the flight period can clearly extend from late

June through to early November, exact limits depending a little on the season. The peak time for the species in the UK is from mid-August through to late September.

Conservation

The species is rated as of Least Concern in the IUCN Red List of Threatened Species (IUCN, 2014). In Europe, *Chalcolestes viridis* is widespread and fairly common, often occurring in large populations. The species can persist in areas affected by man, and the population trend is stable. In Britain, *C. viridis* has spread considerably since its first appearance in Suffolk during 2007 and range expansion is clearly continuing. There are thus presently no major conservation concerns within the UK, though at a local level excessive pollarding of water-side trees has the potential to negatively impact the species, at least in the short term. Induced fresh growth may, however, later become attractive to the species.

Discussion

Chalcolestes viridis has been resident in Britain for less than a decade, and the species is still relatively unfamiliar to most observers. It appears to be thriving, and range expansion continues apace. Fortunately much is known about the biology of *C. viridis* from work on the Continent, it being a common species suitable for both professional and amateur research. In Britain, much of the species' behaviour and ecology is likely to be closely similar to that reported in the literature, and information has been summarised here for the benefit of UK observers. Further studies to determine whether there are any specific adaptations to the UK's climatic and environmental conditions would, however, be worthwhile.

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