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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.

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- 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.
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  - Hammond, C.O. 1983. *The Dragonflies of Great Britain and Ireland* 2nd Edition (revised by R. Merritt), Harley Books, Colchester, 116pp.
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- 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	*Aeshna mixta*	*Migrant Hawker*
Calopteryx splendens	*Banded Demoisle*	*Aeshna isosceles*	*Norfolk Hawker*
Calopteryx virgo	*Beautiful Demoiselle*	*Anax ephippiger*	*Vagrant Emperor*
Lestes barbarus	*Southern Emerald Damselfly*	*Anax imperator*	*Emperor Dragonfly*
Lestes dryas	*Scarce Emerald Damselfly*	*Anax junius*	*Green Darner*
Lestes sponsa	*Emerald Damselfly*	*Anax parthenope*	*Lesser Emperor*
Lestes viridis	*Willow Emerald Damselfly*	*Brachytron pratense*	*Hairy Dragonfly*
Sympecma fusca	*Winter Damselfly*	*Gomphus flavipes*	*Yellow-legged Clubtail*
Coenagrion armatum	*Norfolk Damselfly*	*Gomphus vulgatissimus*	*Common Club-tail*
Coenagrion hastulatum	*Northern Damselfly*	*Cordulegaster boltonii*	*Golden-ringed Dragonfly*
Coenagrion lanulatum	*Irish Damselfly*	*Cordulia aenea*	*Downy Emerald*
Coenagrion mercuriale	*Southern Damselfly*	*Somatochlora arctica*	*Northern Emerald*
Coenagrion puella	*Azure Damselfly*	*Somatochlora metallica*	*Brilliant Emerald*
Coenagrion pulchellum	*Variable Damselfly*	*Oxygastra curtisii*	*Orange-spotted Emerald*
Coanagrion scitulum	*Dainty Damselfly*	*Leucorrhinia dubia*	*White-faced Darter*
Erythromma najas	*Red-eyed Damselfly*	*Leucorrhinia pectoralis*	*Large White-faced Darter*
Erythromma viridulum	*Small Red-eyed Damselfly*	*Libellula depressa*	*Broad-bodied Chaser*
Pyrrhosoma nymphula	*Large Red Damselfly*	*Libellula fulva*	*Scarce Chaser*
Enallagma cyathigerum	*Common Blue Damselfly*	*Libellula quadrimaculata*	*Four-spotted Chaser*
Ischnura elegans	*Blue-tailed Damselfly*	*Orthetrum cancellatum*	*Black-tailed Skimmer*
Ischnura pumilio	*Scarce Blue-tailed Damselfly*	*Orthetrum coerulescens*	*Keeled Skimmer*
Ceriagrion tenellum	*Small Red Damselfly*	*Crocothemis erythraea*	*Scarlet Darter*
Platycnemis pennipes	*White-legged Damselfly*	*Sympetrum danae*	*Black Darter*
		Sympetrum flaveolum	*Yellow-winged Darter*
ANISOPTERA	*DRAGONFLIES*	*Sympetrum fonscolombii*	*Red-veined Darter*
Aeshna affinis	*Southern Migrant Hawker*	*Sympetrum pedemontanum*	*Banded Darter*
Aeshna caerulea	*Azure Hawker*	*Sympetrum sanguineum*	*Ruddy Darter*
Aeshna cyanea	*Southern Hawker*	*Sympetrum striolatum**	*Common Darter**
Aeshna grandis	*Brown Hawker*	*Sympetrum vulgatum*	*Vagrant Darter*
Aeshna juncea	*Common Hawker*	*Pantala flavescens*	*Wandering Glider*

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

Species list in accordance with Davies, D.A.L. & Tobin, P. (1984 & 1985) The Dragonflies of the World: A systematic list of the extant species of Odonata. Vols 1 & 2.

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Migrant and dispersive dragonflies in Britain during 2014

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Summary

In Britain, the year 2014 was rather a mixed one as far as migrant and dispersive dragonflies were concerned. The period mid-May to mid-July saw significant immigrations of *Anax parthenope* (Lesser Emperor) and, in particular, *Sympetrum fonscolombii* (Red-veined Darter). Slightly later, during late July/early August, large numbers of *Aeshna mixta* (Migrant Hawker) were also noted in parts of south-east England and a migratory event was probably involved in at least part of this. Events later in the season were, by contrast, very much more low-key, though small numbers of second generation *S. fonscolombii* were noted.

Events relating to our new colonist species were similarly mixed. *Chalcolestes viridis* (Willow Emerald Damselfly) had a good season with significant range expansion being noted. *Lestes barbarus* (Southern Emerald Damselfly) also seemed to fair well. *Coenagrion scitulum* (Dainty Damselfly) and *Aeshna affinis* (Southern Migrant Hawker) however did less well, with fewer than normal sightings and no sign of any continued immigration. Hopefully, the next few years will see a recovery in the fortunes of these last two species.

Account of species

Notable sightings reported to the BDS Migrant Dragonfly Project during 2014 are detailed below; for information on events during 2013, see Parr (2014).

Chalcolestes viridis (Vander Linden) – Willow Emerald Damselfly

This recent colonist has been steadily expanding its range since its appearance in Suffolk during 2007 (Cham *et al*., 2014). The reporting year saw a major push forward, with many new sites discovered within its current core area of Norfolk/ Suffolk/Essex/north Kent, and several records from new counties. In Cambridgeshire a male was photographed at Ely on 12 September (WM), whilst in Hertfordshire small numbers, including an ovipositing pair, were discovered at Amwell Nature Reserve during the same month (DBa *et al*.), with a male also seen at Balls Wood on 14 September (APr). In Surrey, a colony was discovered at Nutfield Marsh on 28 August (DC, JL) and two were later photographed at Littleworth Common on 22 September (LP). During early 2015, the characteristic oviposition scars were also discovered on willows by the River Mole near Gatwick, on the Surrey/Sussex border (LP), showing that individuals must also have been present at this site during 2014.

Unlike the brief and un-repeated sightings at the periphery of the species' range reported during 2012 (Parr, 2014), many of the reports from new counties made during 2014 seemingly relate to colonies in the process of becoming established. Range expansion in southeast England thus continues apace. At present no major new foci have developed, which suggests that any continued immigration has occurred within broadly similar geographical limits to the initial wave. A surge of sightings from the Norfolk Broads in autumn 2014 (PH) possibly hints at some sort of new immigration event in 2014 but this remains unproven.

***Lestes barbarus* (Fab.) – Southern Emerald Damselfly**

In addition to the previously-published records for 2013 (Parr, 2014), it is now known that a female was photographed near Holmes Hill, E. Sussex, on 17 July 2013 (SRa). During 2014, records were again received from the well-known sites at Winterton Dunes in Norfolk and Cliffe Marshes in north Kent. Sightings at Winterton were limited to single males seen on 2 & 7 August (TH, PH) and two females noted on 3 September (DH). As the species can be rather inconspicuous, it is however possible that further individuals were present. Records in the Cliffe area were, by contrast, relatively numerous. Some double-figure counts were made and sightings spanned the period 3–31 July at least. Clearly a well-established breeding colony would now seem to be present in this area. Away from these known strongholds, significant numbers were, in addition, noted from a private site in the Sandwich Bay area of Kent over the summer (Hodgson & Beugg, 2015); this may suggest the presence of yet another breeding colony. Finally, elsewhere in Kent, a male was seen and photographed near Reculver over the period 30 June–24 July (MH). This is perhaps a fresh immigrant, though it is just possible that it, too, reflects the presence of a breeding site.

Lestes barbarus currently appears to be maintaining its foothold as a British breeder, being helped by continuing immigration. Indeed, since it is relatively inconspicuous, the species may be more widespread than currently appreciated. It will be instructive to follow its future fate in southeast England.

Lestes dryas Kirby – Scarce Emerald Damselfly

This still rather scarce and localised species continues to show signs of significant range expansion. Interesting records include a sighting from Brandon, Suffolk, on 24 July (APa). In addition, several records from Kent, most notably from near Reculver (MH), were well away from the known strongholds in the northwest of that county.

Coenagrion scitulum (Rambur) – Dainty Damselfly

Following several years when populations of this newly re-established colonist (Brook & Brook, 2011) appeared broadly stable, 2014 proved to be a disappointing year. Although exuviae were discovered at two of the regular sites in the Isle of Sheppey area of Kent (JGB), not a single flying adult was noted during the year. Both of the sites where exuviae were found now, worryingly, also looked rather unfavourable for the species, having lost most of their submerged aquatic vegetation (perhaps due to the effects of the 2013/14 winter with its flooding and surge tides). Since the Kent population is based on private land that is both difficult to access and to survey, the fate of the species is however not easy to judge from these observations alone. Preliminary fieldwork in 2015 again found exuviae (JGB), indicating that the species had survived its 2014 low point, but long-term trends remain unknown. Given continuing range expansion on the Continent, even if the Kent population ultimately fails – as appears to have been the case for the colony discovered on the Channel Islands around the same time as the recent UK sites were discovered (Parr & Long, 2015) – then re-colonisation at new sites remains a distinct possibility.

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

This fairly recent new colonist (first appearing in 1999) had a good year during 2014, with many records both from its core areas and from regions near the periphery of its current range. No major new range expansion was noted, this having slowed considerably over the last 6/7 years (Cham *et al*., 2014), but populations in the north appeared to strengthen. A sighting from Strensall Common near York on 31 August (per KG) thus becomes the new most northerly inland record for the species in the UK. Individuals were also noted south of Scarborough, NE Yorkshire, during August (per KG) after an absence of three years. In addition to these general trends, some observations from the East Anglian coast may suggest that further limited immigration from the near Continent took place during the year, probably reflecting a good season for the species in that region as well. The pattern of sightings at Eccles-on-Sea, Norfolk, thus revealed “a small influx” during mid-summer (NB), whilst a record of a singleton attracted to a UV moth trap at Landguard on the Suffolk coast over the night of 23–24 August (NO) is also of some note. Records of Odonata at light frequently refer to migrants (Parr, 2006) and this was the only report of the species from the site during 2014.

Aeshna affinis (Vander Linden) – Southern Migrant Hawker

This recent colonist had a quiet season in Britain during 2014, with no sign of any continued immigration and rather few records from its breeding strongholds around the greater Thames Estuary. In southern Essex, isolated records were received from the well-known sites at Hadleigh and Wat Tyler Country Parks during July, with an immature female having been photographed at the former site early in the period (PM). There were also sightings from Chafford Gorges Nature Reserve on 13 July (KP) and Rainham Marshes on 29 July (JHo). The sporadic nature of all sightings, and the general presence of just single individuals, is perhaps not encouraging. In north Kent, the species may, however, have faired slightly better. Several individuals were recorded from the North Kent Marshes around the Cliffe area during mid/late July (per JGB), and there was also a report of a male slightly further east from near Grove Ferry on 31 July (MH). It will be instructive to continue monitoring the health of our new Thames Estuary populations.

Aeshna mixta Latreille – Migrant Hawker

Although *A. mixta* is now a very common resident in much of England, Wales and parts of Ireland (Cham *et al*., 2014), this has not always been the case. Less than a century ago the species was rather scarce in Britain and was better known as a migrant (Corbet *et al*., 1960, Mendel, 1992). Even today, resident populations are still recognised as being supplemented by arrivals from the continent (see e.g. Parr, 2014). *A. mixta* had a very good year in Britain during 2014 and this seems likely to have resulted, at least in part, from substantial immigration. Some impressive counts early in the flight season included 700 at Dunwich Forest, Suffolk, on 30 July (MT), 50+ at Halesworth, Suffolk, on 30 July, with the species also unusually obvious in the surrounding area (DBr), “literally hundreds” at Fairlight on the Pett Levels, E. Sussex, on 31 July (SRo), 100 east of Robertbridge, E. Sussex, on 2 August (FK) and 100+ at both Upper Hollesley Common, Suffolk, on 3 August (SG) and nearby Sutton Common on 5 August (SA). Later in the season, when swarms of this species are more normal, some noteworthy counts were still made. Sightings thus included 200+ at Dunwich Forest, Suffolk, on 5 September, with only smaller numbers the following day (JHa), as well as 100 at Spurn Point, E. Yorkshire, on 12 September and 120 there on 15 September (BS).

Although synchronous emergence of local individuals might account for some of the aggregations noted at the beginning of the flight period, the highest counts at this time were mostly in coastal areas of eastern and south-eastern England, where migrants from the Continent would be likely to concentrate. An immigrant origin for some individuals thus seems likely, especially in view of direct observations of *A. mixta* arriving in off the sea at Blakeney Point, Norfolk, during August (AT). A count of 1000 along the coast at Mirns, The Netherlands, on 26 July (Waarneming.nl, 2014) would be in line with unusual events similarly taking place on the near Continent in early summer. A paper exploring the events of 2014 in more detail is currently in preparation (Parr, 2015).

Anax ephippiger (Burmeister) – Vagrant Emperor

There were no confirmed sightings of *A. ephippiger* from Britain during the year, though dragonflies seen near Faringdon, Oxfordshire on 27 February (per JC), at East Gilling, N. Yorkshire on 3 March (per KG) and near Swindon, Wiltshire on 7 March (per CI) seem likely to have been this species. Late winter records of this largely Afro-tropical migrant are well-known (Cham et *al*., 2014). In the Channel Islands, a female photographed at Petit Port, Guernsey, on 29 November (AS) represents the first confirmed record of this species from the Islands.

Anax parthenope Sélys – Lesser Emperor

Reports of *A. parthenope* were received from roughly 25 sites during the year (a few observations were not well documented and their veracity is thus difficult to judge), this being a significant improvement on the poor showing during 2013 (Parr, 2014) and more typical of recent levels. Records spanned the period 7 June–3 August (Fig. 1) and peaked in mid June – a period that also saw numerous reports of *Sympetrum fonscolombii* (see below). The two species are indeed known to sometimes, though not invariably, migrate together (Parr *et al*., 2004). Reports were received from Cornwall, Devon, Somerset, the Isle of Wight, Hampshire, Kent, Berkshire, Norfolk, Cambridgeshire, Warwickshire and Lincolnshire. Cornwall, and especially Norfolk, saw records from several sites and it is clear that at least eight, and probably several more, individuals were present in Norfolk during mid-June. Sites such as Felbrigg Hall, Filby Broad and Ormesby Broad all held individuals on 12 June and oviposition was noted at Filby Broad on 13 June (KS, PH). Clearly a major immigration occurred during early summer 2014 but sightings probably also included a few locally-bred individuals. In Kent, records were thus received from Dungeness, where the species has long been seen on an annual basis, and also from New Hythe Lakes, where exuviae were discovered a few years ago (Parr, 2012). Although occasional autumn records of *A. parthenope* have been forthcoming over the years, none were received during 2014.

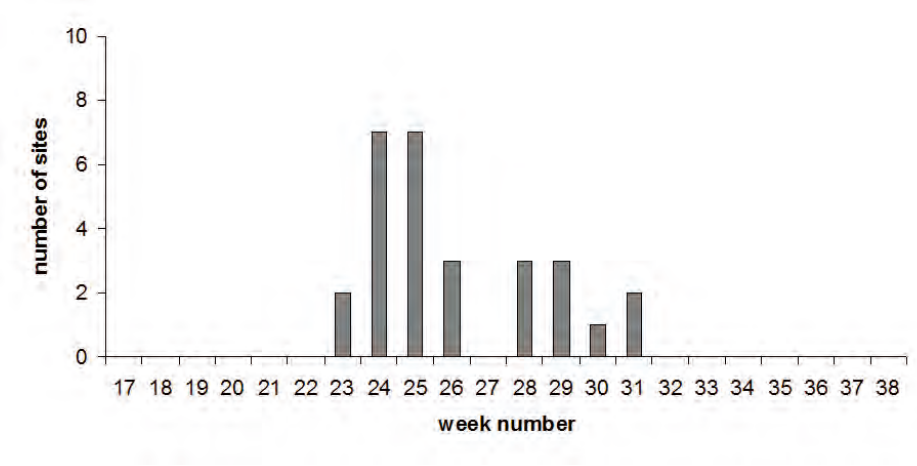

Figure 1. Temporal spread, by week, of new site records for *Anax parthenope* (Lesser Emperor) during 2014. Week 23 refers to the period 2–8 June, week 31 to the period 28–3 August.

Libellula fulva Müller – Scarce Chaser

The first county record for Oxfordshire was made when a male was photographed at Otmoor RSPB Reserve on 6 July (TS).

Libellula quadrimaculata L. – Four-spotted Chaser

One was seen at Skokholm Island, Pembrokeshire, on 18 June (MS), a day after one or more migrant *Sympetrum fonscolombii* had appeared there. This is only the second record for the Island.

Sympetrum danae (Sulzer) – Black Darter

A single male *S. danae* was reported from Dungeness, Kent, on 21 September (per DWa). The species is highly localised in southeast England and this is the first record from this coastal site since the famous continental darter immigration year of 1995 (Attridge, 1996; Silsby, 1996). Few other signs of significant migration were, however, noted during the year.

Sympetrum fonscolombii (Sélys) – Red-veined Darter

Once considered a rare and erratic visitor to our shores, substantial immigrations of *S. fonscolombii* have now become a nearly annual event during spring and early summer. The reporting year was to be no exception, with good numbers

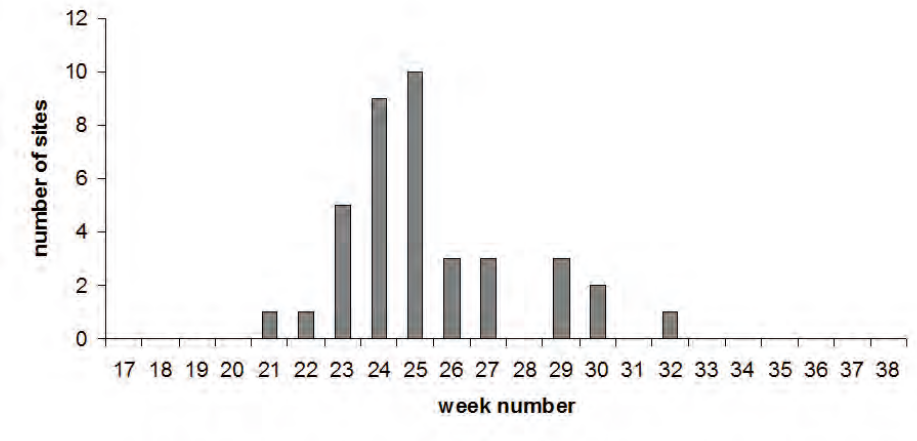

Figure 2. Temporal spread, by week, of new site records for mature adult *Sympetrum fonscolombii* (Red-veined Darter) during 2014. Week 21 refers to the period 19–25 May, week 32 to the period 4–10 August.

of migrants being seen (and an immature male noted near Reculver, Kent, on 8 June (MH) perhaps indicating that a few locally-bred individuals were also present). Single red darters *Sympetrum* spp. seen in Carmarthenshire and Surrey during mid-May were probably male *S. fonscolombii*, as no other British darters are normally seen in mature colouration at this time of year. The first confirmed report was from Felbrigg, Norfolk, on 25 May (SC) and, over the following two and a half months (Fig. 2), individuals were noted at three further sites in Norfolk, as well as in Cornwall (six sites), Hampshire (two sites), the Isle of Wight, Greater London (three sites), West Sussex, East Sussex, Kent (two sites), Suffolk, Worcestershire, Glamorganshire (two sites), Pembrokeshire, Lincolnshire, East Yorkshire (four sites) and Lancashire. Maximum counts at most sites were in the region of 1–6 individuals, though some sites near the south coast, especially in Cornwall, produced higher levels. Over 30 were thus seen at Windmill Farm NR, Cornwall, in late June (DWr).

Following the early season influx, immature adults from a second generation were then noted during late summer. The first record was on 16 August, when an immature female was seen at Badminston, Hampshire (PW). The subsequent two months saw further records from this site, as well as from Windmill Farm in Cornwall (DWr), Rye in E. Sussex (TW), Orfordness in Suffolk (DF), Spurn Point in E. Yorkshire (BS) and Llanilid in Glamorganshire (AH). Circumstances suggest that, at most of these sites apart from at Orfordness, the dragonflies would have been locally-bred; the records from Spurn are of particular interest in that the rapid life-cycle leading to a second (autumn) generation in a year is typically associated with more southerly localities in Britain. Despite successful breeding at several sites during the summer, the number of progeny observed was, however, always rather low, with only single-figure counts (most typically just 1–2) at any one time. Indeed, the lack of further significant immigration into the UK during late summer/autumn might suggest that other sites in western Europe had similarly shown low productivity and maybe most larvae arising from breeding attempts following the early season influx of *S. fonscolombii* were following a slow, one year, developmental cycle. The final record of the year was of an immature seen at Badminston on 4 October (PW).

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

No obvious migrations of this species were observed in Britain during 2014, though, with the simultaneous presence of large resident populations, movements can be difficult to detect. Some limited migratory activity may well have taken place in northwest Europe during mid-summer 2014, for in the Channel Islands several individuals were noted on 26 July from Les Écréhous, a small reef with no suitable breeding habitat situated between north-east Jersey and France (Parr & Long, 2015).

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

As with *S. sanguineum*, movements of this species are easily overlooked. Since it comes at a time when exceptionally large numbers of *Aeshna mixta* were also present at the site, a high count of 250 at Dunwich Forest, Suffolk, on 30 July (MT) may perhaps be related to migration. Later in the season, individuals were attracted overnight to moth traps at Portland Bill, Dorset, on 5 & 29 August (MC) and at Bawdsey, Suffolk, on 27 & 30 September as well as on 15, 27 & 28 October (MD). Records of Odonata at light frequently refer to migrants (Parr, 2006).

Conclusions

The 2014 reporting year was rather a mixed one for migrant and dispersive dragonflies in Britain. *Sympetrum fonscolombii* and *Anax parthenope*, our currently most regular migrants, again showed significant arrivals, and there were indications that numbers of *Aeshna mixta* were also on the move. By contrast, there were few sightings of our rarer or more erratic migrants, though small numbers of ‘possible’ *Anax ephippiger* were noted early in the year. Our recent colonist species similarly experienced mixed fortunes. Some, such as *Chalcolestes viridis* and *Lestes barbarus*, clearly faired well, whilst others such as *Coenagrion scitulum* and *Aeshna affinis* apparently had a much less successful year, with reduced numbers seen and no evidence of continued immigration. All these rather mixed events are set against the background of 2014 having been the warmest year on record in (central) Britain (Met Office, 2015), clearly showing that average temperatures alone are not the sole determinant of what mobile species reach the UK and how they fair on arrival. Never-the-less, general climatic trends do continue to favour high levels of migration and an increasing importance of 'southern' species in our local Odonata fauna. As always, continued vigilance of migrant species is thus to be encouraged, not least because recent population trends and range changes on the near Continent suggest that new species for Britain may well appear in the next few years. Continued surveillance and monitoring of our new colonist species would also be beneficial, as there is still very much that we do not know about these species in our country.

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Voltinism in *Erythromma viridulum* (Charpentier) (Small Red-eyed Damselfly): a newly colonised damselfly species in the UK

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Summary

Odonates have displayed strong responses to changing climate through shifting range margins and changes in phenology and voltinism. Newly colonising species may also be competing with previously established species. This study analysed voltinism and feeding behaviour of a recent coloniser, *Erythromma viridulum* (Small Red-eyed damselfly). The results indicate that the populations sampled were likely to be semivoltine, and growth rates suggest that early instar larvae present in July would overwinter in that stage and emerge the following year. This implies that voltinism has not changed in British populations since the species colonised this country. Gut content analysis of larvae found that larval prey items changed through progressive instars but indicated that *E. viridulum* is unlikely to feed upon other odonate species in the UK.

Introduction

Seasonal temperature rise is causing increased developmental rates in odonate larvae, accelerating life-cycles and shifting phenology (Pickup & Thompson 1990, Grewe *et al.*, 2013). This is due to the intimate relationship between temperature and the biological processes of odonates (Hassall & Thompson, 2008). In Britain, both univoltine (one generation per year) and semivoltine (one generation in two years) populations have been found to be advancing their emergence dates as temperature thresholds for development are reached earlier in the year (Hassall *et al.*, 2007). In European populations of *Gomphus vulgatissimus* (Common Clubtail), Braune *et al.* (2008) demonstrated that voltinism (i.e. the number of generations per year) increased with decrease in latitude and increase in temperature, which variables are, of course, correlated. Hence, increase in temperature due to climate change would be expected to cause increases in voltinism in dragonflies, noticeably at high latitudes, reducing generation times by up to two years (Söndgerath *et al*., 2012). Such a response has been observed in European butterflies and moths, causing increased multivoltinism (more than one generation per year) in some species (Altermatt, 2009; Pöyry *et al.*, 2011).

Erythromma viridulum (Small Red-eyed damselfly) is a species that is rapidly expanding its range across Northern Europe and has fairly recently colonised the UK (Dewick & Gerussi, 1999; Cham, 2004). Unlike *Erythromma najas* (Red-eyed Damselfly) and a number of other UK native damselflies, *E. viridulum* emerges in late-summer, peaking in August (Cham *et al.*, 2014). This strategy may explain its colonising success, as later development than those species with which it shares breeding sites, such as *Coenagrion puella* (Azure Damselfly), *Enallagma cyathigerum* (Common Blue Damselfly) and *Ischnura elegans* (Blue-tailed Damselfly), may decrease competition. Larval odonates are dominant predators in freshwater habitats, preying upon a range of smaller invertebrates, including other odonate species (Corbet, 2004). Through filling different temporal niches, *E. viridulum* larvae may ensure sufficient food availability for larval growth, which subsequently influences adult size, fitness and clutch size (Convey, 1988; Hassall *et al.*, 2014). It is possible that the success of *E. viridulum* as a coloniser may also be a result of outcompeting native species for resources or even by its larvae consuming other odonate species.

High phenotypic plasticity is considered to have aided the colonisation of *E. viridulum* (Hassall *et al.*, 2014). UK populations have greater body sizes than in the rest of Europe. In northern continental European populations, *E. viridulum* is semivoltine, in the Poitou-Charentes region of southwest France it is usually univoltine (Rouillier, 2009), and in the meditteranean region it is either univoltine or, in Greece at least, bivoltine (two generations each year) (Grand & Boudot, 2006; Hassall *et al*., 2014). A consistent pattern of voltinism in the UK has yet to be demonstrated. A study by Keat (2007) revealed that well-established populations in Bedfordshire and Essex were likely to be semivoltine. However, as populations become established over time it is possible that they may become increasingly univoltine as climate continues to warm (Cham *et al.*, 2014). The current study focuses upon life cycle characteristics of *E. viridulum* at a population-scale, studying well-established breeding populations at UK sites. Investigations into their voltinism and studies of larval gut analysis provide further information about the ecological strategies of the species at the northwestern margin of its distributional range.

Materials and Methods

Larval sampling

Larvae were collected from four sites in southeast England: Bedfordshire (two sites), Essex (one site) and Greater London (one site) (Table 1). These sites were selected since breeding populations of *Erythromma viridulum* had either been studied previously by Keat (2007) and Cox (2013) or they were known to support large breeding populations (Cham, pers. comm.). The sites were colonised by the species over a range of years between 2000 and 2004**.**

Table 1. Colonisation dates of Erythromma viridulum at the sampled sites based on NBN records and information from Keat (2007).

Site	Location	Grid Reference	Colonisation date
Barn Elms, WWT Wetland Centre	Barnes, Greater London	TQ228770	2001
Pochard Lake, Chigborough Nature Reserve	Essex	TL876086	2000
Flitton Moor	Bedfordshire	TL056360	2003
Willington Gravel Pits	Bedfordshire	TL096501	2004

Sampling was carried out over three periods in 2014. Preliminary surveys were made at the two Bedfordshire sites on 9th April and at the Barnes site on 14th April, all sites were sampled between 2nd - 10th May, and further samples were obtained from Pochard Lake and Flitton Moor on 1st July. Larvae were collected using a square-framed net swept throughout the water column amongst a variety of vegetation, to ensure a breadth of microhabitats was sampled. Larvae were identified using Cham (2009).

Larval Measurements

Larvae of *E. viridulum* were measured using a dissection microscope and an eyepiece graticule. Head widths and body lengths were recorded to the nearest 0.1mm, observed by positioning larvae dorsal side up against a scale. Head width was measured as the maximum distance at the level of the compound eyes, and body length as the distance from the tip of the labium to the base of the paraproct (Corbet 2004) (Fig. 1). Body length against head width and head width frequencies were plotted for each sample. Although separate larval cohorts may be observed in such plots, they may be obscured by individual variation, particularly in small samples. However, modelling techniques are available to determine the likely number of year classes present, thereby indicating the level of voltinism of the sampled populations. Hence, Gaussian mixture modelling (GMM) was used to estimate a best-fitting model of distribution of body length and head width data, while density estimations of the distribution of head

Figure 1. The head width (A) and body length (B) measurements for *Erythromma viridulum*.

widths within the whole population were estimated using GMM to assess the modality of head widths in the collected samples (Thibault *et al*., 2011, Fraley et al., 2012). The 'mclust' package was used to determine the likely number of clusters, derived using the expectation-maximization algorithm to estimate maximum-likelihood of modality and the Bayesian Information Criterion (BIC) measure to assess model fit (Fraley *et al*., 2014). Each data point in the body length/head width plots is assigned to the most probable cluster.

Larval gut analysis

Gut analyses were performed by dissecting the foregut, after carefully removing the head, pulling the foregut with it and placing it on a microscope slide in a Hydro-matrix mounting medium. A cover slip was applied and the foregut contents examined using a compound microscope. Prey was identified using invertebrate identification keys (Fitter & Manuel, 1994; Dobson *et al*., 2012).

Results

Size analysis

The April sampling at Flitton Moor produced only one *E. viridulum* larva, which had a head width of 2.83mm and body length of 11.17mm. No larvae were

Table 2. Mean head width and body length sizes of *Erythromma viridulum* larvae collected at the sampled sites in May and July.

	May			July		
Site	n	Head width (mm)	Body length (mm)	n	Head width (mm)	Body length (mm)
Barn Elms	3	2.11 ± 0.39	8.28 ± 1.46	-	-	-
Pochard Lake	30	1.91 ± 0.07	6.46 ± 0.32	45	2.94 ± 0.11	12.80 ± 0.47
Flitton Moor	10	2.75 ± 0.20	12.51 ± 1.13	14	2.67 ± 0.20	10.93 ± 0.95
Willington Gravel Pits	2	1.50 ± 0.33	6.92 ± 2.75	-	-	-

found at Barn Elms or Willington Gravel Pits in April. In May, 45 *E. viridulum* larvae were collected from the four sample sites, with the majority collected at Pochard Lake and Flitton Moor. In July a further 59 larvae were collected from these two sites (Table 2).

At Pochard Lake, a total of 75 specimens were found, with greater numbers collected in July when there was a notable increase in Hornwort (*Ceratophyllum* sp.) present at the surface of the lakes. In May, larvae were all early instars of similar sizes, having mean head widths of 1.91mm and body lengths of 6.46 mm (Table 2). In July, both early and late instars were present, including large larvae close to emergence, and head widths ranged between 1.17mm and 4.17mm and body lengths between 6.33mm and 19.00mm. The mean head width and body length was 2.94mm and 12.80mm respectively (Table 2). Thus, between the May and July samples, the average head width of larvae had increased by 1.03mm and average body lengths showed an increase of 6.34mm. This indicates an average growth rate of 0.02mm in head width and 0.12mm in body length per day between the two sampling dates, assuming constant rate of growth. However, there were still some relatively small larvae within the July sample.

Two different methods of analysis were used to provide insights into the number of age classes present. A GMM compared the distribution of body lengths against head widths (Fig. 2A,B). Data from the May samples produced best-fits towards an “EEE” model (ellipsoidal, equal-volume, shape and orientation) containing two clusters (log-likelihood = -41.84, BIC = -110.05). This model was high-performing and the majority of observations were well-classified

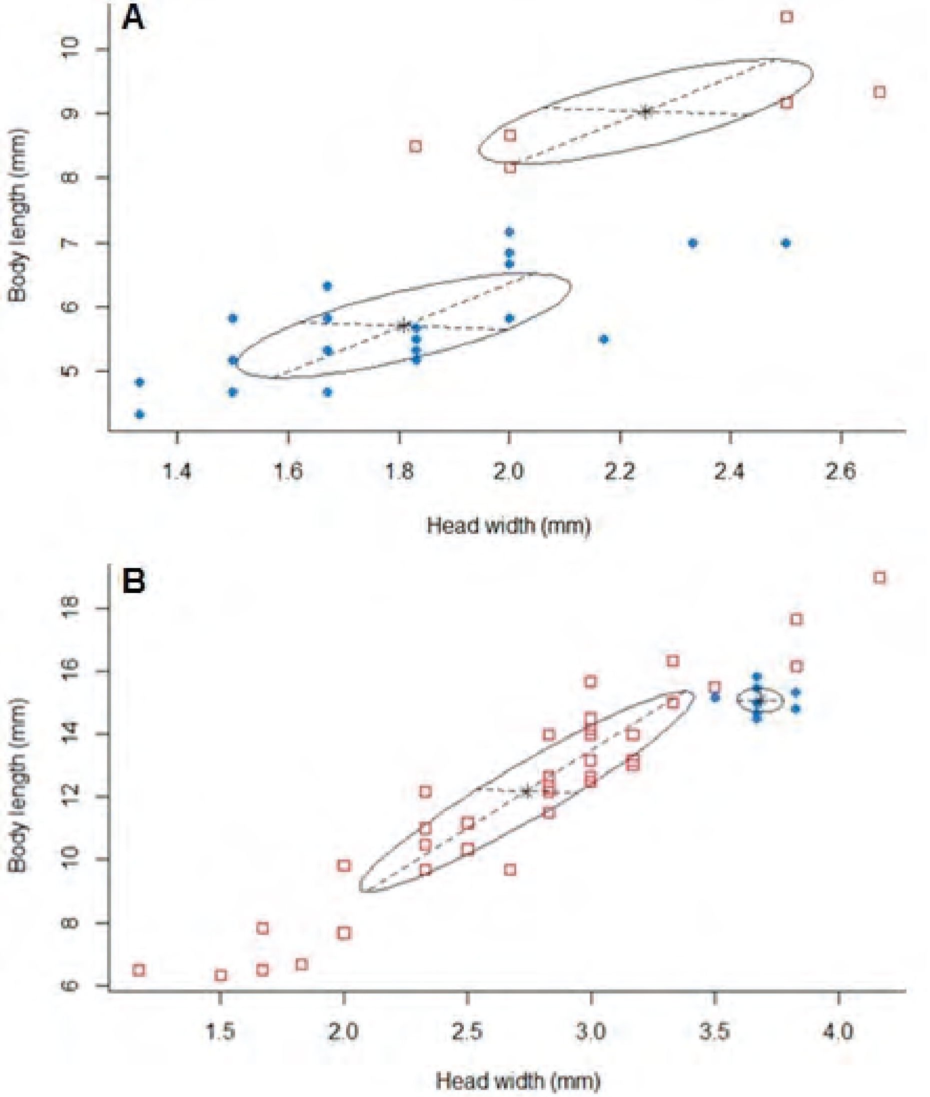

Figure 2. The GMM results of the body length and head width data for Pochard Lake. Data are fitted with the best fitting distributional model for the May (A) and July (B) samples, with different clusters shown by different coloured symbols and elipses circling the mean distribution of the clusters. +, mean.

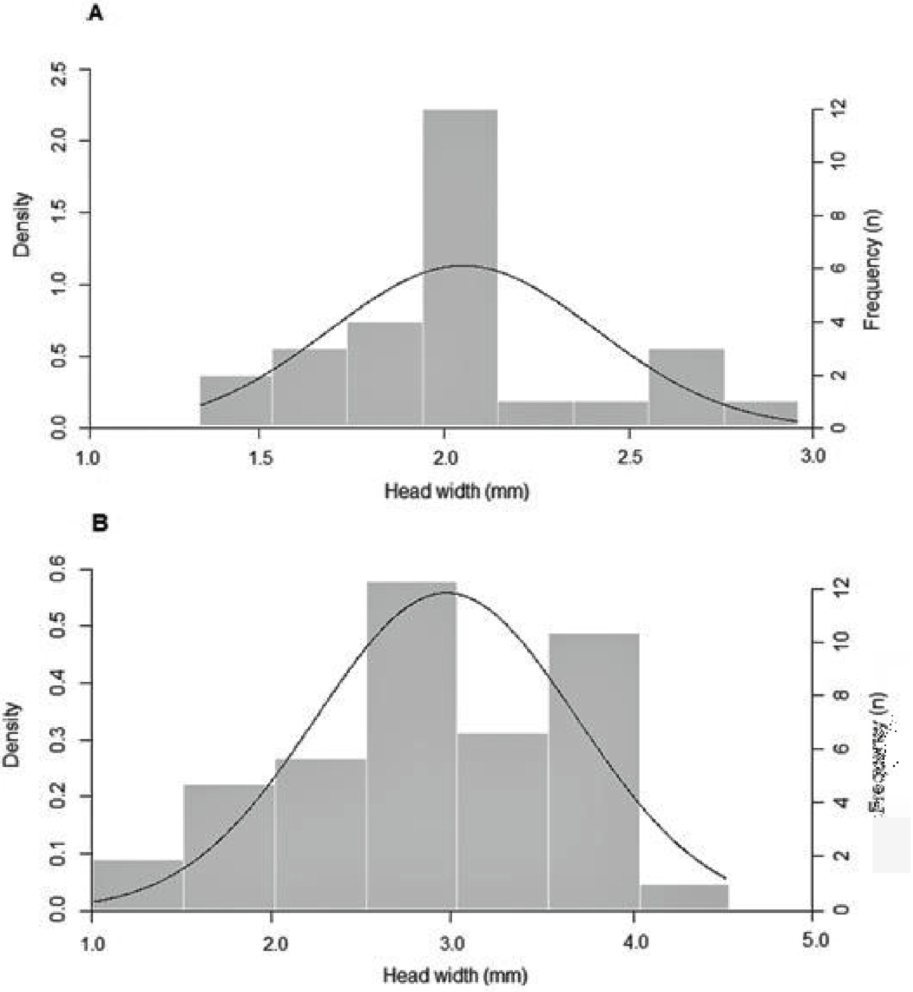

Figure 3. The frequency of larval head widths in the May (A) and July (B) samples from Pochard Lake (bars; right hand scale) and the modelled probability densities likely to be present in the population (line; left hand scale).

into two distributions (sum of uncertainty = 0.09). The July data, which had higher BIC scores, was a ‘VVV’ type model (ellipsoidal, varying volume, shape and orientation model) also with two clusters (log-likelihood = -101.66, BIC = -245.20). This model had higher uncertainty (sum of uncertainty = 1.59) and a lower prediction probability than the May sample. However, both models indicated two distinct clusters. Interestingly, the majority of the lower size group in May had shifted to the next size grouping (presumably the next instar) in July. Several small individuals appear ungrouped in the July sample, suggesting that three instars could have been present rather than the two suggested by the model.

The second method of determining modality assessed the distribution of head widths. Both May and July datasets showed best-fit to univariate models (Fig 3A, B). For the May data the log-likelihood was -10.18 and the BIC was= -26.95), whereas the July data had a log-likelihood of -48.72 and a BIC of -105.05. Although there is some indication visually that there are two peaks in both the May and June datasets (Fig. 3), this is not borne out by the model analysis. The negative predictability power of the models and conflicting results compared to the visual representation of the data may be a result of the normality of the data and low sample size.

At Flitton Moor fewer larvae were collected (Table 2). The May samples showed wide variations in sizes and were similar to those collected in July, with head widths ranging between 1.17mm and 3.67mm in both periods. The mean head width for May (2.75mm) was similar to that in July (2.67mm). However, the mean body length in May (12.51mm) was 1.58mm larger than that of larvae collected in July (10.93mm) (Table 2).

Both the May and July data for body length plotted aginst head width generated a best fit to an “EEE” distribution model (Fig. 4A,B). The May data fitted to a model with nine clusters, with no grouping between observations (log-likelihood = 9.81, BIC = -49.92). For the July data, the ‘EEE’ model was also the best model but the highest performance was fitted with three clusters (log-likelihood = -23.33, BIC = - 75.69), suggesting three different age classes were present. However, the sample size at Flitton Moor was small in both May and July.

Head width data (Fig 5A,B) showed some overlap between groupings, indicating body length may be a better determinant of an individual’s instar. Head width analysis for the May data demonstrated a best-fit towards a univariate, unequal variance model containing two clusters, with two peaks at 1.58mm and 3.02mm (log-likelihood = -5.88, BIC = -23.74). The July data also showed the highest performance with a univariate model but, for these data, the fit is with a normal model with one component with a distribution peak at 2.67 (log-likelihood =

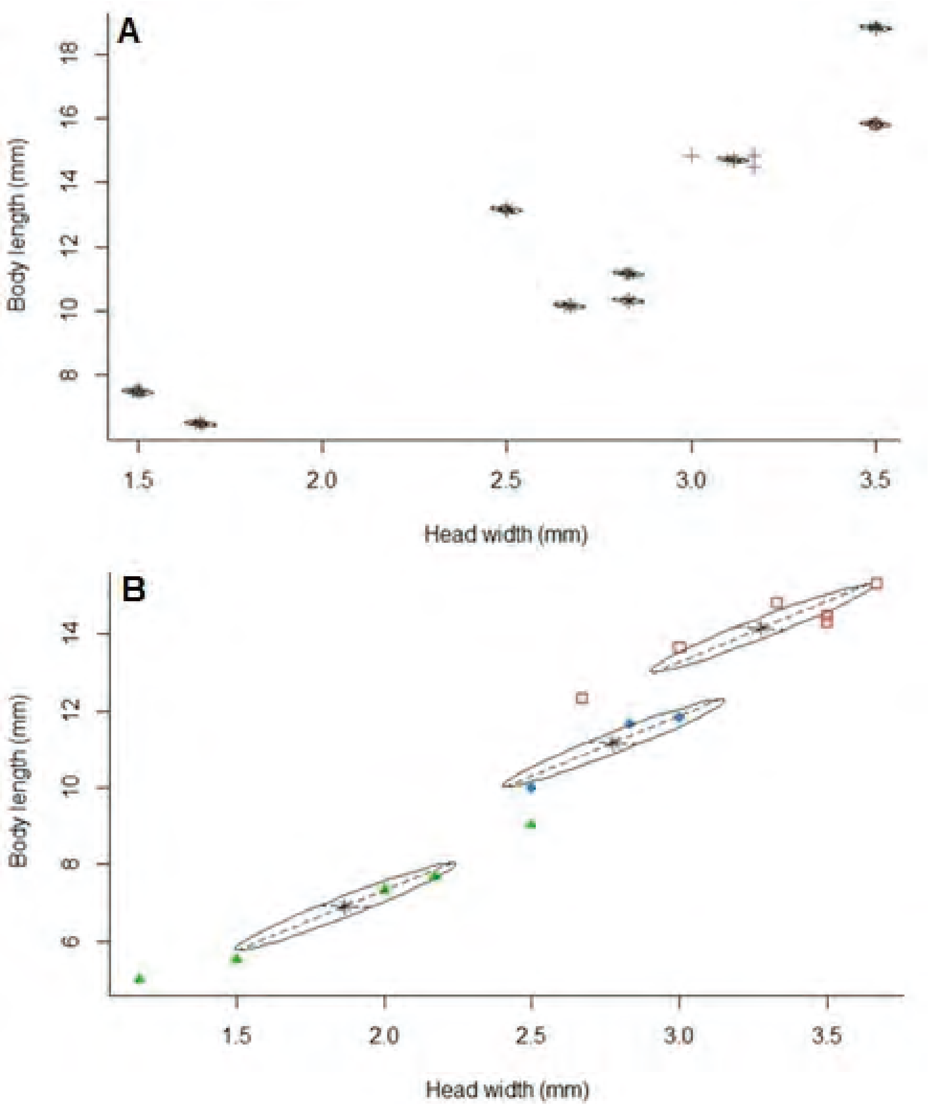

Figure 4. The GMM results of the body length and head width data for Flitton Moor. Data are fitted with the best fitting distributional model for the May (A) and July (B) samples, with different clusters shown by different coloured symbols and elipses circling the mean distribution of the clusters. +, mean.

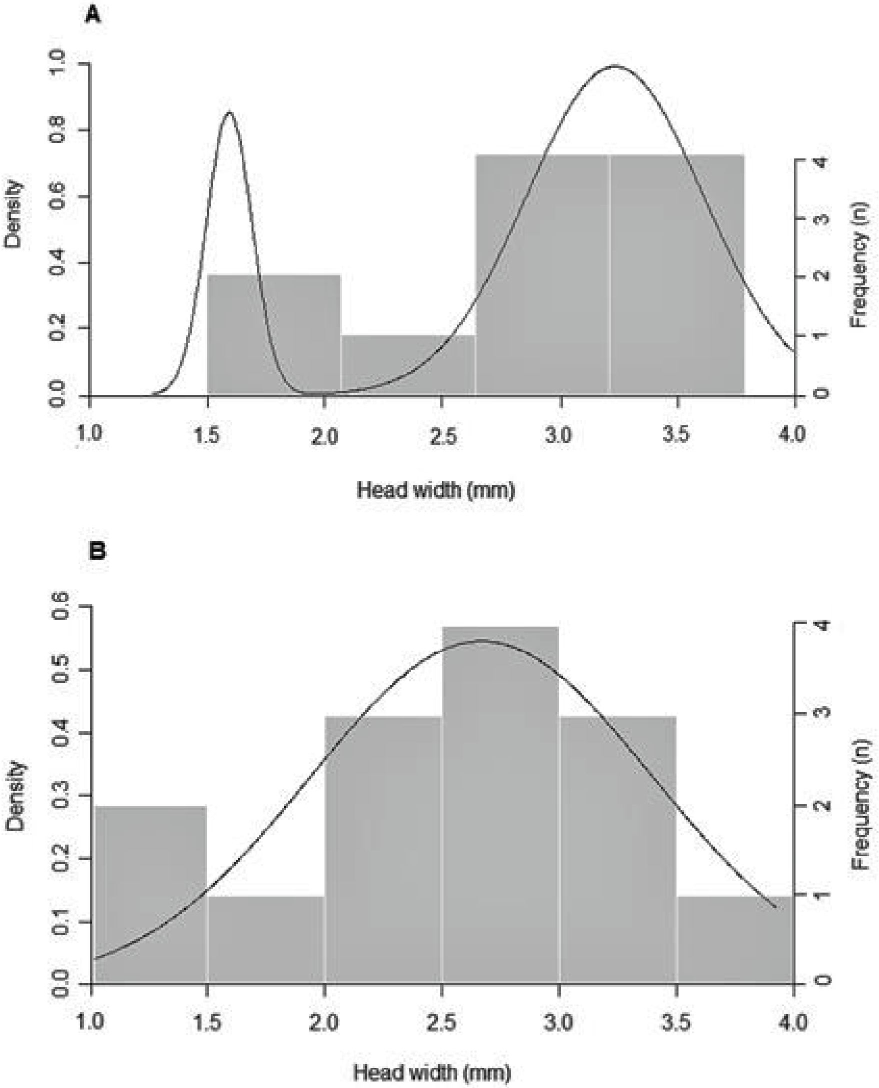

Figure 5. The frequency of larval head widths in the May (A) and July (B) samples from Flitton Moor (bars; right hand scale) and the modelled probability densities likely to be present in the population (line; left hand scale).

-15.43, BIC = -36.14), even though the graph (Fig. 5B) suggests the possibility that two peaks are present. The ambiguity between the two analyses for the July data may well be a result of the relatively small sample sizes from Flitton Moor.

Gut content analysis

The number of larvae with empty foreguts was greater in the May samples than in the July samples. Those with gut contents showed no evidence that *Erythromma viridulum* was predating upon other odonate species. Most of the identifiable prey in the foreguts consisted of chironomids, rotifers, cladocerans and copepods (Fig. 6). In the July samples a larger number of identifiable prey items were present. This may be due to prey being smaller in the smaller larvae collected in May and therefore being harder to identify. Furthermore, the July larvae had a greater number of prey items present in the gut contents, particularly from Pochard Lake, indicating greater feeding activity later in the season and as the larvae increased in size (Table 3). At both Pochard Lake and Flitton Moor, the July samples showed an increase in the proportion of copepods and cladocerans consumed and a decrease in the proportion of chironomid larvae (Fig. 6). This may reflect a decrease in the availability of the latter as they emerged as adults or larval diets becoming more varied as, with increasing size, they are able to prey upon a wider variety of different sized prey species. At Flitton Moor, *Asellus* sp. (Water Slater) became part of the diet.

Discussion

Larval samples from two well-established breeding sites in southeast England were analysed to establish both the voltinism and diet of the two populations, and whether voltinism varied with the amount of time the species had been established. In Britain, *Erythromma viridulum* emerges in late summer. At Pochard Lake in Essex, where the largest numbers of *E. viridulum* larvae were collected, the species was first recorded in 2000, whereas the species is thought to have established at Flitton Moor in Bedfordshire in 2003. Despite the difference in establishment dates, both sites had an overall similar distribution of larval age-classes present. The May and July samples at Pochard Lake appeared to be composed of two cohorts, suggesting a semivoltine population was present. The larger larvae present in July are likely to emerge in the current year, whereas the smaller larvae, based upon average growth rates seen at the site, are likely to emerge in the following year. Due to time constraints, a sample was not taken in September to determine whether larvae were still present. However, it seems highly likely. At Flitton Moor, the July sample had a smaller mean size of larvae than those collected in May. This was likely due to the smaller cohort being too small to collect in May but being large enough

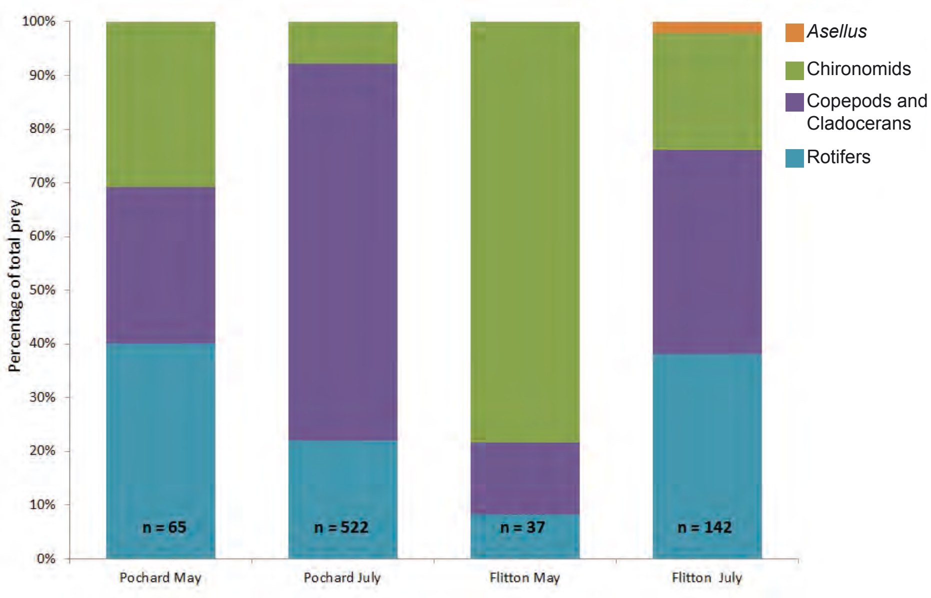

Figure 6. The proportion of major prey items in the foreguts of the *Erythromma viridulum* larvae at Pochard Lake and Flitton Moor in May and July.

to collect in July. Finding larvae early in the season proved difficult and only one individual was found in April and fewer larvae were collected in May than later in the season. This was possibly due to young larvae being too small to collect in the 1mm mesh sampling net and with the Hornwort, their primary habitat and refugium, being located at the bottom of the lakes, thereby making it more difficult to sample successfully. However, the two peaks in the head width distributions in both samples and the three cohorts indicated in the body length/head width plots for the July sample suggest a semivoltine population is also present at Flitton Moor, the cohort with small head widths present in July being highly likely to overwinter in the lake due to their small size.

A similar study by Keat (2007) at two sites in Bedfordshire and Essex produced remarkably similar results to those of this study. Keat's analysis (Keat, 2007) also included a sample in August when large numbers of small larvae were still present. Keat (2007) concluded that the species was probably semivoltine in these localities, as such small larvae are highly unlikely to emerge in the same year but would overwinter and emerge the following year.

The results of the gut content analysis found no odonate body parts in the

Table 3. The number of *Erythromma viridulum* larvae with empty guts in samples collected in May and July from Pochard Lake and Flitton Moor.

	Pochard Lake		Flitton Moor	
	May	July	May	July
Larvae collected	30	15	10	14
Number of empty guts	11	5	1	0

foreguts of the *E. viridulum* larvae collected, suggesting they are not consuming the larvae of other dragonfly species. This was similar to the conclusions of a study by Cox (2013), where samples from the London Wetland Centre indicated that *E. viridulum* were the predominant larvae present at the site and there were no signs of odonate body parts present in their foreguts. Feeding patterns observed between the specimens collected in May and in July showed variation in the larval diet at different developmental stages.

Conclusions

The results of this study corroborate those of Keat (2007) and suggest populations of *E. viridulum* in southeast England are semivoltine. There is no indication of populations switching from semivoltine to univoltine life cycles between 2006 and 2014. The results of the gut content analysis of the larvae showed that similar prey items were consumed at each of the sites but that, in July, the larvae increased the proportion of copepods and cladocerans consumed at the expense of chironomid larvae. There was no indication that the species was feeding upon the larvae of other odonates, suggesting that *E. viridulum* does not exclude other odonate species by preying on their larvae.

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Species Review 9: *Macromia splendens* (Pictet 1843) (The Splendid Cruiser)

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Summary

Macromia splendens (The Splendid Cruiser) is the only Western Palearctic representative of an essentially tropical family, the Macromiidae. This European endemic is one of our largest dragonflies and yet, until recent years, hardly anything was known about its life history or distribution. This essentially riparian species favours man-adapted habitats and particularly hydroelectric barrages. It is classified as vulnerable in the European Red List of dragonflies but its populations are stable. It is hoped that this review will encourage more people to study this local and beautiful insect.

Introduction

Macromia splendens (The Splendid Cruiser) is the sole Western Palearctic representative of the family Macromiidae, which is now known to be separate from the closely related Corduliidae (Dijkstra & Klausnitzer 2014) in which it was formerly classed (e.g. Davies & Tobin, 1985). The Macromiidae comprises four genera:

- *Macromia* – Eastern Palearctic, Nearctic and Oriental regions – 90 species (Dijkstra & Klausnitzer, 2014)
- *Phyllomacromia* – Sub-Saharan Africa – 35 species (May, 1997)
- *Epopthalmia* – Oriental region – 5 species (Davies & Tobin 1985; Bridges, 1994)
- *Didymops* – Nearctic – 2 species (Davies & Tobin 1985; Bridges, 1994)

There are no members of the family in the Neo-tropical region. The genus *Macromia* is primarily tropical, inhabiting permanent forest streams. Outside of the tropics, the number of species is greatly reduced and our European representative *Macromia splendens* is remarkable in its isolation from other members of the genus (Fig 1). Geographically, its nearest relatives within the Macromiidae are found in sub-Saharan Africa. However, the species in this, the Ethiopian Region, have been assigned to a separate genus, *Phyllomacromia,*

Figure.1. World distribution of *Macromia, Phyllomacromia* and *Epopthhalmia* (Macromiidae), excluding the Nearctic where only *Macromia* and *Didymops* occur.

by May (1997), which is more closely related to *Epopthalmia*, which occurs in tropical Asia and India. In fact, the nearest relatives belonging to the genus Macromia are found in the Eastern Palearctic and are separated from *M. splendens* by more than 5,000 miles.

Discovery

It is remarkable that *Macromia splendens*, which is one of the largest and, in my opinion, most beautiful of European insects, was so little known until very recent years. I first came across it when researching dragonflies in Sussex back in the 1970s. By chance I came across a paper by Morton (1925) entitled “*Macromia splendens* at last”; his tale is worthy of recounting. The species was first discovered by M. Amedee Guinard from the neighbourhood of Montpelier in southern France. He sent a female to M. Pictet and subsequently a male and two females to de Selys. Pictet (1843) described the species based on the first female and with a supplementary note by De Selys describing the male and assigning the species to the genus *Macromia*. The next reference is from Fallou (1868), announcing that M. Delamain "has found near to Jarnac [north west France] a large number of individuals of *M. splendens*, which had hitherto only been reported from around Montpelier". Morton (1925) commented that "less has been written about it [*M. splendens*] than almost any other European dragonfly." He further recalled seeing a specimen in Robert Maclachan's collection from the Bouches du Rhone, which is close to the Montpelier locality, and that in 1911, with his friend Dr Ris, he visited the area finding 34 species but no *M. splendens*. He re-visited in 1913 and 1914 but again with no success. Finally, in early July 1923 and quite by chance, in Cahors on the River Lot, he found "*Macromia splendens* at last". In 1924 Morton returned to the site and was again successful but was France the only country where *M. splendens* could be found? Navas (1924) referred to an example of *M. splendens* sent by a Dr Pau from Segorbe (Catellon) or the Sierra Camerena in eastern Spain. He also listed a locality at Poigres in Portugal. In summary, in 1924 six localities were known:

- Montpelier, France – the original locality (Pictet, 1843)
- Jarnac, France (Fallou, 1868)
- Segorbe or Sierra Camerena , Spain (Navas, 1924)
- Poigres, Portugal (Navas, 1924)
- Bouche du Rhones?? France - Maclachlan collection (Morton, 1925)
- Cahors, River Lot, France (Morton, 1925,)

Grasse (1930) described the larvae but it was not until 1965, when the celebrated entomologist Maurits Lieftinck (Lieftinck, 1965) turned his attention to *M. splendens*, recounting two excursions, in June of 1961 and 1964, when he was successful in rediscovering the species in the valley of the River Lot. Lieftinck provided a map showing the known distribution at that time. The French localities included a number of sites in the far south around Montpelier, a cluster along the Rivers Lot and its tributary the Cele together with the original Jarnac record. More perplexing was the situation in Iberia. Lieftinck (1965) mentioned the Segorbe record but goes on to state that "all [his] enquiries into the whereabouts of an authentic Spanish individual remain ineffectual." However, two sites were given for Portugal :

- Soure, a coastal locality west of Coimbra discovered by Prof. A. F. De Seabra. Leiftinck examined the specimen which he thought would have been taken from the Rio Mondego
- Poigres or Poiares, about 25 km east of Coimbra.

In summary, forty years on from Morton's paper the known distribution had hardly expanded from the original localities; indeed the Jarnac (France) and all three of the Iberian localities remained unconfirmed. Inspired by Leiftinck's visits, Alois Bilek, a German entomologist, spent two periods of four weeks in 1966 and 1967 studying *M. splendens* on the Rivers Lot and Cele in Midi-Pyrénées, France (Bilek, 1969). Bilek's paper became my key reference, encouraging me to visit the Lot river system in 1979, where I first observed the species, and again in 1980.

The known distribution took a step forward in a completely new direction in the 1980s when two larvae were found in the Rio Tavizna (Ferreras Romero, 1983). This small river in the very southern part of Spain was almost 500 km from the nearest known sites. Tiberghien (1985) included this record in his paper, which summarised the distribution known in the mid 1980s. The known distribution in 1987 was given by Askew (1988) (Fig. 2) and yet it was another ten years before three researchers extended the known distribution. Adolfo Cordero (Cordero, 1996) discovered the species for the first time in Galicia in Northern Spain in 1995. Contemporaneously, Rudolf Malkmus recorded it from the lower reaches of the Guadiana river in southern Portugal; yet another new site (Malkmus, 1996). Finally, I, along with my colleague Peter Mitchell, recorded the species along the Rio Ceira, which is a tributary of the Rio Mondego, and thus confirmed the old sites around the city of Coimbra, Portugal (Chelmick & Mitchell, 1996). Since the mid 1990s a considerable expansion of the known range of this species has been established.

Distribution and key references

In summary, the original Jarnac (France) sites have been confirmed and expanded to the Gironde (Jourdain, 2004) and to the northern edge of the Charente Region in France (Prudhomme & Suarez, 2007) which represent the most northerly sites for *Macromia splendens*. However, the most spectacular expansion has been in Iberia, simply as a result of greatly improved recording. The current known distribution, which is reproduced here (Fig. 3), is from Boudot & Dommanget (2015); it also shows the locations of six key studies that I have used in this review and which constitute the principal body of work on this species.

- The Alois Bilek work (Bilek, 1969) on the rivers Lot and Cele, Midi-Pyrénées, France
- Adolfo Cordero Rivera's work in Galicia, Spain carried out in the late 1990s (Cordero Rivera *et al*., 1999; Cordero Rivera, 2000)
- The study by Leipelt & Suhling of larval biology and habitats on the river

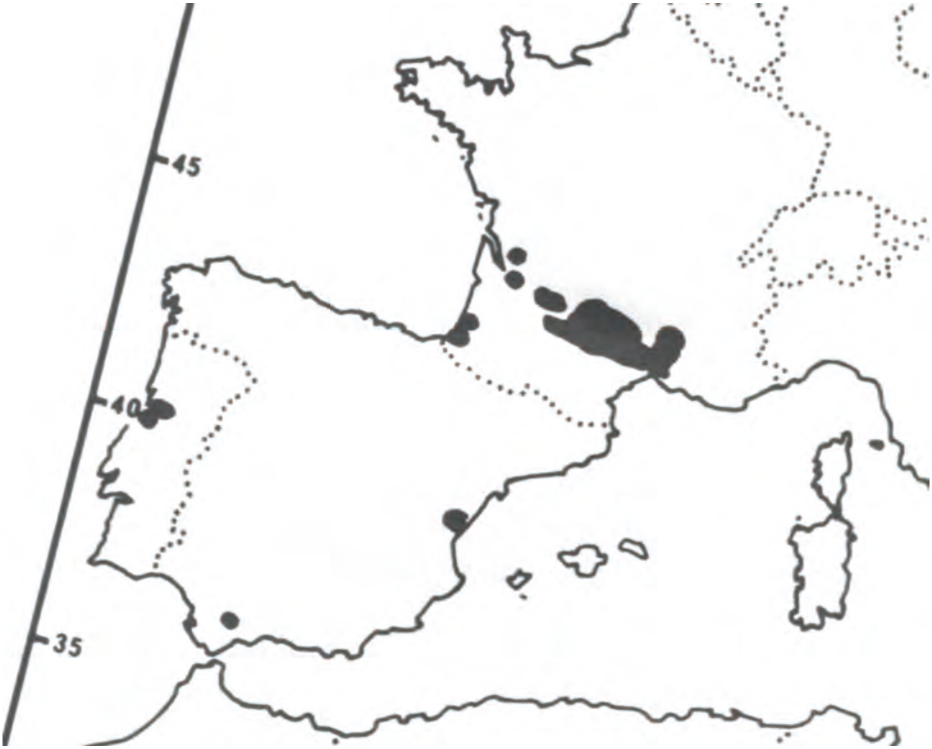

Figure 2. The distribution of *Macromia splendens* as known in 1987. From Askew (1988).

Gardon, France (Leipelt & Suhling, 2005)

- Studies by the author on the Guadiaro river system in southern Spain (Chelmick, 2015a)
- Work on exuviae collected from Terra Alta, Catalunya (Martinez-Martinez *et al*., 2015)
- Jean-Louis Dommanget's comprehensive study from 1979 until 2000 on all aspects of the insect's life history on the River Tarn, France (Dommanget, 2001)

Cordero Rivera (2000) stated that one of the limitations to the distribution of *M. splendens* is that it only occurs where the mean annual temperature exceeds 13°C and this is clearly a factor (Fig. 4A). However, in southern Spain, where this temperature occurs over most of the country, rainfall, or more correctly the lack of it, is a key limiting factor (Fig 4A). In summary, in southern Spain, rainfall is a limiting factor to the distribution of *M. splendens* whilst in northern Spain, where rainfall is sufficient (more than 600 mm per annum), much of the

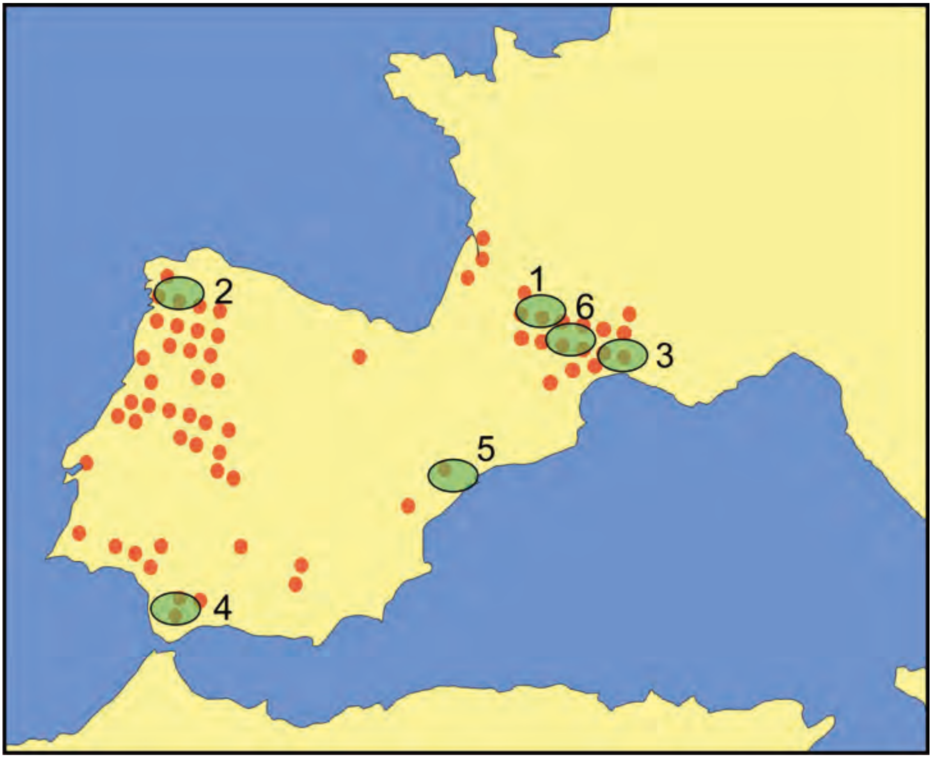

Figure 3. The current (2013) known distribution of *Macromia splendens.* After Boudot & Dommanget (2015), together with key reference studies: 1, Rivers Lot & Cele, Midi-Pyrénées, France (Bilek, 1969), 2, Galicia, Spain (Cordero Rivera *et al.*,1999; Cordero Rivera, 2000), 3, River Gardon, France (Leipelt & Suhling, 2005), 4, Guadiaro river system, Spain (Chelmick, 2015), 5, Terra Alta, Catalunya, Spain (Martinez-Martinez *et al.*, 2015), 6, River Tarn, France (Dommanget, 2001).

region is too cold. Dommanget (2001) stated that *M. splendens* requires warm summers where the shade temperature exceeds 25°C for more than 60 days in the year. He makes no mention of rainfall but in The Tarn valley in France this is not a limiting factor. Looking at the 13°C contour (Fig 4A), the Rhone valley in southern France shows a sharp decrease in temperature and, although climate conditions appear suitable in Italy, there are no records from that country. Grand (2002) stressed that colonisation of habitats east of the Rhone Valley may be inhibited by the strong northern winds, the Mistral, which commonly blow along the Rhone Valley during the flight season. It would appear that a combination of the Rhone Valley and the Alpes Maritimes to the east have provided sufficient barriers to the expansion of *M. splendens*, whose nearest relatives occur some 5,000 miles to the east.

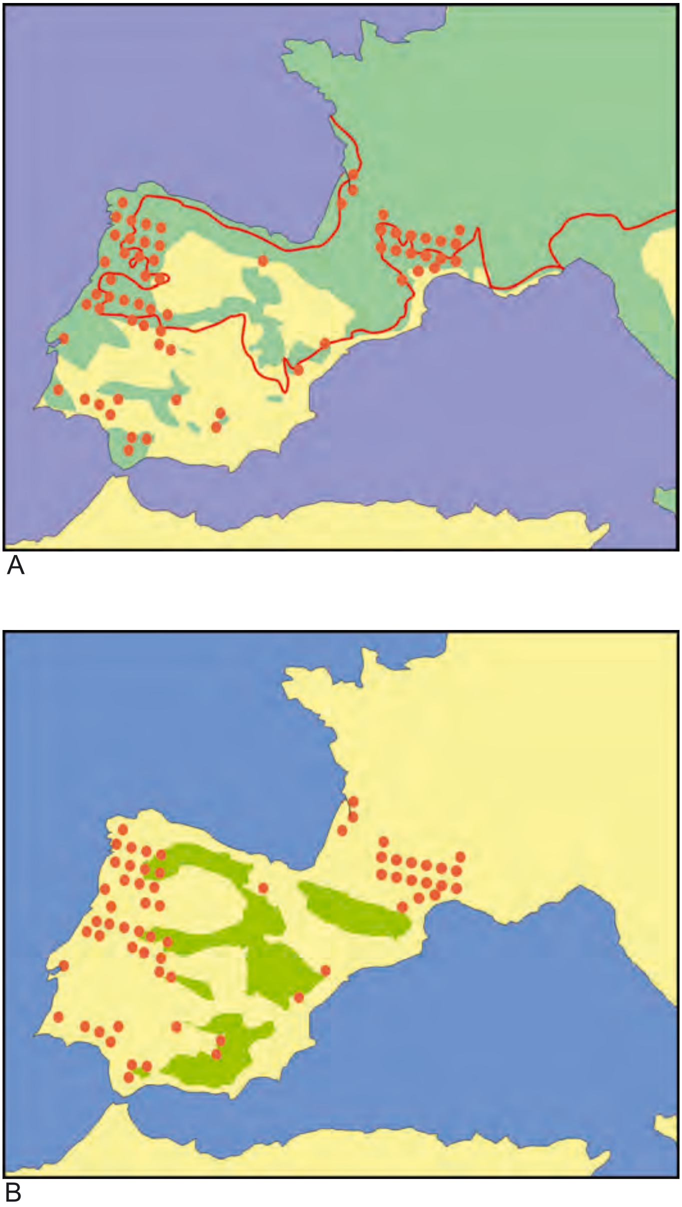

Figure 4. The current (2013) known distribution of *Macromia splendens* showing (A) the 13°C contour (red) and annual rainfall above 600 mm (green areas) and (B) areas over approximately 1000m a.s.l. (green). After Boudot & Dommanget (2015); climate information based on Steinhauser (1970).

One final factor limiting distribution is that of altitude. Spain has large areas over 1,000 m a.s.l. (Fig 4B). Cordero Rivera (2000) stated that *M. splendens* is rarely found above 350 m a.s.l. although Dommanaget (2001) noted that, in France, there have been records from as high as 620 m a.s.l. There are no records from rivers that run from the Pyrenees either north into France or south into Iberia. Hence it would appear that the larvae are unable to cope with cold melt waters.

Description and Life Cycle

Eggs

I was unable to find any reliable information on the eggs of *Macromia splendens* but my good friend and authority on European dragonflies, Jean-Pierre Boudot, pointed me in the direction of Dommanget's study on the River Tarn (Dommanget, 2001). This study provides a photograph of the eggs, which are described as "ovoid and of gold-yellow colouring with a mucilaginous covering which develops on contact with water". This covering presumably enables the eggs to adhere to the substrate. Dommanget (2001) stated that, where the water temperature is between 18^{o}C and 22^{o}C, the hatching period is between 19 and 22 days with the vast majority hatching at 20 days. Dommanget (2001) makes an interesting point regarding the numbers of eggs laid. When females are caught and milked for eggs they provide only between 6 and 10 at any one time. This is a very low number in comparison with a female *Sympetrum* sp., which will produce much larger numbers.

Larvae

First described by Grasse (1930), the larva of *Macromia splendens* is one of the most spectacular amongst odonates. It is large (31 mm from head to tip of abdomen), has extensive spines and extremely long legs (Plate 1A, B). Leipelt & Suhling (2005) stated that the larval life cycle is two years and Dommanget (2001) found that larval life lasts 22 months spread over three calendar years. My own work concurs with both these conclusions. The final instar develops in the autumn of the year prior to emergence, the adult being ready to emerge in the following Spring without further change. In this sense the insect is a spring species as defined by Corbet (1962).

The morphological changes from at least the F-2 instar (Plate 1A) to the final instar (Plate 1B) are relatively minor other than overall size and the length of the wing cases. At any stage the larva is unmistakeable from any other species that is likely to be encountered in Europe. The larval habitat has been the subject

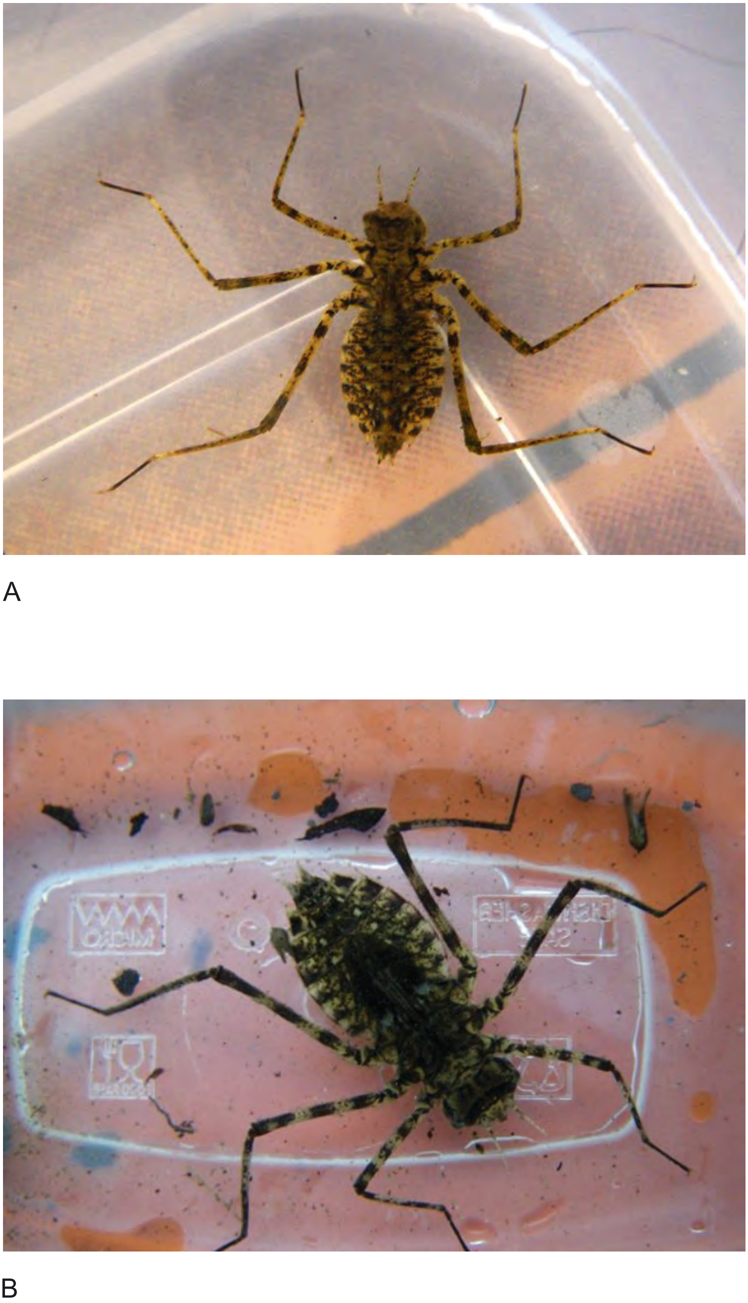

Plate 1. Larvae of *Macromia splendens*. (A) F-2 larva, (B) Final instar larva.

of some speculation. Cordero Rivera (2000) suggested that the larvae live in tree roots. However, Leipelt & Suhling (2005) stated that this is not the normal situation and suggested that the larvae life in detritus and sand in the bed of the river. They also suggested that they live in small depressions found at the base of the vertical banks which are common along the stretches of river where *M. splendens* breeds. My own experience and that of Graham Vick (pers. comm.), who collected and bred the species in the 1980s, is that the larvae are to be found primarily in detritus with leaf litter, sand and mud and Dommanget (2001) reached the same conclusion. The larvae come in a wide range of colours from almost black to sandy brown (Plate 2), indicating that they possibly adapt to suit the colour of their surroundings and may well live in a range of environments. The larvae lead a very sedentary life. I have kept them in aquaria and studied them over many years. They conceal themselves by covering their bodies with the substrate, leaving only the antennae and eyes above the surface. After removal of the sandy substrate from their bodies they are still difficult to see (Plate 3A); even more so when they are covered (Plate 3B).

Leipelt & Suhling (2005) suggested that the larvae remain stationary during the day, moving around to hunt only during the hours of darkness. My own work suggests an even more sedentary life cycle. I have watched two larvae over the period of one complete night. During that time one of them moved a total of 7 cm and remained covered for all the time that I observed it. In the Guadiaro river system, where most of my observations have taken place, the endless fish fry and tadpoles render any need to move quite superfluous; the protruding eyes and long antennae of the larva easily locating prey without need for further exertion.

Plate 2. Exuviae of *Macromia splendens* to show the range of individual colours.

A

B

Plate 3. *Macromia splendens* in its preferred feeding/ambush position. (A) Larva with its covering of detritus removed, (B) the larva after it had re-covered itself, showing only its eyes and antennae above the surface.

Pre-Emergence As stated above, Leipelt & Suhling (2005) found larvae in small depressions at the base of vertical rocks. Up until this year, I had never found larvae in these situations. However, in May 2015 on the Guadiaro, I was successful at my first attempt in finding a final instar larva in just such a depresion at the base of a cliff. This leads me to the view that the majority of the larval life is spent in detritus etc. but, as the larvae approach emergence, they migrate close to the selected emergence point: tree roots, roots of aquatic vegetation or depressions in rock faces. The larva at this stage no longer spends time concealing itself; it appears simply to be waiting for the correct emergence conditions. Such conditions can take a considerable amount of time to develop. In 1980 I made my second visit to the River Cele in southern France, where I had, the previous year, found *M. splendens* for the first time. My timing was similar to the previous year except for the weather! The eruption of Mount Helens in the US had caused a major change to European weather patterns and huge storms prevailed over the valleys of the Lot and Cele for the entire three week period of my trip. The sparkling idyll of a lowland river in 1979 had become, and remained, a raging torrent, nullifying any possibility of *M. splendens* emergence. How does an insect, bearing in mind that it will now be an adult in the larval body and can no longer feed, cope with such conditions? I can give some small insight into its flexibility. Having collected a larva in May 2015, I decided to make observations of its emergence behaviour and duly transported the larva to a temporary aquarium in my hotel room. That night at about 22.45 in the darkness the larva left the water and looked ready to emerge. I checked again at 1:00 and the larva had completely disappeared; my containment system was less than perfect. At 7:30 I awoke and, to my surprise and considerable pleasure, I saw the larva moving down the curtains. It eventually dropped back into the water. The larva had spent more than nine hours out of the water and had travelled a minimum of 4.0 m. After about 30 minutes in the water it left the tank again and looked ready to emerge but, probably sensing too much light, it returned to the tank where it remained for a further seven nights. Chelmick (2015b) provides a more extensive description of this odyssey.

Emergence Grand & Boudot (2006) stated that emergence in *M. splendens* “commence tot le matin” [early in the morning]. Graham Vick (pers comm.) stated that he reared a larva that emerged during the night. The larva (a male) that I reared (see above) eventually emerged on 29 May (seven nights after its original attempt). It emerged from the water at 18:45 and by 22:00 (3.25 hours) the wings were opened and by 22:42 the adult insect was ready to fly (Plate 4). Cordero Rivera *et al*. (1999) have also bred out larvae. In two cases, as with mine, the emergence took place at night whilst the one shown in their paper emerged at around 05:00. Dommanget (2001) recorded emergence from 08:30 until 16:00 and noted that some larvae travelled only 30 cm whilst others moved as much as 6.0 m from their water exit. Cordero Rivera *et al*. (1999) stated that

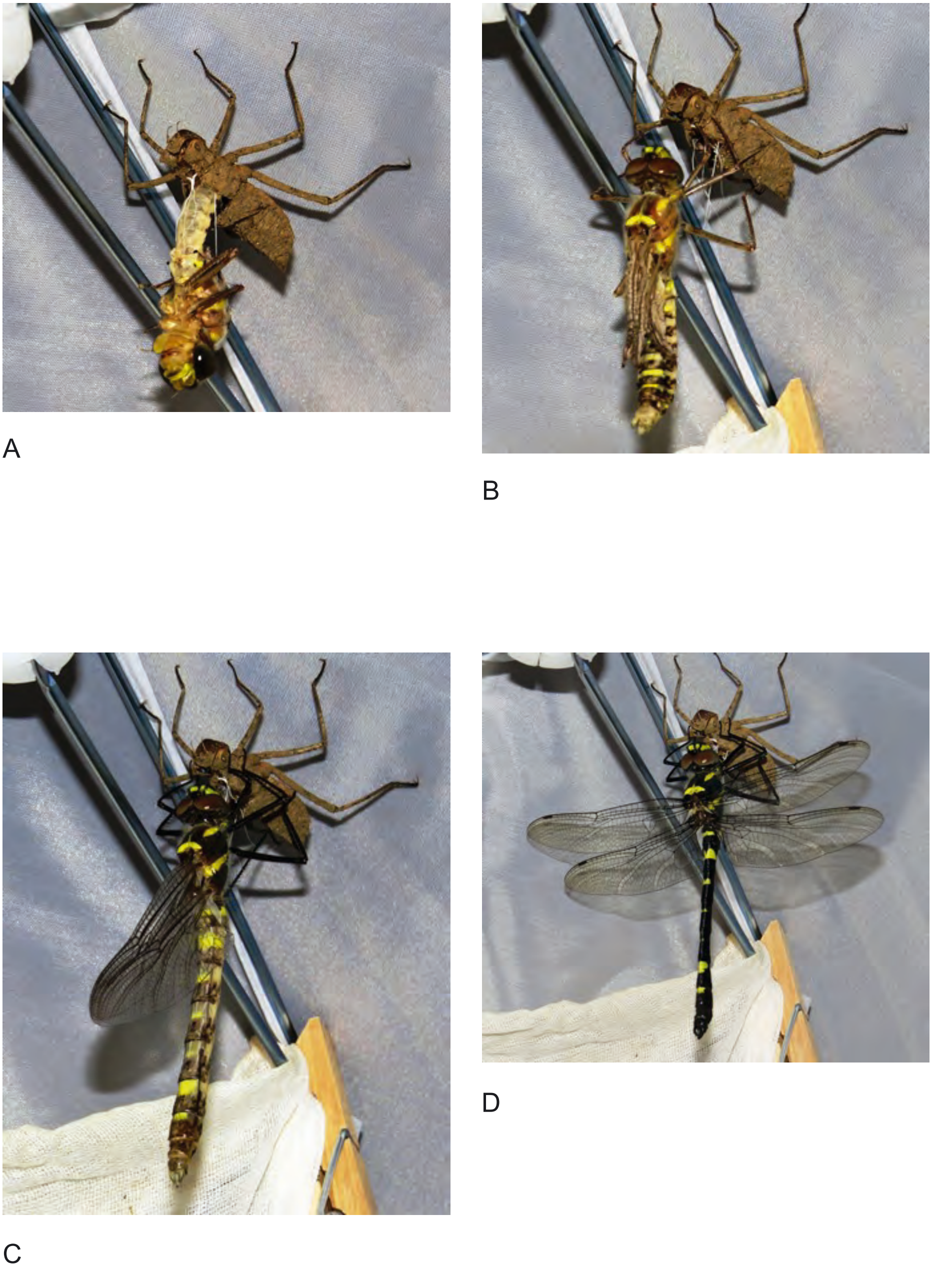

Plate 4. Stages in the emergence of *Macromia splendens.*

the entire emergent process needed two hours. This is rather shorter than I observed and Dommanget (2001) found that emergence was always longer than the two examples recorded by Cordero Rivera *et al*. (1999).

In the larva that I reared, the temperature in the emergent area was maintained above 20°C until the insect had completed its development. The heater was then removed and, by the following morning, the temperature had decreased to 11.0°C. The adult insect, totally reliant upon outside temperature, was virtually comatose. The first point to make here is that, before the heater was installed, the larva remained motionless; it was only stimulated to emerge by the provision of the heat. Thus it is likely that low ambient temperatures at emergence time must be a major limiting factor to the northern expansion of *M. splendens*. Secondly, in Spain, early morning temperatures during May can be around 20°C, thus providing sufficient energy to allow the adult to fly off to the safety of the trees at first light. Lieftinck (1965) discussed his finding of agitated Grey Wagtails (*Motacilla cinerea*) at the water's edge on the river Lot in the early morning. On investigation, a number of dragonfly wings were found floating on the surface of the river, including 12 of *M. splendens (*Lieftinck, 1965*)*. There can be no doubt that predation at this most vulnerable emergence stage is a major factor in losses of adult insects and this is made even more critical by the relatively small populations, as explained below. As one moves north in Spain and then into France so suitable (circa 20°C) emergent early morning temperatures occur later in the year, which may well explain why, over its geographical range, there is considerable variation in its flight period.

Emergence sites On the river Guadiaro, in southern Spain, emergence takes place normally between 30 and 50 cm above the water. Grand & Boudot (2006) stated that they are found near the bank at depths of 30cm to 150cm under the shade of trees or at the base of walls. Rock faces, particularly where they have overhanging sections or caves, are preferred as the larvae often emerge upside down. However, there is no rigid rule and trees and even herbaceous vegetation are often used (Plate 5A, B)). Caves adjacent to suitable rivers should always be searched. I recall staying at the hotel des Grottes on the River Cele in the 1980s. Beneath the hotel and adjacent to the river there was a small cellar inaccessible from the land. Undeterred, my young son's inflatable boat was pressed into service and, with little effort, I gained entry into the cellar where a large number of *M. splendens* exuviae were found, doubtless accumulating over a number of years until the next storm surge would wash them away.

In most cases exuviae are found with little or no accumulation of debris although some can be quite encrusted. My emergence experiment (above and Chelmick, 2015b) may provide an explanation for this. I had to move the location of the tank containing the larva. In the original room it was quite clean. The larva was

A

B

Plate 5. Exuviae of *Macromia splendens* (A) on a tree on the bank of the river Hozgarganta, (B) on vegetation. Note that, in the latter, an exuvia of *Boyeria irene* used that of *M. splendens* for its own emergence.

placed in the tank in the new location in very murky water. As it settled, so the larva became covered in fine mud and sand; it made no attempt to clean or bury itself during this period, presumably needing to save all its energy for emergence as it was quite unable to feed. The resulting exuvia was thus encrusted with this material.

Numbers of exuviae can give an indication of population size. If that is the case then *M. splendens* does not have large populations. Bilek (1969) collected 23 exuviae over 56 days and I collected 80 exuviae over 90 days. However, a much larger collection was made in Catalunya by Martinez-Martinez (2015) who found a total of 277 exuviae. This last study took place over a four year period at 11 key sites, each site being approximately 500 m long. The largest number of exuviae found at one site in the best year, 2011, was 24 whilst the average for all the sites in 2011 was 10 exuviae. This implies a relatively low density. My own collection of only 80 exuviae was made over a ten year period and shows similarly low numbers. To put these collections in perspective, had I been collecting other exuviae of species that occur regularly with *M. splendens*, i.e. *Oxygastra curtisii* and *Gomphus graslini*, then numbers would be increased by a factor of ten; further, if I had collected *Boyeria irene* then numbers would be into the thousands. In my opinion *M. splendens* simply does not occur in large numbers and populations must always be considered to be vulnerable to problems of low temperatures at emergence (as shown above) and to irresponsible collecting.

Dommanget (2001) collected 544 exuviae at one of the large hydroelectric barrages on the River Tarn (France) in 1987. This clearly shows how such habitats are particularly suitable for *M. splendens*. What is particularly remarkable is that the numbers of exuviae of other anisopterans collected at such barrages were much lower, the total numbers of exuviae found at two barrages on the Tarn from 1986 to 1992 (Dommanget, 2001) being:

■	*M. splendens*	1059
■	*Gomphus* spp.	486
■	*Boyeria Irene*	64
■	*Oxygastra curtisii*	313

These results are the reverse of the usual at *M. splendens* habitats and this species is clearly far better suited for this man made environment than its generally more abundant co-habitees.

Adults

It is only when we consider the adult stage that we begin to understand why *Macromia splendens* has been so little known or researched until recent years. Hawkers (Aeshnidae) are conspicuous (how can one miss *Anax imperator* as it cruises leisurely across pool or stream?), darters (Libellulidae) sit and display in the hot sun and gomphids are hardly the strongest fliers. However, consider the Emeralds (Corduliidae and Macromiidae); in my opinion the most beautiful of dragonflies and yet, in the biblical sense, they hide their light under the proverbial bushell. The Emeralds are the shrinking violets of the dragonfly world and none more so than the genus *Macromia*. In Germany, the Emeralds are known as Die Falkenlibellen (Falcon dragonflies) and the German vernacular name is Flussherrscher which in English is 'Sovereign of the River' (Wildermuth, 2008). I cannot think of a more apt vernacular name because when I saw my first *M. splendens* in France in 1979, I could barely believe that it could fly so fast and could be so hard to spot (Plate 6A, B). Why am I discussing the insect in flight first? Because that is almost certainly how you will see this insect for the first time. When you do see it, its size, speed and directness of flight make it unmistakeable but very easy to miss unless you know what you are looking for. In this respect the only comparable species would be *Cordulgaster boltonii*, which does occur in similar habitats, but is most certainly not the 'Sovereign of the River', having a much slower, more ponderous flight and settling often. The only other emerald that occurs with *M. splendens* is *Oxygastra curtisii* which looks similarly dark but has a much more hesitant flight and is much smaller.

The males of *M. splendens* fly low along the edges of stream or river bank at incredible speed (they never hover) at a fairly consistent height of between 300 and 600 mm above the surface of the water, often diverting into the bushes or crevices in their search for females. Cordero Rivera *et al*. (1999) carried out capture and marking experiments. They concluded that the males remain on the river for relatively short periods of up to 16 minutes and then, either for reasons of having successfully captured a female or simply to divert for feeding, they disappear. I was able to confirm this observation this year (2015) on the river Guadiaro in southern Spain. My visit was early in the season (21-23 May) when numbers of adults are quite low. The males were indeed on territory for around 15 minutes and then left. Later in the season (mid-June) other males would come in to take over the territory; indeed on the river Genal (a tributary of the Guadiaro) I have observed as many as seven males fighting for territory. The territorial behaviour is somewhat similar to that of *Cordulia aenea*. *M. splendens* arrives on the river early in the day and even in dull conditions the males can be seen patrolling as early as 08:00, when they are alone on the river. The first male will patrol a huge territory of up to 150 m in length or the full perimeter of a river pool. As other males arrive so the territory size reduces

A

B

Plate 6. *Macromia splendens* in flight. Photographs by Christina Chelmick.

but it never seems to fall much below 30 m in length. When two males meet they fly together and disappear from the river for a few seconds with only the dominant male returning. Cordero Rivera *et al*. (1999) and Graham Vick (pers. comm.) are of the view that the majority of adult activity on the breeding habitat takes place in the morning. However, my observations on the river Guadiaro are that *M. splendens* flies all day long from as early as 08:00 until 18:00. Between 13:30 and 15:30 adult numbers were low and there were times when the males were not present but adults were on territory throughout the day with no obvious reduction in the afternoon. In addition, the adults fly late into the evening. Gert de Nijf (pers. comm.) told of a recent trip to southern France where he watched *M. splendens* adults hunting almost until dusk over his campsite and away from the river. In much of northern Europe this behaviour would not be possible for more than a few days in the year as ambient evening temperatures would be too low.

In southern Spain, the first records of adults are from 1 May (Arturo Bernal pers. comm.). On the Guadiaro there are differences in flight period. The warmest of the three rivers, the Hozgarganta, has adults flying on territory from mid-May, whilst on the Genal and Guadiaro itself, the adults do not appear until the end of May and occur throughout June. I have been present in the valley in July but have never observed adult *M. splendens* at this time. In the north of Spain and in France the flight period is rather later in the year. Cordero Rivera *et al*. (1999) stated that, in Galicia, adults are on the wing until the end of July, with the earliest oviposition being recorded on 23 June. I observed oviposition on the river Hozgarganta on 23 May this year (2015). In France, Grand & Boudot (2006) stated that adults appear from mid June (exceptionally the end of May) and are present until the third week in August; in Poitou-Charentes in western France their peak of activity is during the first two weeks of August (Jourde & Laluque, 2006). Dommanget (2001) stated that water temperatures on the Tarn in France are around 21.5°C in July. Such temperatures are found on the Guadiaro in mid-May. It is therefore hardly surprising that the flight season is so different north to south.

In prime habitat you would think that *M. splendens* would be the dominant insect, with few rivals. The problem is *Anax imperator* (the Emperor Dragonfly). This latter species is a very aggressive territorial insect and rarely tolerates others of its, or any other, species. In Portugal, my colleague Peter Mitchell saw a *M. splendens* attack and kill a male *A. imperator* (Chelmick & Mitchell, 1996). This was an exceptional incident and usually, where *A. imperator* has established territory, *M. splendens* will keep out of the way. This *M. splendens*/*A.imperator* relationship on the river Guadiaro defines prime habitat for *M. splendens*. On stretches of river where one side is open *A. imperator* will dominate, whereas in stretches where both sides are enclosed either with bushes/trees or rocky cliffs

A. imperator appears less ‘comfortable’ and *M. splendens* takes over. Once the males leave the river they head off into the countryside to hunt or settle and where, if you are very fortunate, you will be able to observe the adult insect (Plate 7A, B).

Description The size of the adult insect (Dijkstra & Lewington 2006) is:

Total length	70-75 mm
Length of abdomen	48-55 mm
Length of hind wing	42-49 mm

In terms of overall size *M. splendens* is similar to *Cordulegaster boltonii* with which it bears a passing resemblance and which is the only dragonfly with which it could be confused. However, the yellow markings are much less extensive in *M. splendens*.

The abdomen of *M. splendens* is jet black with a yellow bar on the upperside of S2. In the male there are small yellow spots on S3 to S5 and a large yellow spot on S7 and a slightly smaller yellow spot on S8 (Plates 7, 8A, 9). The female has yellow spots on S3-S7 (Plates 8B, 9). Cordero Rivera *et al*. (1999) noted considerable variation in the yellow spots on the dorsal surface of segments 7 & 8 of the abdomen. I have not seen this variation in the Guadiaro populations, which are invariably consistent with the example shown in Plates 7 & 8. The thorax is dark metallic green with a strong yellow band running between the wings. There is a yellow crescent in front of the forewings and two strong yellow lines along the top of the thorax. The legs are long and black. The wings have a light coloured costa and thin black pterostigma. There are extensive yellow markings on the frons and mandibles. The eyes range from bright green to bluish green.

Interestingly, eye colour provides an example of just how the study of this insect has been so neglected. The first attempt at an illustration of the living *M. splendens* is provided in Aguesse (1968). The planches [plates] for this work were produced by Paul Robert, a gifted entomological illustrator. His plate 5 shows *M. splendens* (Plate 10). The irridescent green thorax and black abdomen are accurate but the eye colour is predominantly brown, as of a newly emerged insect or, more likely, of a dead collected specimen. Entomology at the time of Aguesse was almost exclusively based upon collecting; little time was spent in observing the living insect. It is quite possible that Robert was unaware of any non-structural colouration; the beautiful green/blue eyes (Plate 7) losing colour on death. What is more remarkable is that the brown eyes were featured in all identification works until Dijkstra & Lewington (2006) showed the green of the living insect.

A

B

Plate 7. Adult males of *Macromia splendens* (A) from southern Spain, (B) from near Caceres in Extremadura, Spain. (B) Photograph by Isidro Frutos.

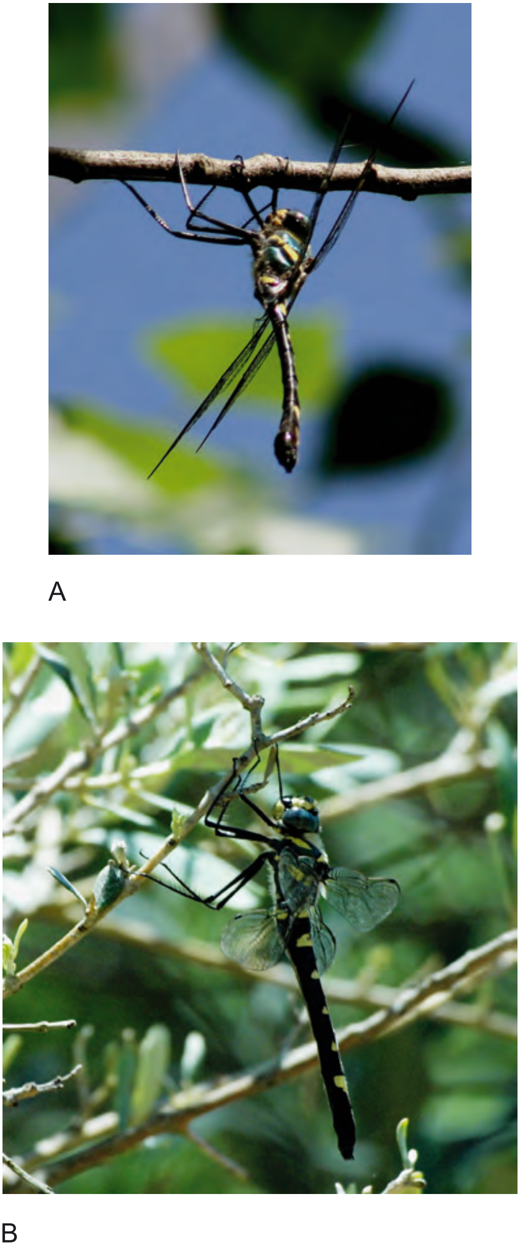

Plate 8. Adults of *Macromia splendens* in southern Spain (A) Male high in the trees by the Rio Genal, (B) female on the “Campo” of the Rio Genal. (A) Photograph by Bryan Pickess.

Plate 9. A pair of *Macromia splendens* in the wheel position (in cop.) near Caceres in Extremadura, Spain. Photograph by Isidro Frutos.

Robert's illustration (Aguesse, 1968) also shows *M. splendens* perched on a rock face (Plate 10). I have never observed it resting in this position, those long legs being far more suited for suspension rather than for perching. Once again it is quite probable that Robert was unfamiliar with the habits of this enigmatic insect and had to create its life habits from his own imagination.

What are the chances of finding adult *M. splendens* settled? I have been studying this insect on the river Guadiaro since 2003: in total around 100 days of field work, mostly during the flight season. I have seen settled *M. splendens* on only a handful of occasions and in all cases it was pure serendipity; a female settled on a bush taking a break from hunting (Plate 8B). Peter Mitchell spotted a male settle on a tree next to the Rio Genal and Bryan Pickess managed to take a good set of pictures (Plate 8A).

Plate 10. Paul Robert's illustration of *Macromia splendens.* From Aguesse (1968).

The task of finding a settled *M. splendens* is, therefore, quite daunting. However, my friend Arturo Bernal took me to a site in Southern Spain where the river is hard to observe but the adjacent 'campo' as it is known in Spanish, is dominated by low shrubs and adjacent pasture. In mid-June, when the adult population is high, there is presumably considerable competition for river territories, leaving many adults to wait their turn and hunt or rest. Due to the low scrub the adults can be observed hunting and, more importantly, laying up settled at photographable height, the insects quite indifferent to the many lenses pointed at them at close proximity.

Reproduction and Oviposition

Female emerald dragonflies are always hard to observe; they return to the water to find a mate and, after mating, only to lay their eggs. When a male is successful and catches a female the pair immediately fly high into the trees where copulation takes place and where detailed observation is impossible. I have observed this behaviour on a frustratingly large number of occasions. Indeed, up until this year copulation had hardly ever been observed and only, to my knowledge, photographed once (Cordero Rivera *et al*., 1999) and this obtained by tethering a female using the fishing line technique. One male captured the female and mated for about 10 minutes and soon after a second male was in copula for only 2 minutes. However, this year following the first Iberian symposium on Odonata (SIO) in Cordoba in May, I was introduced to an encouragingly large number of Spanish Odonatologists. One of them, Isidro Frutos, posted a number of superb pictures of *M. splendens* on Facebook, including some in copula (Plate 9), taken on 7 June 2015, at what Isidro describes as the 'Paraiso de *Macromia*' (*Macromia* heaven) near Caceres in Extremadura, Spain. Such photographs will hopefully encourage other observers to look for this natural copula. My experience of copulation only occurring high in the trees is clearly not always the case.

After mating, the females try to avoid contact with the males and hence oviposition is a very fleeting process. The females visit the water when males are away, often very early in the morning or late in the afternoon, flying in and dipping their abdomens into the water four of five times before disappearing. If they are present for longer than a minute this is unusual. The females appear to prefer to oviposit around rocks or where trees have fallen into the water. I mentioned above how *A. imperator* can cause problems for *M. splendens* when on territory but it can work the other way! On my recent trip I was watching a female *A. imperator* ovipositing at a large pool; after a few moments a female *M. splendens* flew almost to my feet and started her random oviposition flight, which lasted for no more than 30 seconds. As the *M. splendens* left so also did the *A. imperator* fly up and disappear from the river, only reappearing some minutes later. It was as though the *A. imperator* female had been disturbed by the presence of the *M. splendens*.

Habitat

Macromia splendens has a two year larval life and requires permanent water. Most reference works consider it to be a riverine species, although its need for moving water is unclear. Grand & Boudot (2005) stated that, in France, the insect occurs in calm sections of large rivers, hydroelectric barrages and small streams with deep pools. Cordero Rivera *et al*. (1999) found a colony on a reservoir and hence it appears that flowing water is not the principal requirement. Indeed Dommanget (2001) (see above) has shown how suited *M. splendens* is to these man-made habitats. On the river Guadiaro, and in particular on its tributary the Genal, the most favoured stretches are those that are artificially maintained at a high water level with temporary dams that are created for the summer holiday makers. In the most important *M. splendens* stretch on the river Genal, where up to seven males have been seen competing, this narrow stretch of river is hemmed in by rock on one side and by trees on the other (Plate 11A). This appears to inhibit *Anax imperator* but holds no fears for *M. splendens*, which dominates this part of the river. The dam (Plate 11B) provides an open area where *A. imperator* is dominant. However, it also maintains the depth of water in the narrow section of the river essential for *M. splendens*. My colleague Paul Winter (pers comm.) visited this site in early June 2015. On June 11 there was no dam and no *M. splendens* on the main stretch of river. He visited again two days later after the dam had been rebuilt and deep water prevailed. To his delight, patrolling *M. splendens* was present. The creation of the dam may also explain why this site, so good for adults, produces very few exuviae. The adults certainly breed here but, presumably, as the dam deteriorates over the winter so the larvae are washed down river into the deeper pools where they develop.

Large rivers are not by any means the only habitats. The Rio Hozgarganta in late summer is little more than a series of deep pools and, it would appear that, so long as the pools are permanent, *M. splendens* larvae can survive. Even quite narrow streams, as long as there are deep pools, are frequented by the adult insects and I have also found larvae in such small habitats.

Conservation

In the European Red List of dragonflies (Kalkman *et al*., 2010) *Macromia splendens* is categorised as Vulnerable and, therefore, with a moderate risk of extinction. Contrarily, its known range has greatly increased in recent years but this, as has been explained above, is the result of much increased recording. The principal requirement appears to be warm, lowland streams and rivers with deep permanent pools so that the larvae can complete their two year life cycle. Pollution must historically have been a problem, particularly in Iberia where rivers were treated as garbage dumps. This situation is now much improved and environmental awareness is now very high on the Spanish agenda, with *M. splendens* almost certainly capable of flourishing in a much wider range of rivers today than historically. One other way that man has helped *M. splendens* is in the construction of barrages which provide deep river sections and reduce flow rates. This is true both in France, where many of the favoured rivers have small barrages for hydroelectric schemes, and in Spain where, in order to attract visitors, temporary summer barrages are erected, usually just in time for breeding *M. splendens*. It is encouraging to note that man, in his attempts to attract more people to rivers, is also inadvertently attracting *M. splendens*. Long may this situation continue.

A

B

Plate 11. (A) The most important *Macromia splendens* stretch on the Rio Genal, southern Spain, (B) The Rio Genal showing the dam created for holiday makers.

Acknowledgements

None of this work would have been possible without the understanding and infinite patience of my wife Christina, who has the added bonus of being a professional photographer and providing me with the stunning flight shots of *M. splendens*. Jean-Pierre Boudot has been of great assistance in providing information and encouragement. Isidro Frutos has kindly allowed me to use his superb photos. I must thank my friends who have accompanied me on trips to Spain for their patience and understanding in the search for this elusive insect; Peter Mitchell deserves a special mention as he has been on almost all of my trips and whose sharp eye first spotted a settled *M. splendens*. Bryan Pickess has helped with much of the habitat description and in the identification of plants. Fons Peels, Anthony Winchester, Roger Wicks and John Luck have all assisted and finally thanks to Arturo Bernal for his local knowledge.

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Ultrastructural evidence for antennal chemoreceptors in *Aeshna grandis* L. (Brown Hawker)

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Summary

The results of an SEM investigation of the antennae of larval and adult *Aeshna grandis* (Brown Hawker) have revealed that both larva and adult possess a range of sensilla and that the morphological structures present are similar to those found in investigations carried out on other odonate species. While a chemoreceptive ability cannot be concluded categorically, from a structural view point both the larvae and adults of *A. grandis* possess *sensilla coeloconica*, which have often been associated with chemoreception. From the existing body of work it is likely that odonate larvae and adults use a more diverse range of cues than previously thought during searching, feeding and habitat choice, one of which is chemoreception.

Introduction

Odonates have long been considered to locate their prey visually and indeed have large eyes to aid this. However, there is evidence that both adult and larval odonates can also use tactile and chemical stimuli and the antennae are an obvious location for both types of receptor. Thus chemosensory recognition of predators has been demonstrated in larvae of *Enallagma* sp. (Chivers *et a*l., 1996) and of prey in adults of *Ischnura elegans* (Blue-tailed Damselfly) (Piersanti *et al*., 2014a). Furthermore, an olfactory response to various volatile chemicals by the antennae of adult *Libellula depressa* (Broad-bodied Chaser) and *Ischnura elegans* has been demonstrated electrophysiologically (Rebora *et al*., 2012; Piersanti *et al*. 2014b). Sensilla on the antennae have also been shown to have a hygroreceptive function in both larvae (Rebora *et al*., 2007) and adults (Piersanti *et al*., 2011) of *Libellula depressa*.

Tactile or mechanical stimuli are perceived by sensilla formed from deformable cuticular protrusions (hairs). These hairs are modified in various ways but in each case the dendrite of a sensory neuron is attached at the base of the hair. Keil (1998) has reviewed the nature of these hair-like structures in insects, where the simplest are the *sensilla trichodea*. The shaft acts as a lever, reducing large deflections to small movements at its base. It can move in almost any direction (Tautz, 1977; Keil & Steinbrecht, 1984; Barth, 1986). *Sensilla chaetica* are similar, also with a tactile function (Schoonhoven, 1967; Albert, 1980; Zacharuk, 1980; Baker *et al*., 1986; Faucheux, 1995). *Sensilla filliformia* retain a hair-like form but their movement is restricted by a cuticular cup surrounding the base (Keil, 1998). They are very sensitive and can only be deflected in one plane and have the same function as the trichobothria of arachnids, responding to air currents and to low-frequency air vibrations (Gnatzy & Schmidt, 1971; Harris & Mill, 1977; Gnatzy & Tautz, 1980). Campaniform sensilla (*sensilla campaniformia*) lack the hair shaft and respond to deformation of the cuticle, thereby sensing cuticular stresses. Little seems to be known about the flask-shaped *sensilla ampulliformia* but they may also be tactile receptors.

Olfactory/gustatory information (chemoreception) in insects is received by modified hairs. Specialised trichoid sensilla have pores on the sensilla shaft or have one at its tip and these are innervated by neurons, the dendrites of which run into the shaft. Rebora *et al*. (2010) have described what they refer to as porous and aporous sensilla on the latero-ventral surface of the antennae of adult odonates. The former consist of porous pegs in shallow pits (*sensilla coeloconica*) with three dendrites entering the peg. Rebora *et al*. (2010) suggested that these are olfactory sensilla. The numbers of pegs in the pits determine whether they are called simple or compound *sensilla coeloconica*. Gaino & Rebora (2001) defined a compound coeloconic sensillum as being innervated by two groups of three neurons which fill the lumen of the peg. The aporous sensilla are also peg sensilla but they are located inside deep cavities and the pegs are on a cuticular protrusion (*sensilla styloconica*). There are two types of styloconic sensilla, one of which has four dendrites entering the peg (Type 1); the other has three dendrites (Type 2) (Piersant *et al*., 2011). Rebora *et al*. (2010) suggested that they may be thermo-hygroreceptors. Some *sensilla basiconica* may also be involved in this function (Schoonhoven, 1967), whereas others have been reported to have an olfactory function (Zacharuk, 1980; Sun *et al*., 2011). It is also possible that some of the *sensilla trichodea* may be contact chemoreceptors, with one dendrite attached at the base of the shaft to detect movement and others entering the shaft to detect chemical stimuli.

A range of receptor structures has been described for odonates. On the antennae these receptors include *sensilla trichodea*, *s. chaetica*, *s. filliformia*, *s. basiconica*, *s campaniformia* and *s. ampulliformia* (Crespo, 2011). In adult *Libellula depressa* the flagellum has both *sensilla coeloconica* and two types of *sensilla styloconica*, the latter being located in deep pits (Rebora *et al*., 2008). Contact chemoreceptors have been located on the cutting valves of the ovipositor in *Aeshna cyanea* (Southern Hawker) and *Ischnura elegans* (Rebora *et al*., 2013) and on the epipharynx of the labium in *Ischnura elegans* (Rebora *et al*., 2014).

Hence a chemosensory capacity is becoming apparent as part of the sensory tools of odonates. Indeed a recent study on the behaviour of larvae of *Aeshna grandis* has demonstrated their ability to respond to chemical stimuli (Coulter *et al*., in prep.). To further explore the possibility of chemoreception a morphological examination of the antennal structure of *Aeshna grandis* was carried out.

Materials and methods

A Field Emissions Incorporated (FEI) Inspect S50™ Scanning Electron Microscope (SEM) was used. Low vacuum was used for general morphology. For more detailed examination of individual receptors, a high vacuum was used after pre-treatment of the specimen with hexamethyldisilazane (HMDS). HMDS enables a specimen to be dried while retaining its original dimensions and morphology and gives results comparable to those obtained using critical point drying (Bray *et al*., 2005).

Sample preparation

The antennal structures were examined on six adults and eight larvae of *Aeshna grandis*, the head capsule widths of the latter ranging from 3.5mm to 4.8mm. Each antenna was immersed in approximately 100 µl of HMDS and placed in a fume cupboard for 20 minutes to allow the HMDS to evaporate. Both head capsules and individual antennae were mounted on stubs, using stub mounting pads. Scanning electron micrographs (SEMs) were taken at a range of settings.

Results

The similarity of the gross antennal structure in both adults and larvae was confirmed (Plates 1, 2). Investigation of the antennal fine morphological structure indicated a distinct change between the larval and adult stages, both in the overall antennal structure and in the types of sensory structures present. In both stages the antenna comprises a scape, a pedicel and a jointed flagellum. The last is just over 1 mm long in the larva and the flagellomeres are at most 3.5 x as long as they are wide. In the adult, the flagellum is over 2 mm long and is much more slender than in the larva, with flagellomeres being at least 10 x as long as they are wide.

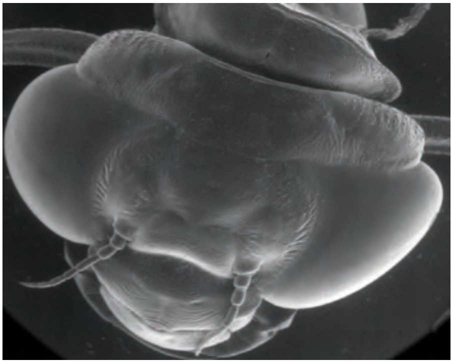

Plate 1. The head of a larval *Aeshna grandis* showing the antennae.

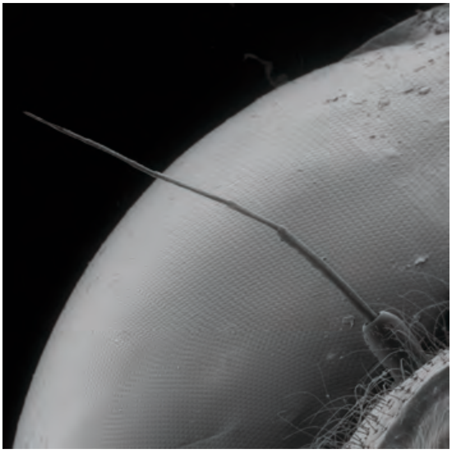

Plate 2. The head of an adult *Aeshna grandis* showing one of the antennae.

Larva

The larval antenna possesses a range of sensory hairs (*sensilla trichodea*) of various sizes along its length, some of which are long and slender, extending for almost the full length of a flagellomere (Plate 3) while others are somewhat shorter (Plates 4, 5); There is also a hair at the tip of the flagellum (terminal hair) (Plate 5). In addition there are short pegs (modified hairs), ranging in length from 0.8µm to 12.5µm, which project from small pits (*sensilla coeloconica*) (Plates 4, 6). One of these is located on the posterior side near the tip of the distal flagellomere (Plates 5, 7). S*ensilla coeloconica* were not found on the scape or the pedicel.

Adult

The adult flagellum does not possess *sensilla trichodea* along its surface and there is no terminal hair. However, it does possess an array of single and compound *sensilla coeloconica* (Plate 8) on the lateral and ventral sides of the flagellomeres. There are more *sensilla coeloconica* on the adult flagellum than on the larval one and some of those on the adult flagellum are larger, their pegs ranging in length from 2.0µm to 20.5µm. The adult antenna has an expanded flagellomere socket where it meets the pedicel and there are a large number of small projections located within the socket (Plate 9).

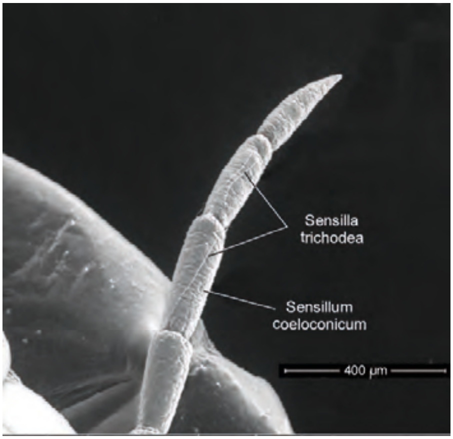

Plate 3. The distal flagellomeres of an antenna of a larval *Aeshna grandis* showing long *sensilla trichodea* and a *sensillum coeloconicum.*

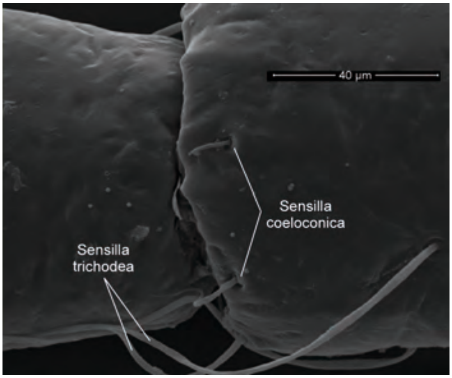

Plate 4. The junction between two flagellomeres of a larval *Aeshna grandis* to show short *sensilla trichodea* and two *sensilla coeloconica*, each with its projecting short peg.

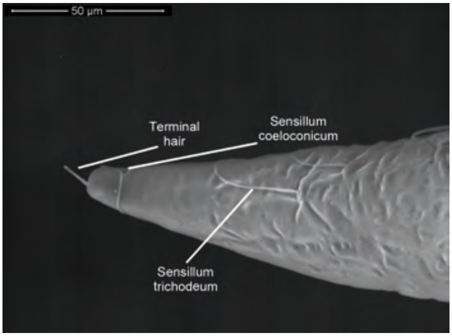

Plate 5. The terminal hair (*sensillum trichodeum*) and the sub-terminal s*ensillum coeloconicum* on the last flagellomere of the antenna of a larval *Aeshna grandis*.

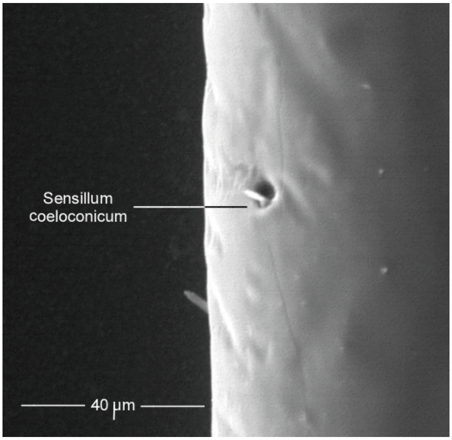

Plate 6. A *sensillum coeloconicum* with a small peg on the flagellomere of an antenna of a larval *Aeshna grandis*.

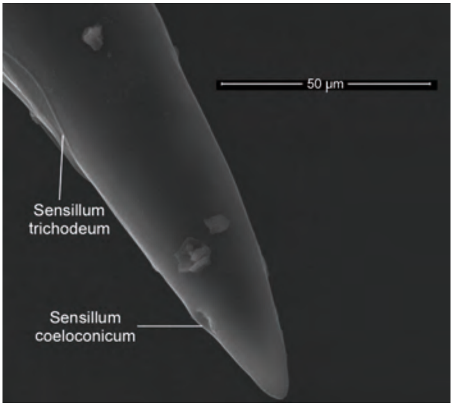

Plate 7. The sub-terminal *sensillum coeloconicum* on the last flagellomere of an antenna of a larval *Aeshna grandis.*

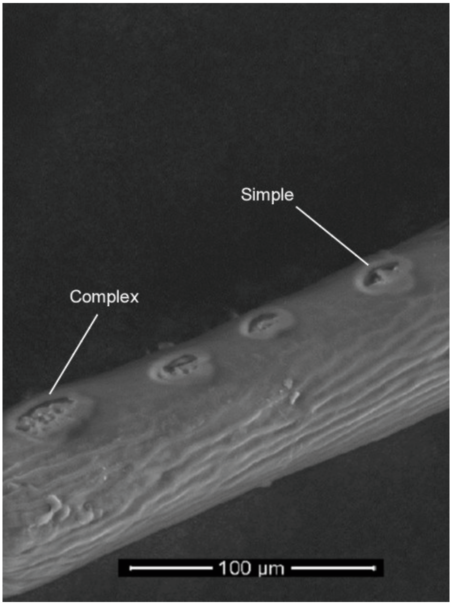

Plate 8. Simple and complex *sensilla coeloconica* on an antenna of an adult *Aeshna grandis*.

Discussion

Sensory receptors

The evidence that Odonata possess a chemosensory capacity and utilise it for assessing their habitats and for seeking food is building. The current study of *Aeshna grandis* has demonstrated that the antennae of both the larva and the adult possess a range of sensilla, the morphological structures of which are similar to those found in other odonates (Slifer & Sekhon 1972; Rebora *et al*., 2007, 2010, 2013). This current research on *A. grandis* has also shown that there is a difference in the sensilla present in larvae and adults of this species.

Larva

Aeshna grandis larvae, as in other odonates, possess more than one type of sensillum on their antennae - *sensilla trichodea* and *sensilla coeloconica*, one of the former being a terminal hair. Long trichoid sensilla of the type found in *A. grandis* are generally considered to detect mechanical stimuli (Tautz, 1977; Keil, 1998; Barth, 1986). However, some long thin sensilla are known to function

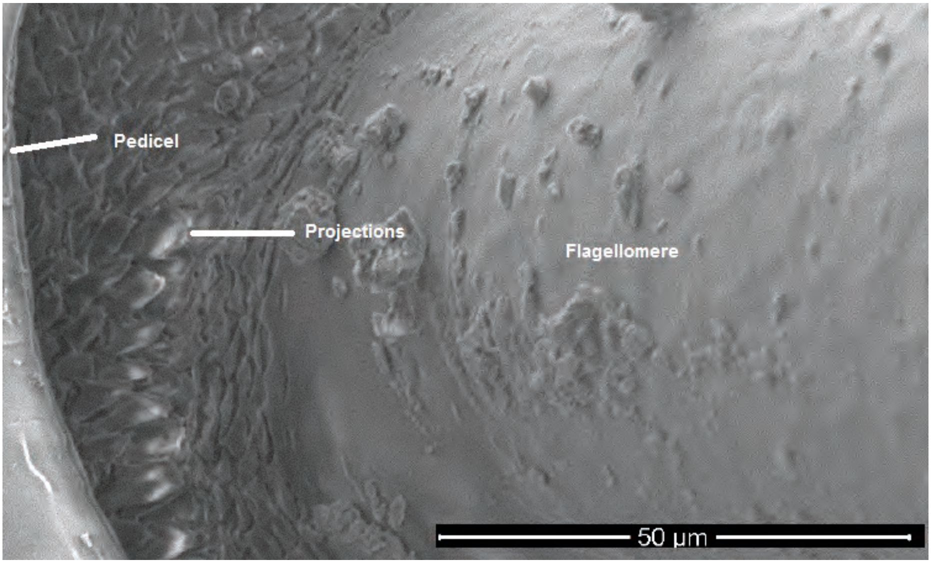

Plate 9. The antennal pedicel-flagellar junction of an adult *Aeshna grandis* to show small projections with 'toothed' tips in the socket.

as contact chemoreceptors, monitoring both movement and chemical stimuli, as has been found in arachnids (Harris & Mill, 1977) and aquatic turbellarians (Hardege, 1999; Hardege *et al*., 2004). The terminal hair on the antennae of *A. grandis* is in a good position to act as a contact chemoreceptor.

In larvae, the *sensilla coeloconica* have been ascribed a dual function: thermoreception (Rebora *et al*., 2007; Piersanti *et al*., 2011) and hygroreception (Rebora *et al*., 2007). Rebora *et al*. (2007) studied *Libellula depressa* and suggested that the hygroreceptive function may enable larvae to detect residual areas of water or moist areas when ponds start to dry out. This function was confirmed behaviourally by Piersanti *et al*. (2007). The small, single *sensilla coeloconica* on the terminal antennal segment and those along the surface of the antennae of *A. grandis* may also have a chemosensory function (Gaino & Rebora, 1999, 2001).

Enallagma spp. have been shown to demonstrate chemosensory recognition of predators (Chivers *et al*., 1996). Fulan & Almeida (2010) showed that odonate larvae actively moved towards dead tadpoles and, in a recent study (Coulter *et al.,* in prep), *A. grandis* has been shown capable of detecting dead prey in the absence of any visual stimulus.

Adult

Structures have been identified on the antenna of many adult odonates. Thus Slifer & Sekhon (1972) examined the antennal flagella of six species of zygopteran and 11 species of anisopteran (excluding *Aeshna grandis*) and found both simple and compound *sensilla coeloconica* on the flagella, and that these were more numerous in anisopterans than in zygopterans. More than one type of peg was present in the pits while pores were present in the wall of some of the pegs. *Aeshna umbrosa* (Shadow Darner) has six single *sensilla coeloconica* and 10 compound *sensilla coeloconica* on its antennae (Slifer & Sekhon, 1972). Rebora *et al*. (2008) noted that the structure of the *sensilla coeloconica* is in accord with known insect chemoreceptors. In *A. grandis* both simple and complex *sensilla coeloconica* were found in the present study. Chemoreceptors are also noted elsewhere on the odonate body. Thus probable contact chemoreceptors have been found on the cutting valves of the ovipositor, possibly being important for detecting suitable oviposition sites (Rebora *et al*., 2013), and on the epipharynx of the labrum (Rebora *et al*., 2014).

Although *sensilla styloconica* appear to be absent from *A. grandis* antennae, they have been described on the antennae of several odonates (Rebora *et al*., 2008, 2010). It was suggested by Rebora *et al*. (2008) that they have a thermo/hygroreceptive function and the presence of this sensory modality by receptors on the antennae was confirmed by Piersanti *et al*. (2011).

Chemosensory recognition of prey has been demonstrated in *Ischnura elegans* and there are sensilla on the antennae which respond to prey odour (Piersanti *et al*., 2014a). These researchers also showed that antennal sense organs in both *I. elegans* and *Libellula depressa* responded to a variety of odours (Rebora *et al*., 2012; Piersanti *et al*., 2014b).

In behavioural studies on *Orthetrum cancellatum* (Black-tailed Skimmer) Gewecke *et al*. (1974) and Gewecke & Odendahl (2004) highlighted the importance of the scape and the pedicel in air speed perception and flight control. This suggests that the projections identified in the *A. grandis* pedicel-flagellomere socket could have a role to play in this context.

Electrophysiological investigations have been carried out on adult dragonflies which appear to show they respond to plant volatiles, hypothesised to be used for detecting suitable oviposition sites (Rebora *et al*., 2013). Piersanti *et al*. (2014b) explored the responses of *I. elegans* and *L. depressa* adults to a range of aldehydes, carboxylic acids and amines. The tested substances included green vegetation volatiles, decomposition chemicals such as ammonia, and the odours of waterborne bacteria associated with the breakdown of organic material in ponds and other standing water bodies. They noted a very small difference in response between males and females of the species tested. This ability to respond to odours from decomposing material is significant in terms of the chemosensory response which might be expected from *A. grandis.* This species is known to place its eggs in the crevices of submerged logs (Corbet *et al.*, 1960) and other locations with rotting or long submerged wood (Tyrrell, 2004). Equally, the recognition of plant volatiles as indicative of habitats for suitable prey is exemplified in this species by observations made by Cham & Banks (1986). They noted, in two separate locations, instances of *A. grandis* adults repeatedly brushing against nettles (*Urtica dioica*) in order to disturb chironomid flies – a potential food source, concealed beneath their leaves. Since sight was unlikely to be the initial trigger for such action, chemoreception may have drawn the adult dragonflies to the location, although it cannot be ruled out that they may have encountered the chironomids by chance.

Hence a chemosensory capacity is becoming apparent as part of the sensory tools of odonates and *Aeshna grandis* appears to be a further exemplar of an odonate species in which visual, mechanical and chemical stimuli may play a role in determining the presence and suitability of food; also possibly habitat and oviposition sites.

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