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Cover illustration: Immature female of *Sympetrum fonscolombii*. Photograph by Terry Crow.

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Migrant and dispersive dragonflies in Britain during 2021

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Summary

The 2021 reporting year was a relatively eventful one for migrant and dispersive species in Britain. *Anax ephippiger* continued its recent run of autumn influxes, with well-documented records from nearly 20 localities between 9 September and 22 November, and with several 'possibles' also being reported. *Sympetrum fonscolombii* showed well during spring and early summer, with all but one individual being fully mature when first discovered, rather implying that most individuals were immigrants rather than locally bred. Perhaps surprisingly there were, however, few autumn records of the species, implying that both the emergence of a locally bred second generation and also any late season immigration had been limited. Of our other traditional migrant species, *Anax parthenope* and *Aeshna affinis* were both widely reported during the year, but the growing strength of local breeding populations that have become established over the last decade or so made detailed analysis of migration difficult, particularly in the case of *A. parthenope*.

In addition to conventional migrants, *Aeshna isoceles* continued its recent range expansion, with a sighting at Wykeham Lakes in North Yorkshire on 20 July being of particular note. At least some of this expansion may be being driven by immigration from the Continent, but increased internal dispersal must be a major factor. During 2021 there was also evidence for significant mid- to long-distance dispersal within Britain by several other species. *Calopteryx virgo,* for example, appeared on the Isles of Scilly during late August, some 45 kilometres away from the nearest known breeding sites on the Cornish mainland. A male *Orthetrum cancellatum* was also recorded from Scilly during the year, this being only the second record for the islands.

Finally, it is worth noting that *Chalcolestes viridis*, one of Britain's recent colonist damselflies, had yet another successful season with considerable range expansion, particularly in a north westerly direction. An individual seen near Wolverhampton on 23 September represents the new "most westerly" sighting for Britain while, further south, three records in the general area of the New Forest are also of note.

Account of species

Notable sightings reported to the BDS Migrant Dragonfly Project during 2021 are detailed below; for information on events during 2020, see Parr (2021).

Chalcolestes viridis (Vander Linden) – Willow Emerald Damselfly

Chalcolestes viridis continued its rapid range expansion in England, with areas such as Leicestershire, Nottinghamshire, Derbyshire and many parts of Yorkshire as far north as Scarborough producing good numbers of new sightings (Fig. 1). The most westerly record for *C. viridis* in Britain is now from Smestow Valley Nature Reserve on the western edge of Wolverhampton, where a male was seen on 23 September (JCa). Although no new 'most northerly' British record was set during 2021, two sightings from the Youlton area of North Yorkshire during mid-September (LBo), one from nearby Staveley Nature Reserve on 8 October (KGt *et al.*) and one from Gilling Lakes on 10 October (KGt) are of some note. Further south in England, expansion appeared more limited, though there were three reports from the general area of the New Forest, significantly to the west of past sightings. These records involved a female at Titchfield Haven, Hampshire, on 6 September (EP), a male near Verwood, Hampshire, on 15 September (MGa) and a male at Franchises Lodge, Wiltshire, on 26 September (SLe). This isolated cluster of records towards the south coast may perhaps indicate a recent fresh colonisation event, but more likely their apparent isolation simply reflects a degree of under-recording in intervening areas closer to the species' main range.

Lestes barbarus (Fab.) – Southern Emerald Damselfly

The species had probably its best ever year in Britain, with records from 15 sites in south-east England between the Isle of Wight and Norfolk. Reports came from almost all the known recently active breeding sites, though not from the inland colony near Beaconsfield in Buckinghamshire (Parr, 2019), which may now have become extinct following continuing habitat disruption. Although representing new site records, several sightings from the Hoo Peninsula in north Kent were also in the general vicinity of known breeding sites. This may indicate that, since the species is quite easily overlooked, *Lestes barbarus* may well be more strongly established in the greater Thames Estuary area than is currently appreciated. Records of single females at Shoeburyness east beach, Essex, on 10 July (MO) and nearby Gunners Park on 3 August (AAr) may similarly hint at a local breeding site, though could reflect fresh immigration. Clearer evidence for internal dispersal or fresh immigration during 2021 was provided by the sighting of a female near the Norfolk coast at Beeston Common over 19–23 August (FF *et al*.), with ovipositing being noted there on at least one occasion. Other

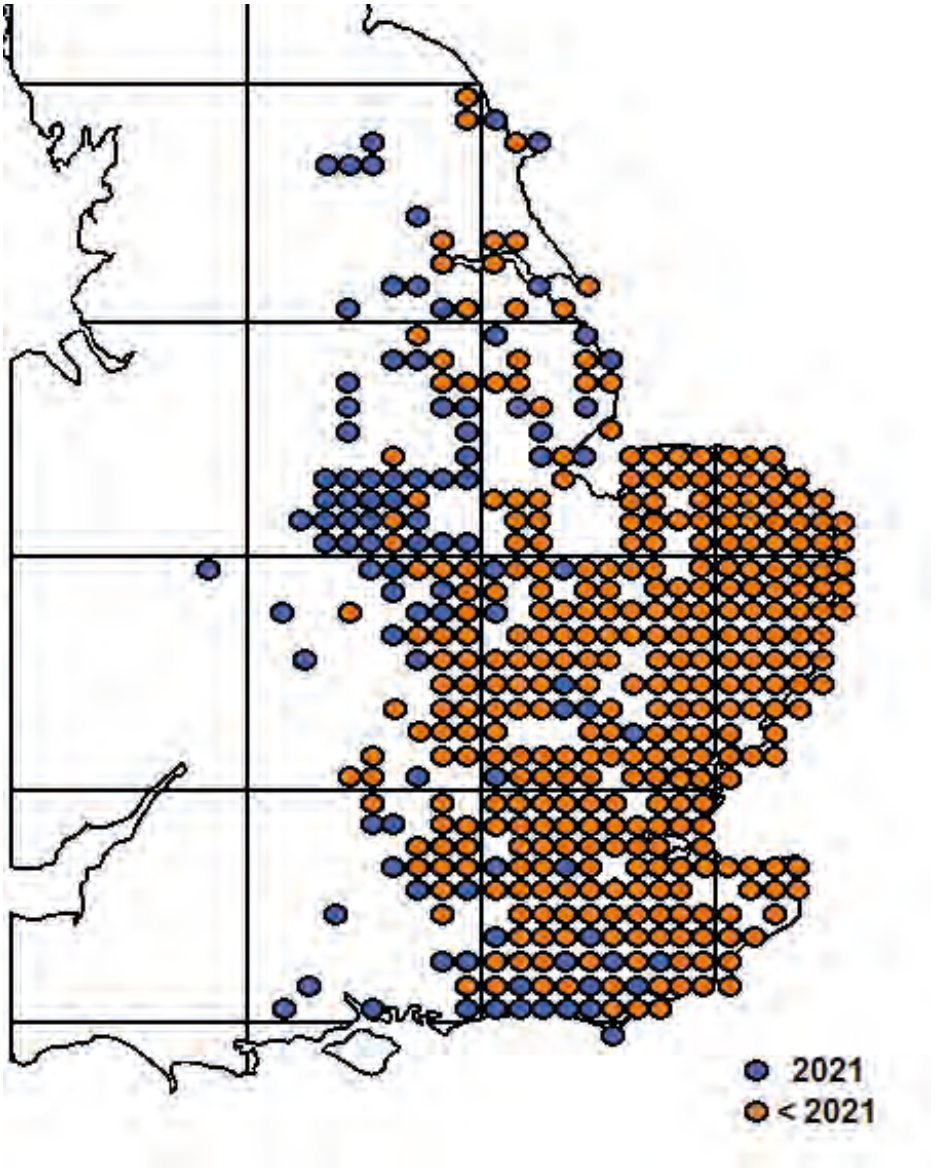

Figure 1. Distribution of *Chalcolestes viridis* (by 10×10 km grid squares), showing new areas producing records during 2021.

Plate 1. *Lestes dryas* (male). Landguard, Suffolk, 17 July 2021. Photograph by W. Brame.

records from entirely novel areas involved a female photographed at Denbies Hill in Surrey on 18 July (LS), another female at St Albans, Hertfordshire, on 21 July (RE) and an individual seen near Wickham, Hampshire, on 10 August (TB). The fact that most/all these unexpected sightings relate to females is of some interest.

Lestes dryas Kirby – Scarce Emerald Damselfly

There were several records from unexpected sites on the East Anglian coast during 2021. In Norfolk, a singleton was seen at Overstrand on 15 August (SLw), with 1–2 then seen at Beeston Common during the period 20–23 August (SCh, FF *et al*.). Up to two were also noted at Landguard Bird Observatory in Suffolk over 15–18 July (WB, NO) with another individual present on 20 August (WB). These sightings likely result from influxes of some description; the simultaneous appearance of both *L. barbarus* and *L. dryas* at Beeston Common should be noted.

***Calopteryx virgo* L. – Beautiful Demoiselle**

A male photographed at Porth Hellick, St Mary's, Isles of Scilly, on 27 August (MGo) is one of very few records from the Islands; it was presumably a wanderer from the Cornish mainland, some 45 km away.

***Coenagrion scitulum* (Rambur) – Dainty Damselfly**

Coenagrion scitulum recolonised Britain around 2010, after having become locally extinct back in 1952/53 (Cham *et al*., 2014). A new site for the species was discovered in Kent during 2021, with small numbers being seen at the Oare Marshes (CC, SWe). This site is in the general area of other recent sites and is likely to result from natural range expansion rather than fresh immigration.

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

There were signs of possible immigration noted on the Norfolk coast during high summer. Singletons were reported from Salthouse beach on 31 July (SLw) and Happisburgh cliffs on 15 August (SWi). A few miles further south, 100+ were noted at Winterton Dunes on 10 August (BJ) and 15 August (SRl); these are unusually high counts for the area.

***Ischnura pumilio* (Charp.) – Scarce Blue-tailed Damselfly**

Following reports from several new areas for the species during 2020 (Parr, 2021), the current reporting year had fewer highlights. Several of the new sites discovered during 2020 produced no further records in 2021, though thriving colonies had clearly become established at others. Interestingly, at Sompting in West Sussex successful emergences were noted in May, but very few females were then seen during the year (Sadler & Chelmick, 2022), many probably dispersing away as the local habitat became less optimal for the species. Despite the quieter year, a few unusual sightings were still made during 2021; a male photographed at Stoke Park in Bristol, Gloucestershire, on 23 June (LBl) was apparently the first record for Bristol, while another male was photographed in the Crown Estate Field at Portland Bill, Dorset, during late August (JM). At least ten individuals were also noted at Didcot, Oxfordshire (though Vice County 22, Berkshire), on 2 July (IL); although this is the first site record and one of only very few records for the modern county of Oxfordshire, the numbers seen perhaps suggest the presence of an already established breeding colony, just possibly established during the events of 2020.

Aeshna affinis (Vander Linden) – Southern Migrant Hawker

During 2021, *Aeshna affinis* was recorded from a wide scatter of sites involving 17 counties in England; these were principally along the south coast and in East Anglia, but there were also scattered records as far north as East Yorkshire and Cheshire. In addition, there was one sighting from Wales, in Pembrokeshire. Breeding colonies are no longer restricted to the Thames Estuary strongholds established during the species' initial colonisation of England just over a decade ago, and sites such as Hempsted in Gloucestershire, Otmoor in Oxfordshire, Quy Fen in Cambridgeshire and Winchelsea in East Sussex continued to produce sightings. Several other records away from the Kent/Essex area likely also refer to locally bred individuals. Certainly, an immature male was photographed at West Rise Marsh near Eastbourne, East Sussex, on 3 July (KGl) and a teneral and exuvia were discovered at Landguard, Suffolk, on 5 July (WB).

Substantial migration also clearly took place during the year. Unexpected sightings came from the south-west coast of England at Beer Head in Devon on 2 August (SWa), Portland Bill in Dorset on 3 August (KD), Studland in Dorset on 4 August (EW) and Worbarrow in Dorset on 6 August (JA). There then followed further unexpected coastal reports from Spurn in East Yorkshire on 10 August (DB), the West Bexington area of Dorset over 20 August–6 September (MM, WA *et al*.), Hilbre Island in Cheshire on 25–26 August (CWi, AC) and from at least seven sites in west Cornwall towards the end of August and into early September (AB, CM, SRe, MWa, DW *et al*.), with a male also being photographed on St Mary's, Isles of Scilly, on 1 September (KW). Late season records saw individuals reported from the Langton Herring/Herbury area of Dorset over 11–20 September (MPp) and a male was seen at Dale Airfield, Pembrokeshire, on 14 September (PG) – this being one of very few current Welsh records. Reports from sites such as West Bexington and Herbury in Dorset and Marazion in Cornwall (CM) involved multiple individuals, and with mating being noted it seems possible that further new breeding colonies may become established as a result of the movements seen during 2021.

Aeshna isoceles (Müller) – Norfolk Hawker

Following records from the site during 2020 (Parr, 2021), *Aeshna isoceles* was again reported in numbers from the Radipole area of Dorset and a self-supporting breeding colony is apparently now present there. Between 8 June–19 July, up to ten *A. isoceles* were also reported from the Chichester Canal in West Sussex, less than 10 km away from Medmerry Nature Reserve where an individual had been seen in 2019 (Parr, 2020). This is highly suggestive of a breeding colony having now also become established in the area. Elsewhere, there were further signs of continuing range expansion. Records came from

Plate 2. *Aeshna affinis* (ovipositing pair). Marazion, Cornwall, 11 September 2021. Photograph by C. Moore.

pretty much the entire coastal strip of Suffolk, with very large numbers present in the Felixstowe Ferry area on 16 June (MPo). Elsewhere, individuals were seen at Amberley Wild Brooks in West Sussex on 3 June (KGt), Eastbourne (West Rise Marsh) in East Sussex on 13–17 June (KGl, SLi, MGo), Dungeness in Kent on 26 June (DB), Baston Fen in Lincolnshire on 9–24 July (AT, MWd), Romford in Essex on 16–21 July (CJ) and, even more dramatically, Wykeham Lakes in North Yorkshire on 20 July (CBr). It is probable that increased internal dispersal within Britain accounts for a number of these new site records, but a degree of immigration from the Continent would also seem likely, particularly in the case of coastal records.

Aeshna mixta Latreille – Migrant Hawker

No obvious movements of *Aeshna mixta* were noted during the year, although migration at low densities can be difficult to detect. Unseasonably early records of two males at Radipole, Dorset, on 15 June (PW) and a mating pair in the Cotswold Water Park, Wiltshire, on 22 June (AJ) could, however, relate to immigrants from further south. Single *A. mixta* were also attracted to moth-traps

at Cuxton, Kent, on the nights of 11 & 29 August (DTa) and at Bawdsey, Suffolk, on the night of 13 September (NS); such records of dragonflies at light frequently refer to migrants (Parr, 2006). Although outside British coastal waters, it is worth noting that a single *A. mixta* landed on the Gyda Oil Platform in the central North Sea c. 300 km east of Aberdeen on 11 August (RG).

Anax ephippiger (Burmeister) – Vagrant Emperor

Once a great rarity in Britain, over the last decade *Anax ephippiger* has become quite a regular visitor to our shores, if still only in relatively small numbers. During 2021, an individual was photographed at Torpoint, Cornwall, on 24 February (JS) and unidentified dragonflies seen near Harlyn, Cornwall, on 26 February (DJ) and at Nursling, Hampshire, on 27 February (JCl) are likely to have also been *A. ephippiger*. Further records followed at Frampton Marsh, Lincolnshire, on 30 July (TCo), Lower Holbrook, Suffolk, on 1 August (BSt) and Durlston Country Park, Dorset, on 23 August (WA). A significant autumn influx was then seen. Between 9 September and 22 November, individuals were confirmed from 17 sites, with several other less well documented sightings also being reported. Although most records were made during the day, one individual was attracted to a moth trap at Prawle Point, Devon, late in the evening of 9 September (DGu). During the autumn influx, records came mostly from the counties of Devon, Kent, Suffolk and Norfolk, but there were also reports from Skokholm in Pembrokeshire on 9–10 September (GE), Nether Poppleton in Mid-west Yorkshire on 21 September (JMH), Bardsey Island in Gwynedd on 15 October (SS) and from at least two sites in the Scottish Islands – at Scatsta, Shetland, on 1 October (ER) and at Kirkwall, Orkney, on 17 October (HH). Most autumn records involved single individuals, but towards the end of September three were present at Waxham in Norfolk (JHr, SCh *et al*.), with some ten or so at nearby Winterton (BSm, PHe *et al*.). Finally, during a period of unseasonably mild weather at the very end of the year, a likely *A. ephippiger* was also reported from St Mary's, Isles of Scilly, on 31 December (WS).

Anax parthenope Sélys – Lesser Emperor

Confirmed records were received from 50 sites in Britain during 2021, with several further sightings of 'possible/probable' individuals. The earliest records came on 7 June from both Sandwich Bay in Kent (SRe) and Ingrebourne Valley in Essex (HV), while the latest sighting, perhaps reflecting an autumn emergence, was from Overcombe in Dorset on 26 September (PHa). It was thus a good year for *Anax parthenope*, though totals were still well short of the species' best-ever year in 2019, when records came from over 80 sites (Parr, 2020). Sightings during the current reporting year were concentrated in southern and south-eastern England, with a significant proportion of localities

Plate 3. *Sympetrum fonscolombii* (immature female). Wildern Local Nature Reserve, Hampshire, 18 August 2021. Photograph by T. Crow.

involved also recording the species during 2019 and/or 2020. With the life-cycle of *A. parthenope* being in the range of a few months to two years in length depending on environmental conditions (Werzinger & Werzinger, 2001; Corbet *et al*., 2006), it seems likely that individuals seen at these sites will often be local breed, though in some instances repeat sightings might result simply from fresh immigrants re-finding particularly favourable habitat. Sites where breeding is now possible include Windmill Farm in Cornwall, Longham Lakes in Dorset, Eastbourne (West Rise Marsh) in East Sussex, Dungeness in Kent, Tice's Meadow Nature Reserve in Surrey, the London Wetland Centre in Greater London, Little Belhus Country Park in Essex, Hilfield Park Reservoir in Hertfordshire, Loompit Lake in Suffolk, the Trinity Broad complex, Felbrigg and Winterton Dunes in Norfolk and also Ripple Lakes in Worcestershire.

In addition to local breeding, significant migration also took place during the year as seen by records from unexpected areas. Highlights included a record from south Wales at Caerau, Glamorganshire, on 12 June (DS) and a drab form female seen at Hartley, Northumberland, on 18 August (JG), the latter being the most northerly record of the year. The period 16–22 July was also notable for a surge in sightings of *A. parthenope* in England, coincident with a period of hot sunny weather (Met Office, 2022). This may be indicative of an influx, but in terms of individual records the precise balance between local breeders, dispersing British individuals and fresh immigrants from the Continent is difficult to determine.

Orthetrum cancellatum (L.) – Black-tailed Skimmer

A male was photographed at Higher Moors on St Mary's, Isles of Scilly, on 30 July (DH), and stayed until at least 26 August (LG). This is apparently only the second record of the species from the Islands.

Sympetrum danae (Sulzer) – Black Darter

September and early October 2021 saw several records of *Sympetrum danae* well away from regular sites for the species, and while internal dispersal within Britain is likely to be involved in many of these unusual sightings, a degree of immigration from the Continent may also have taken place. Of the more notable records, a male was seen and photographed near the coast at Benacre, Suffolk, on 15 September (CBu), despite the species not breeding in the county and indeed being extremely localised in East Anglia as a whole. A male noted at Symondshyde, Hertfordshire, on 16 September (JW) represents the first county record since 2015, while elsewhere a male and female seen at Bempton Cliffs, East Yorkshire, on 24 September (IH) constitute only the second record for the area.

Sympetrum fonscolombii (Sélys) – Red-veined Darter

A small influx into Belgium and the Netherlands over 9–14 May (Waarneming.be, 2021; Waarneming.nl, 2021) appeared to miss Britain, with the first record of the year not being until 30 May at Windmill Farm Nature Reserve, Cornwall (CM). The following three weeks saw many further records; in general the numbers involved were low (typically 1–6 individuals per site), but 24 were noted at Sandwich Bay, Kent, on 11 June (MHe) and 34 at West Rise Marsh, East Sussex, on 13 June (KGl). Almost all dragonflies were fully mature when first spotted, consistent with freshly arrived migrants, though an immature male photographed at Stallingborough, Lincolnshire, on 11 June (DW) may possibly have been locally bred. After the initial influx, new records continued at a slightly lower frequency until roughly mid-July, then started to tail off. In all, spring/summer records came from at least 40 sites, with a strong bias towards southern and eastern coastal counties, and with Cornwall, Devon, Suffolk and Norfolk featuring prominently. More northerly east coast sightings included reports from Thornwick Pools in East Yorkshire on 8 July (AAl), Hunmanby in North Yorkshire on 16 June (JHw) and Newmains Meadow pond in the Scottish Borders on 17 June (DGa). Of those few records on the west coast of Britain, reports from Kenfig in Glamorganshire on 4 June and 29 June–16 July (TW *et al*.) and Ainsdale Sand Dunes in Lancashire on 15 June (DTy) are of particular note.

On 16 August, the first record of a second, autumnal, generation of *S. fonscolombii* was received when an immature female was noted at Wildern Local Nature Reserve in Hampshire (CWh); this individual remained until 18 August (TCr). A locally bred teneral with damaged wings was seen at Sandwich Bay in Kent on 26 August (AL), but only a handful of other late season records were received and clearly little in the way of either local emergences or fresh immigration took place during autumn 2021. The last records of the year were in late September, when an immature female was noted at Broadwater Warren RSPB Reserve in Kent (though Vice County 14, East Sussex) on 22 September (SCr) and a mature male was seen on Brownsea Island, Hampshire, around the same date (HM).

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

It was seemingly a quiet year for movements of *Sympetrum striolatum,* though migration involving only low densities can be difficult to detect.

Discussion

A considerable number of records of unusual species, or more common species in unusual locations, were made in Britain during 2021, either as a result of internal dispersal or immigration from the Continent. At a relatively local level, the two phenomena are indeed related, since weather conditions that favour movement within Britain should also stimulate movement on the near Continent. Longer-distance immigration was also significant during the course of the year with, for example, yet another influx of *Anax ephippiger* being seen during autumn. Other species whose strongholds lie in more southerly regions of Europe, such as *Aeshna affinis*, *Anax parthenope* and *Sympetrum fonscolombii* also showed well, but for species such as *A. affinis* and, particularly, *A. parthenope* that now also breed in Britain, the growing local populations make detailed analysis of continuing immigration difficult. This is because it is becoming increasingly problematic to decide which specific sightings refer to local individuals and which to fresh immigrants. Indeed, for species such as *Aeshna mixta* that colonised Britain in the more historic past, this dilemma has long existed and little is known about their current migratory behaviour. It is hoped that increased international collaboration, along with records at sea or from areas without suitable breeding habitat, will allow further progress to be made in understanding the movements of species that also have resident populations. The recent developments using stable isotopes to determine the likely natal area of individual dragonflies (Hobson *et al*., 2012) might also prove useful in advancing out knowledge of dragonfly migration in our current warming world.

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Some characteristics of the wings of *Cordulegaster boltonii* (Donovan, 1807) (Odonata: Cordulegastridae) from central Spain

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Abstract

Wing characteristics in the Odonata have been widely analysed given their significance in the ecology of the species and their importance for flying patterns. However, until now very little is known about wing morphology in *Cordulegaster boltonii* (Odonata: Cordulegastridae). In this work, six variables are examined in males of this species, in relation to fore-wing and hind-wing venation and their correlation to wing length, wing area and aspect ratio. The number of ante-nodal and post-nodal cross-veins and the number of cells in the anal triangle and anal loop are shown to be the more suitable variables for wing study in this species.

Introduction

The wings of flying insects have been studied to ascertain their structure, composition, aerodynamics and phylogenetic relationships (Sudo *et al.*, 2010; Bomphrey *et al.*, 2016; Huang *et al.*, 2020).

In anisopterans the fore-wings are long and thin in comparison to the hind-wings, which are larger with an expansion near the anal region. The wing morphology of a species can vary with geographical location (Hassall, 2015), habitat type

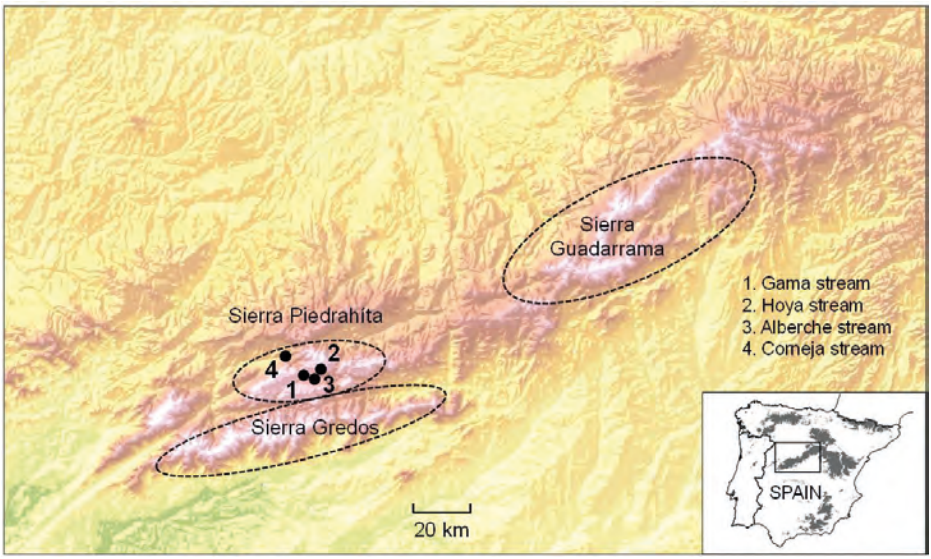

Figure 1. Location of the four streams sampled (dots) in the Sierra Piedrahíta. (altitude ≥ 1000 m a.s.l.). Inset shows the region of Spain shown in the main diagram.

(Outomuro *et al.*, 2013), and migratory or non-migratory behaviour (Suárez-Tovar & Sarmiento, 2016). In some species, it seems that the morphology of the fore- and hind-wings may have evolved differently (Huang *et al.*, 2020).

Wing length, wing area and aspect ratio (i.e. the relationship between wing length and wing width) are characteristics used in studies on dragonflies. Larger wings are considered to facilitate gliding ability (Grabow & Rüppell, 1995) and, likely, manoeuvrability (Wootton, 2020). In addition, larger wings usually have more cross veins, which increases their resistance to fracture (Rajabi & Gorb, 2020). Wing aspect ratio tends to be higher in some species inhabiting areas with low temperature (Hassall, 2015) but not in others (Casanueva *et al.*, 2017). However, at the intraspecific level, the variations in these characteristics and their causes have not been broadly scrutinised (Casanueva *et al.*, 2017).

Cordulegaster boltonii, a hawking anisopteran (Wootton, 2020) which mainly occupies mountain streams, is distributed throughout the western Palearctic (Boudot & Holusa, 2015). This species is sedentary and large with a wingspan up to 10 cm. The wing variation of species in the Cordulegastridae has been poorly studied. However, much attention has been given to the morphology of the body and colour patterns in *C. boltonii* (Boudot & Jacquemin, 1995; Corso, 2019). Handling live specimens to estimate wing length, wing area and aspect ratio is complex (Hassall *et al.*, 2009), and specimens often need to be euthanized. In this work we analyse wing traits that are easy to obtain (number

of cells, number of cross veins) to find out if they are significantly correlated with wing length, wing area and aspect ratio. Data is also provided on *C. boltonii´*s wing structure.

Material and Methods

This study was carried out in the mountains of the Sierra de Piedrahíta, in the centre of Spain (40º25ˈ - 40º29ˈN, 5º09ˈ - 5º13ˈW) (Fig. 1), about 130 km north-west of Madrid. During July in each year from 2010-2021, four streams (the Hoya, Gama, Alberche and Corneja) were sampled. Both the Hoya (1595 m a.s.l.) and Gama (1670 m a.s.l.) streams are tributaries of the Alberche stream (1642 m a.s.l.) and they are 1.1 km apart from each other. Therefore, the Hoya, Gama and Alberche streams can be considered as a single unit. The Alberche stream and the Corneja stream (1330 m a.s.l.) are 9.3 km apart, the former joining the Tagus River, the latter the Douro River (Fig. 2), both rivers flowing through Portugal to the Atlantic Ocean. In between the Corneja and Alberche streams the mountain rises to an altitude of 2062 m a.s.l. at its highest point, thus providing a possible geographical barrier between the two sites. The two sites differ in that the Alberche stream has deforested banks (Plate 1), whereas the lower altitude Corneja stream has abundant tree cover (Plate 2).

Only adult males of *Cordulegaster boltonii* were trapped. Males are smaller than females and have an anal triangle in their hind-wing; this is absent in females. The males were preserved in ethanol and then dissected, and the two right wings were preserved. Right fore- and hind-wings were flattened by a glass plate and scanned using an HP Scanjet 3770 at 2400 dpi. Wing veins were named based on the nomenclature proposed by Riek & Kukalová-Peck (1984) and updated by Rehn (2003).

From all specimens analysed, the following variables were measured from both fore-wing and hind-wing (Fig. 3):

a) The number of ante-nodal cross veins and post-nodal cross veins.
b) The number of cells in the discal cell, bridge space, anal triangle and anal loop.
c) Wing total length (from the extreme base of the cubitus posterior vein to the wing apex).
d) Ante-nodal length and post-nodal length.
e) Wing area.

Ante-nodal length, post-nodal length and wing area were measured using software ImageJ (Abramoff *et al.*, 2004). The nodal index was calculated as

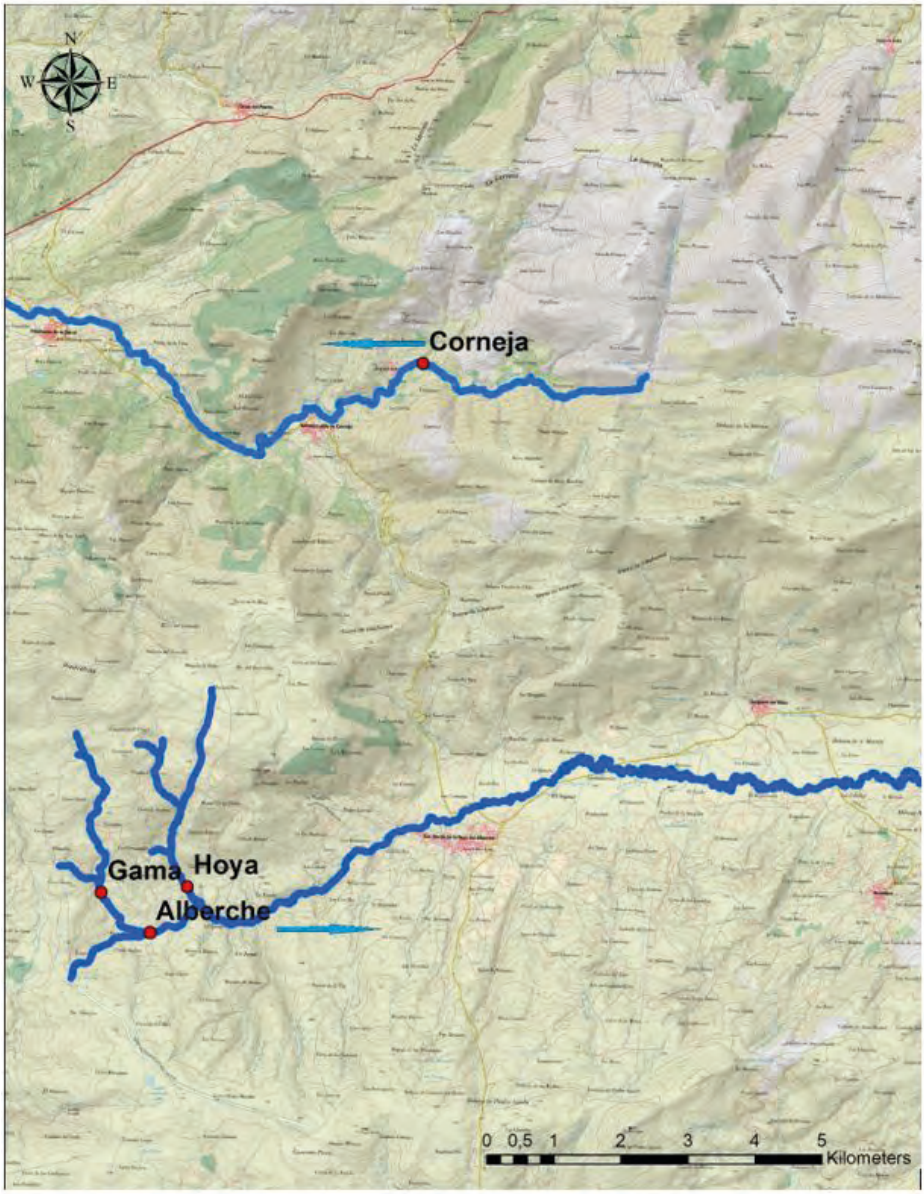

Figure 2. Sampling points (red dots) in the four streams. Blue arrows indicate the direction of flow.

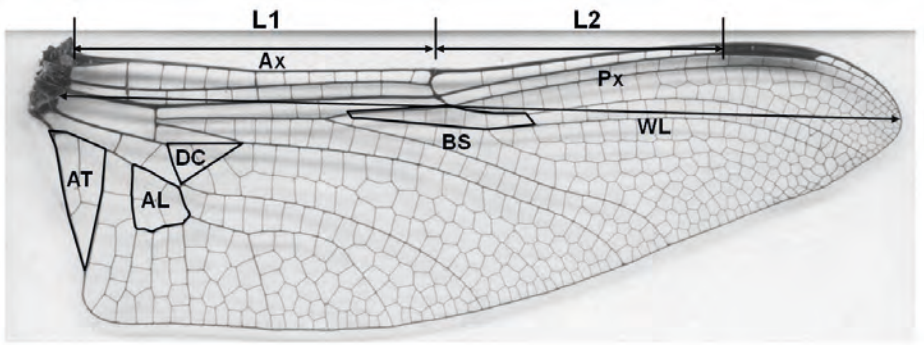

Figure 3. The hind-wing of an adult male *Cordulegaster boltonii* from the central Iberian Peninsula. AL, anal loop; AT, anal triangle; Ax, ante-nodal cross veins; BS, bridge space; DC, discal cell; L1, ante-nodal length, L2, post-nodal length; Px, post-nodal cross veins; W, wing length.

Plate 1. The Gama tributary of the Alberche stream, lying above the tree line.

Plate 2. The Corneja stream showing extensive vegetation.

the number of ante-nodal cross veins / number post-nodal cross veins, which has been previously used to describe species of the genus *Cordulegaster* (Fraser, 1936). Anal triangle, anal loop and node position have been used as characteristics for the identification of taxa in anisopterans (Carle & Kjer, 2002; Abbott, 2006). Even though the basal complex, formed of the arculus, triangle and supertriangle, has an influence on odonate flight (Wooton, 1991; Rajabi *et al.*, 2016), in the present study only the number of cells that make up the triangle has been analysed because, in *C. boltonii*, the supratriangle is always made up of a single cell in both fore- and hind-wings.

A bivariate linear regression analysis model was used to analyse the relationship between the measured variables, nodal index and number of ante-nodal cross veins + number post-nodal cross veins with wing length, ante-nodal length, post-nodal length, wing area and aspect ratio values. The comparison of the values of the variables between fore-wing and hind-wing was done using ANOVA, with a 0.05 level of significance, when they fulfilled the Shapiro-Wilk normality criteria and Levene´s test for homogeneity of variance. When this was not the case, the Kruskal-Wallis test was used. All calculations were done with Past 3.15 software (Hammer *et al.*, 2001).

Table 1. Mean values ± SD (in brackets, range of values) of the measured variables in the fore- and hind-wings of adult males of *Cordulegaster boltonii*. CV, coefficient of variation; F, ANOVA; H, Kruskal-Wallis; P, probability. Ranges are in green; significant values in red.

	Fore wing	CV	Hind wing	CV	Test
Ante-nodal cross veins	18.01 ± 1.21 (16 - 21)	6.7	12.72 ± 1.19 (9 - 15)	9.4	$F_{1,148}$ = 729.31 P < 0.0001
Post-nodal cross veins	13.03 ± 1.34 (10 - 16)	10.3	12.67 ± 1.44 (9 - 15)	11.3	$F_{1,148}$ = 2.53 P = 0.114
Nodal index	1.39 ± 0.15 (1.07 - 1.73)	10.8	1.02 ± 0.15 (0.73 – 1.50)	14.8	H = 94.334 P = 0.0001
Ante-nodal + post-nodal cross veins	31.04 ± 2.06 (27 - 37)	6.6	25.39 ± 1.94 (21 - 30)	7.7	$F_{1,148}$ = 298.28 P < 0.0001
Number of cells					
Discal cell	1.96 ± 0.20 (1 - 2)	10.1	1.99 ± 0.12 (1 - 2)	5.8	H = 0.079 P = 0.778
Bridge space	7.28 ± 1.09 (5 - 10)	14.9	6.93 ± 1.12 (5 - 12)	16.1	H = 5.422 P = 0.0199
Anal triangle			4.20 ± 0.79 (3 - 6)	18.8	
Anal loop			4.80 ± 0.72 (3 - 7)	14.9	
Wing length (mm)	43.33 ± 1.13 (40.54 - 45.64)	2.6	42.42 ± 1.06 (39.78 - 44.63)	2.5	$F_{1,148}$ = 25.86 P < 0.0001
Ante-nodal length (mm)	21.45 ± 0.70 (20.16 - 23.89)	3.3	17.90 ± 0.60 (16.79 - 19.93)	3.3	$F_{1,148}$ = 1111.21 P < 0.0001
Post-nodal length (mm)	13.08 ± 0.54 (11.50 - 14.99)	4.1	14.80 ± 0.63 (13.44 - 16.90)	4.3	$F_{1,148}$ = 321.9 P < 0.0001
Wing area (mm^2)	344.74 ± 15.84 (269.93 - 383.55)	4.6	434.09 ± 20.13 (381.17 - 483.08)	4.6	H = 111.675 P = 0.0001
Aspect ratio	5.45 ± 0.19 (4.81 - 5.83)	3.4	4.15 ± 0.14 (3.82 - 4.56)	3.3	H = 111.775 P = 0.0001

Results

A total of 75 adult males were trapped: two in Hoya stream, three in Gama stream, 41 in Alberche stream and 29 in Corneja stream. The number of ante-nodal cross veins, post-nodal cross veins, nodal index and bridge space cells were significantly higher in the fore-wing than in the hind-wing, although there was considerable overlap in the number of post-nodal cross veins and bridge

Table 2. Values of the coefficient of correlation (r) and its probability (P) among the variables from fore- and hind-wings of adult males of *Cordulegaster boltonii*. Significant values are in red.

		FW		HW	
		r	P	r	P
Ante-nodal cross veins	Wing length	0.213	0.066	0.245	0.033
	Wing area	0.213	0.066	0.208	0.073
	Aspect ratio	0.041	0.724	0.084	0.469
	Ante-nodal length	0.206	0.075	0.191	0.100
Post-nodal cross veins	Wing length	0.226	0.051	0.139	0.232
	Wing area	0.227	0.049	0.088	0.449
	Aspect ratio	0.033	0.775	0.094	0.419
	Post-nodal length	0.373	0.001	0.251	0.029
Nodal index	Wing length	-0.080	0.491	0.050	0.664
	Wing area	-0.103	0.379	0.049	0.675
	Aspect ratio	0.022	0.845	0.005	0.966
Ante-nodal + post-nodal cross veins	Wing length	0.272	0.019	0.253	0.028
	Wing area	0.272	0.017	0.193	0.098
Bridge space	Wing length	-0.067	0.563	-0.111	0.339
	Wing area	-0.001	0.992	-0.156	0.179
	Aspect ratio	-0.100	0.357	0.050	0.665
Anal triangle	Wing length			0.266	0.021
	Wing area			0.198	0.088
	Aspect ratio			0.125	0.282
Anal loop	Wing length			0.272	0.018
	Wing area			0.188	0.105
	Aspect ratio			0.151	0.193

space cells between fore- and hind-wings. The discal cell always had 1 or 2 cells in both wings, with no difference between their mean values (Table 1).

Fore-wings were significantly longer than hind-wings and, in the former, the node was closer to the thorax than in the hind-wing (Table 1). Conversely, the hind-wing area was greater than that of the fore-wing and the distance between the node and the pterostigma was also greater. Thus, the aspect ratio was higher in the fore-wing than in the hind-wing (Table 1).

In the fore-wing, wing length was correlated only with the number of ante-nodal

Table 3. Tests between sampled variables found in the fore- and hind-wings of adult males of *Cordulegaster boltonii* from the Alberche, Hoya and Gama streams (N = 46) and the Corneja stream (N = 29). F, ANOVA; H, Kruskal-Wallis; P, probability. Significant values are in red.

	Variables	Test	P
Fore wing	Ante-nodal cross veins	$F_{1,73} = 2.25$	0.1379
	Post-nodal cross veins	$F_{1,73} = 0.56$	0.4567
	Ante-nodal cross veins / post-nodal cross veins	H = 0.068	0.7940
	Bridge space	$F_{1,73} = 3.24$	0.0758
	Ante-nodal length	$F_{1,73} = 19.06$	0.0000
	Post-nodal length	$F_{1,73} = 6.95$	0.0102
	Wing length	$F_{1,73} = 14.90$	0.0002
	Wing area	$F_{1,73} = 14.32$	0.0003
	Aspect ratio	H = 0.153	0.6953
Hind wing	Ante-nodal cross veins	$F_{1,73} = 0.05$	0.8250
	Post-nodal cross veins	$F_{1,73} = 2.08$	0.1538
	Ante-nodal cross veins / post-nodal cross veins	H = 1.19	0.2795
	Bridge space	H = 0.50	0.4795
	Anal triangle	$F_{1,73} = 0.13$	0.7208
	Anal loop	$F_{1,73} = 1.59$	0.2108
	Ante-nodal length	H = 22.243	0.0001
	Post-nodal length	$F_{1,73} = 7.49$	0.0078
	Wing length	$F_{1,73} = 20.94$	0.0000
	Wing area	$F_{1,73} = 15.11$	0.0002
	Aspect ratio	$F_{1,73} = 1.41$	0.2383

cross veins + post-nodal cross veins, while in hind-wing the correlation was significant with the number of ante-nodal cross veins and the number of ante-nodal cross veins + post-nodal cross veins; also with the number of cells in the anal triangle and the anal loop (Table 2). Furthermore, the post-nodal length was significantly correlated with the number of post-nodal cross veins in both fore-wing and hind-wing but there was no correlation in either wing between the ante-nodal length and the number of ante-nodal cross-veins (Table 2).

Regarding wing area, the only significant correlations were with the number of post-nodal cross veins and the number of ante-nodal cross veins + post-nodal cross veins in the fore-wing, the former only just being significant (P=0.049); no variable in the hind-wing was correlated with wing area (Table 2). Aspect ratio was not significantly correlated with any of the variables analysed.

The average values for the number of cross veins, the number of cells in the bridge space and the aspect ratio in both fore- and hind-wings were statistically similar between samples from the Corneja and Alberche streams (Table 3). In contrast, wing length, ante-nodal length, post-nodal length and wing area were significantly higher in both wings at the Corneja stream. The aspect ratio did not vary between streams in either the fore-wing or the hind-wing (Table 3).

Discussion

This study is the first to provide data on variables in the wings of *Cordulegaster boltonii* from the Iberian Peninsula. The characteristics of the wing in specimens from central and northern Europe are not known. However, Terzani (2016) showed a range of values of ante-nodal cross veins, post-nodal cross veins and anal loop cells in Italian specimens. These were higher than those of the Iberian specimens, but there were a similar number of cells in the anal triangle (2-7 cells) from both sites. Ocharan (1987) obtained the hindwing length of males from the Iberian Peninsula (mean 40.9 mm, range 38.6-43.3 mm), but used a different methodology to measure the wing length, and so comparisons with our data are not possible.

The total number of ante-nodal + post-nodal cross veins was the only variable that was significantly correlated with wing length in both wings, and the number of post-nodal cross veins was correlated with post-nodal length. Therefore, as expected, the number of cross-veins is an indicator of both the total length of the wing and the position of the node with respect to the pterostigma. The position of the node on the wings influences the flight of dragonflies (Wootton, 1992; Wootton & Newman, 2008) and Suárez-Tovar & Sarmiento (2016) proposed that migrating dragonflies have their node close to the body and a small pterostigma, thereby facilitating gliding flight. *Cordulegaster boltonii* is a non-migrant, sedentary species that does not need to travel long distances (Hančíková, 2014), so that the changes in wing shape are reflective of wing structure that improve speed and manoeuvrability in flight.

Anal triangle and anal loop variables presented high coefficients of variation and were correlated with wing length. This suggests that both variables are good indicators of the size of a specimen and that they may differ between geographical areas, which is consistent with observations in other odonates (Alvial *et al.*, 2019).

The two analyzed populations (Alberche and Corneja streams) differ in wing length and wing area and in ante- and post-nodal length, but do not differ in vein

patterns in the fore- and hind-wings. These two populations belong to different hydrographic basins, and the similar vein patterns in both populations suggest that this is independent of geographical position, or that they are not subject to the same selective pressures as wing aspect. *Cordulegaster boltonii* males make short movements during their flight period, generally not exceeding 5 km (Hančíková, 2014). Since the two populations are 9.3 km apart and are separated by higher ground, there may not be any exchange of individuals between them, something that requires more studies to be verified. In dragonfly flight the ante-nodal zone plays an important role in lift and thrust forces (Zhao *et al.*, 2012). Having the node closer to thorax favours a lower degree of wing torsion and a higher speed of flight (Wootton, 1991). Therefore, individuals in the *C. boltonii* population located in the Alberche stream, should be able to reach higher speeds than those in the Corneja stream population.

In dragonflies, the various regions that make up the wing are integrated, so that the evolution of each region can influence the final shape of the wing (Blanke, 2018). For this reason, it is important to know precisely if a certain area of the wing changes at an intraspecific level, because this may suggest adaptations of the species to local environmental conditions. In addition, vein configuration of the fore-wing seems to be correlated with vein configuration of the hind-wing (Blanke, 2018). However, our results show that, in *C. boltonii*, only the number of cross-veins (post-nodal veins and total number of transverse veins) is simultaneously correlated in fore- and hind-wings with total or partial wing length, and that in hind-wings there are five variables correlated with the total or partial length of the wing, whereas in fore-wings there are only two. This suggests that the hind-wing may be more suitable for analysing adaptations of this species to local conditions. In other dragonflies, there is evidence of changes in wing shape related to variations in habitat vegetation coverage, in which fore-wing and hind- wing change independently (Outomuro *et al.*, 2013).

This study has shown that aspect ratio is not correlated to the vein patterns, but it is with wing length. Therefore, the aspect ratio value could be obtained from the wing length. Wing length has been used in numerous odonate studies to analyse geographic variations (Hassall, 2015), interspecific variations (e.g. Chitsaz *et al.*, 2020), body size and hunting strategy (Worthen & Jones, 2006). Until now, morphological variations in *C. boltonii* have been based on the colouration of the thorax and abdomen, and the shape of the anal appendages (e.g. Ocharan, 1987; Boudot, 2001; Corso, 2019; Scheneider *et al.*, 2021), or in the biometry of the exuviae (Casanueva *et al.*, 2020; Hernández *et al.*, 2022), but not on the characteristics of the wings. The variables analysed here could be used in studies of geographical variability of the morphology of this species.

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