J. Br. Dragonfly Society, Volume 31 No. 1, April 2015

CONTENTS

Journal of the British Dragonfly Society

Volume 31 Number 1 April 2015

BDS

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

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

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

ADDRESSES
Editor:
P.J. Mill
8 Cookridge Grove
Leeds, LS16 7LH
email: gpmill@supanet.com

Secretary:
H.G. Curry
23 Bowker Way
Whittlesey
Peterborough, PE7 1PY
email: secretary@british-dragonflies.org.uk

Librarian / Archivist:
D. Goddard
30 Cliffe Hill Avenue
Stapleford
Nottingham, NG9 7HD
email: david.goddard8@ntlworld.com

Membership Secretary
L. Curry
23 Bowker Way
Whittlesey
Peterborough, PE7 1PY
email: membership@british-dragonflies.org.uk

Back numbers of the Journal can be purchased from the BDS Shop at £2.00 per copy to members or £5.50 per copy to non-members.
email: shop@british-dragonflies.org.uk

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

Ordinary membership annual subscription £20.00.
Overseas subscription £25.00.
Benefactor membership £40 (minimum)
All subscriptions are due on 1st April each year.

Other subscription rates (library, corporate) on application to the Membership Secretary, who will also deal with membership enquiries.

BDS Website: www.british-dragonflies.org.uk

Cover illustration: Male *Coenagrion mercuriale*. Photograph by Phillip Watts.

The Journal of the British Dragonfly Society is printed by Artisan Litho, Abingdon, Oxford.
www.artisanlitho.co.uk

INSTRUCTIONS TO AUTHORS

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

- Word processed manuscripts may be submitted in electronic form either on disk or by e-mail.
- Manuscripts should be one and a half spaced, on one side of the page only and with margins at least 25mm on both sides and top and bottom. Footnotes should be avoided.
- Use of these terms is acceptable: 'exuvia' for cast skin (plural: 'exuviae'); 'larva' (instead of 'naiad' or 'nymph'); 'prolarva' to designate the first larval instar.
- Dates in the text should be expressed in the form: 24 July 2010.
- References cited in the text should be in the form '(Longfield, 1949)' or '...as noted by Longfield (1949)'. All references cited in the text (and only these) should be listed alphabetically at the end of the article in the following forms:
  Hammond, C.O. 1983. *The Dragonflies of Great Britain and Ireland* 2nd Edition (revised by R. Merritt), Harley Books, Colchester, 116pp.
  Longfield, C. 1949. The Dragonflies of the London area. *The London Naturalist* **28**: 90-98.
- Titles of journals should be written out in full.
- Figures, plates and tables should be presented on separate, unnumbered pages.
- Legends for figures, plates and tables should be presented together in sequence on separate, unnumbered pages.
- The legend for each table and illustration should allow its contents to be understood fully without reference to the text.

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

SCIENTIFIC AND ENGLISH NAMES OF BRITISH ODONATA

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

Registered Charity No. 800196

The habitat requirements and changing distribution of *Calopteryx splendens* (Harris) (Banded Demoiselle) in Northumberland.

Jennie Lowdon

8 Fell Terrace, Burnopfield, Newcastle upon Tyne, NE16 6DW.

Summary

Calopteryx splendens (Banded Demoiselle) (Harris) is one of many Odonata species expanding their range northwards in Great Britain. This study investigates this shift within the county of Northumberland, alongside an analysis of habitat characteristics (using River Habitat Surveys) and their influence on site selection. The availability of further habitat in the county was also examined, with many currently unoccupied but suitable sites found.

Introduction

Calopteryx splendens (Banded Demoiselle) (Harris) is considered to be predominantly southern in its distribution, with Merritt *et. al.* (1996) commenting on its restricted range over lowland areas of southern and midland Britain and of Ireland before 1990 (Corbet, 2008). However, it is expanding its range northwards in Great Britain (Brooks *et al*., 2007; Mill *et al*., 2010; Cham *et al*. 2014). This has occurred on both the western (Clarke, 1999) and eastern sides (Jeffries, 2001; Ward *et. al.*, 2004; Jeffries *et. al.* 2005; Corbet, 2008) of the country. Several anisopterans that inhabit still water are also extending their range northwards. These include: *Aeshna cyanea* (Southern Hawker), *A. mixta* (Migrant Hawker), *Anax imperator* (Emperor Dragonfly), *Orthetrum cancellatum* (Black-tailed Skimmer), *Sympetrum sanguineum* (Ruddy Darter) and, to some extent, *Libellula depressa* (Broad-bodied Chaser) (Merritt *et. al.,* 1996; Brooks *et al*., 2007; Mill *et al*., 2010; Cham *et al*., 2014).

In Northumberland, most rivers flow eastwards to the North Sea (Fig. 1). From south to north these are the Blyth, Wansbeck, Lyne, Coquet and Aln. Further north the rivers Breamish and Glen join the river Till, which flows northwestwards to join the river Tweed, entering the North Sea at Berwick-on-Tweed. These rivers flow through various environments, e.g. southern lowlands (river Pont), uplands (river Breamish) and to the north of the Cheviot Hills rivers Glen and

Till), with many rivers being fast and turbulent, and lacking extensive in-stream vegetation (Ward & Mill, 2005). This is in contrast to the southerly meandering, lowland rivers with emergent vegetation that *C. splendens* inhabits (Ward & Mill 2005).

Figure 1. The distribution of *Calopteryx splendens* in Northumberland, 2011. NT. etc., 100 Km squares. ■, sites at which *Calopteryx splendens* was present; □, sites at which *C. splendens* was absent.

By 1988, *C. splendens* had arrived on the river Wansbeck in the south of Northumberland, where it was recorded from one site by Silcock (1988). Its presence there was confirmed in 1996 by Jeffries, who also recorded it in the same year from the river Blyth and its main tributary (the Pont) and from a pond near Seaton Burn, all in the south of the county (Jeffries, 2001). However, he found no specimens on either the river Lyne or the river Aln (Jeffries, 2001). In 2003, *C. splendens* was found further north, at Rothbury on the river Coquet (Jeffries *et al*., 2005), a region where negative records had been obtained the previous year by Storey (2002). Up to 2003, the species was still recorded as absent on the river Lyne and on the river Aln and the Northumberland tributaries of the river Tweed (Breamish, Till and Glen) in the more northerly part of the county. However, it had reached south-west Scotland by 2005 (Batty, 2007).

Viable territory appears important in enabling this expansion as, like many odonate species, *C. splendens* has specific habitat requirements. In the case of *C. splendens*, the main requirements are fairly shallow, smooth-flowing water with submerged vegetation, high banks and tall herbaceous vegetation (Rozenweig, 1991; Raab *et. al.*, 1996; Jeffries, 2001), with narrower stretches of river being favoured (Jeffries *et al*., 2005). Areas with tall herbaceous vegetation are more likely to occur in areas with no bankside agriculture or grazing (Ward & Mill, 2005). This provides an environment where successful breeding and oviposition can take place (Corbet, 1962), as well as providing perching sites for males (Ward & Mill, 2005). The presence of trees and shrubs (site shading) are deemed unfavourable (Shutte, 1997; Jeffries, 2001; Ward & Mill, 2005), as they create a visual barrier, blocking a males' vantage point from which to protect its territory (Ward & Mill, 2005). However, it appears that their requirements are not as limiting as once thought (Jeffries, 2001), with their recent appearance in northern England and southern Scotland, where riverine environments differ from those further south, suggesting adaptation to environmental conditions, which in turn facilitate its movement northwards (Ward & Mill, 2008). The aims of this study were to examine any recent northerly shift in the range of *C. splendens* in Northumberland and to analyse habitat characteristics and their influence on site selection by this species.

Methods

Distribution

This study is a follow up to that of Jeffries *et. al.* (2005). Fifty sites were visited during July and August 2011 during the regional flight period, on days when weather provided conditions warm enough for adult activity. A set observation time of twenty minutes was applied to each site visit, with the presence or absence of adults recorded at a single spot, chosen where river visibility was highest. Negative records were noted to ensure that any future expansion studies have accurate records on which to build. The sites chosen covered all of the main rivers visited by Jeffries *et al.* (2005) (Blyth, Wansbeck, Lyne, Coquet, Aln and Till) and included a number of the sites that they noted. Other sites were also visited, the most northerly of which was at the bridge at Ford on the river Till (Table 1).

Habitat characteristics

River Habitat Surveys (RHS) were used to assess any differences between sites with positive *C. splendens* records and those from which it is absent, as they offer comprehensive characterisation and assessment of physical, vegetation and land management variables. Their standardisation enables consistent recording and direct comparison between sites, which can in turn be analysed alongside distribution data to determine habitat features relevant in site selection. RHSs are typically carried out along 500m stretches of river, with observations made at ten equally spaced points (Environment Agency, 2003). However, in this study, as in that of Jeffries *et al.* (2005), each habitat survey was carried out as a single spot check in the area immediately around the location of distribution data recording. As vegetation can change over time, RHSs were completed in conjunction with distribution data, enabling a direct comparison between presence/absence and habitat variables.

In accordance with Environment Agency guidelines regarding RHS completion (Environment Agency, 2003), fringing reed banks were only recorded as present if they extended at least half way up the river bank and covered at least 50% of the river bank within the survey site, and comprised species such as *Phragmites australis* (Common/Norfolk reed) and *Sparganium erectum* (Branched Bur-Reed). The presence of such species in smaller quantities were recorded as emergent vegetation. Emergent vegetation consisted of reeds (e.g. *Sparganium erectum)*, sedges (e.g. *Carex* spp.), rushes (e.g. *Juncus* spp.), grasses (e.g. *Phalaris arundinacea)* and horsetails (e.g. *Equisetum fluviatile*), which are rooted below water-level or along the water's edge (Environment Agency, 2003).

Principle Component Analysis (PCA) was used to identify and summarise the predominant patterns in the data. River Habitat Surveys contain numerous variables, e.g. 'density of vegetation', 'land use', 'tree density' and 'river flow type', with various options for recording, e.g. presence/absence and density. In order to allow direct comparison between variables, either '0' (where an option didn't apply to a site) or '1' (where it did apply) was assigned to each variable for each site. PCA graphs show clusters of sites that have variables in common.

Chi-square tests with Yates' Correction were carried out to further examine individual habitat features revealed within the broader patterns of the PCA.

Results

Distribution

The presence of *Calopteryx splendens* was confirmed on the river Blyth, the river Wansbeck and the river Coquet. On the river Blyth it was found at 11 of the 16 sites visited. One of the sites where it was absent was fairly close to the estuary; the other four were generally further upstream on the Blyth or its tributary, the river Pont (Fig. 1). On the river Wansbeck, it was recorded at four sites but was not present at the sites visited on three of its tributaries the Burn, Font and Hart. It still remains absent from the river Lyne (three sites). Only three sites were visited on the river Coquet and it was present at two of these. On the river Aln it was present at five of the six sites visited, the one from which it was not recorded being furthest upstream. It was also recorded from three sites on the river Till but was absent from those sites investigated on its tributaries, the Breamish and the Glen (Fig. 1).

Habitat characteristics

The emergent vegetation consisted of reeds, sedges, rushes, grasses and horsetails.

The results from the PCA analysis of habitat features in relation to occupancy by *Calopteryx splendens* indicate that unmodified banks are attractive to adults whereas bare banks with less than 50% vegetation and with rock, scree or boulders along with bank tops devoid of vegetation have a negative effect (PC2 - 13.2% of the variation) Similarly, PC3 (12.5% of the variation) indicates that lack of bank erosion and the absence of boulders and exposed bedrock are attractive to adults, whereas eroded banks exposing the underlying bedrock have a negative effect. The variables in PC1 (17.1% of the variation) indicate ambiguity with regard to the importance of bank-side trees. The first three PCs account for 42.8% of the total variation. In summary, adult *C. splendens* have a preference for the presence of emergent and bank-face vegetation with a surrounding area comprising rough, flat, unimproved pasture (Plate 1). Conversely, the absence of *C. splendens* is associated with a lack of emergent vegetation and banks that are virtually devoid of vegetation and with exposed rock, scree or cobbles (Plate 2) (Fig. 2).

Emergent vegetation (e.g. *Equisetum fluviatile*) density data supports the above

Table 1. Sites visited. The rivers and their tributaries are listed from south to north, the sites from downstream to upstream (see Fig. 1). +/ □ , presence/absence of *Calopteryx splendens*; Grid Reference, British National Grid Reference; *, site new to this survey (i.e. not visited by Jeffries (2005)).

River	Site	+/ □	Grid Reference
Blyth			
	Bedlington Bridge	□	NZ 266812
	Plessy Woods	+	NZ 241796
	Plessy Woods	+	NZ 234796
	Bellasis Bridge	+	NZ 190777
	Thornyford	+	NZ 156772
	Shilvington Bridge	+	NZ 149798
	Ogle Bridge	+	NZ 134798
	Trewick Bridge	□	NZ 111795
	Blyth Bridge (East)	□	NZ 094799
Pont			
	Kirkley Mill (bridge)	+	NZ 166766
	Cornyhaugh Farm	+	NZ 164764
	High Berwick Bridge	+	NZ 168742
	Central Ponteland (nr Bridge)	+	NZ 166728
	Medburn	□	NZ 131710
	*Bridge outside Medburn	□	NZ 125709
	Eachwick	+	NZ 120710
Wansbeck			
	Sheepwash	+	NZ 256860
	Mitford	+	NZ 152853
	Meldonpark Corner	□	NZ 122856
	Low Angerton (bridge)	+	NZ 093843
	Middleton (bridge)	+	NZ 053841
	Wallington (bridge)	□	NZ 033839
Hart Burn			
	Hartburn Bridge	□	NZ 091859
	Kirkhill Bridge	□	NZ 033878
Font			
	*Netherwitten	□	NZ 100901

Lyne				
		Ellington	☐	NZ 278913
		South Linton (bridge)	☐	NZ 257920
		Ulgham	☐	NZ 240925
Coquet				
		Warkworth	+	NU 235050
		West Thirston	+	NU 197009
		Thropton	☐	NU 030021
Aln				
		Lesbury Bridge	+	NU 239115
		Hawkhill Bridge	+	NU 214126
		Alnwick	+	NU 197138
		Bolton Bridge	+	NU 108132
		Broom Park west	+	NU 096121
		Wittingham	☐	NU 063118
Tweed				
	Breamish			
		Harehope Bridge	☐	NU 076204
		Beanly	☐	NU 071183
		Brandon ford	☐	NU 042168
	Till			
		*Ford (bridge)	+	NT 939374
		Doddington Bridge	☐	NT 999307
		Clavering	☐	NU 017294
		Chatton North Lyham	+	NU 058298
		Chatton East	+	NU 060284
		Chatton South	☐	NU 056277
		East Lilburn	☐	NU 046237
	Glen			
		Bridge end (bridge)	☐	NT 970313
		Akeld Steads (bridge)	☐	NT 962302
	Wooler Water			
		Wooler	☐	NT 994281

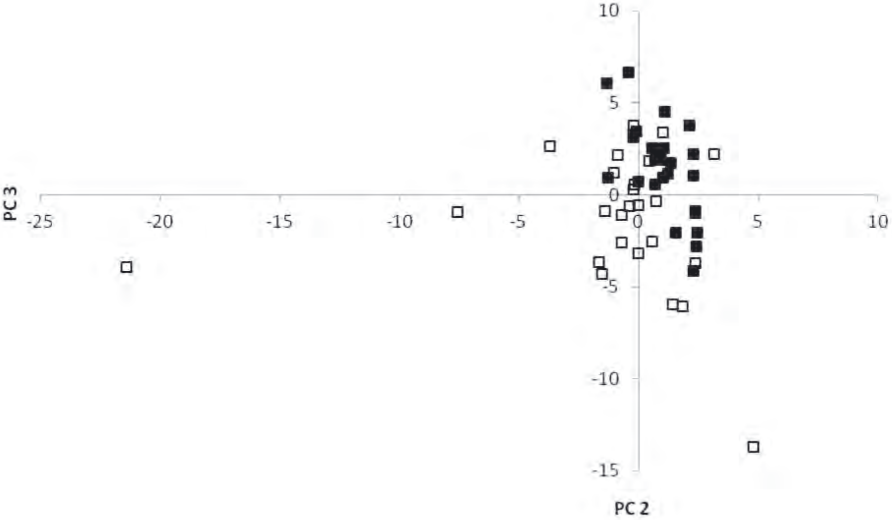

Figure 2. Principle component analysis ordination of the River Habitat Survey data for 50 sites across Northumberland. Each plot represents one of the 50 sites surveyed. ■,sites at which *Calopteryx splendens* was present; □, sites at which *C. splendens* was absent. Sites close together share characteristics; those further apart are notably different. PC2 axis - Positive values (upwards) indicate increasingly unmodified banks; negative results (downwards) indicate increasingly bare banks with less than 50% vegetation and with rock, scree or boulders along with bank tops devoid of vegetation. PC3 axis – Positive values (to the right) indicates increasing lack of bank erosion and the absence of boulders and exposed bedrock; negative values (to the left) indicate increasingly eroded banks exposing the underlying bedrock.

in that *C. splendens* appears to have a distinct preference for sites where there is ≥33% coverage, with positive records noted in 13 of the 16 sites with this amount of cover present and negative data from 12 of the 13 sites lacking emergent vegetation. This is highly significant (P = 0.0004, Chi-Square = 12.74). Where there is emergent vegetation but the coverage is <33% it appears to have little influence on site selection. Furthermore, fringing reed banks (e.g. *Sparganium erectum*) also appear to have an influence, with *C. splendens* present at 16 of the 18 sites containing this vegetation and absent from 24 of the 32 sites devoid of it (P = <0.0001, Chi-Square = 16.37). Whilst it is possible that *C. splendens* and these vegetation types independently prefer the habitats provided by the sites where they are both present, there is undoubtedly a correlation. All other RHS habitat characteristics were insignificant in influencing site selection.

The presence of suitable vegetation differs between rivers. However, there is what appears to be viable, but as yet unoccupied, habitat present in Northumberland. Thus records for a number of sites on the rivers Wansbeck, Aln and Till indicate suitable habitat, a number of which, particularly on the river

Plate 1. Example of an unmodified flat site, with dense emergent, bank-face and banktop vegetation, surrounded by rough/unimproved pasture - River Aln (Bridge at Bolton).

Plate 2. Example of a modified, bare site (rock, scree and cobble) - River Breamish (Brandon Ford).

Till, are currently unoccupied by *C. splendens*. The rivers Lyne and Breamish uniformly lack suitable habitat, which makes it unsurprising that *C. splendens* is absent from these rivers.

Discussion

Distribution

Calopteryx splendens had traditionally been regarded as a predominantly southerly species within the UK (Merritt *et. al.*, 1996; Brooks, 2001). However, more recent studies suggest a gradual northwards range expansion from around 1990 onwards (Clarke, 1999; Jeffries *et. al.*, 2005; Corbet, 2008). This study reveals a northwards range expansion within Northumberland beyond that reported by Jeffries *et. al.* (2005)

The river Pont, a tributary of the river Blyth, represents the southerly edge of the distribution of *Calopteryx splendens* in Northumberland and it is here, along with the river Wansbeck, that *C. splendens* appears to be the most established, having been consistently reported at various sites on these rivers since 1988 (Jeffries, 2001; Jeffries *et. al.*, 2005). However, the recorded range has now progressed beyond that noted by Jeffries (2005). A northerly range expansion is evident and *C. splendens* is now present on the rivers Aln and Till, with the latter (a tributary of the river Tweed) currently representing the northern limit within Northumberland.

There are potential issues with species distribution records as, whilst individuals may be present, they can go unobserved, resulting in negative records. Furthermore, some sites hold no records. Thus, range expansion studies can lack precision. However, *C. splendens* was recorded in the present study at Broomepark (NU 099122) on the river Aln, despite a previously negative account (Jeffries, 2005), suggesting an expansion rather than an undetected presence. Indeed, *C. splendens* is now present at a number of sites on the Aln. Additionally, it is now present within the previously unoccupied easterly extent of the river Coquet. However, there are a number of rivers within the county where the species is still absent. These include the river Font and Hart Burn (tributaries of the river Wansbeck), the river Lyne and the rivers Breamish and Glen (tributaries of the river Till, itself running into the river Tweed). This is despite the presence of *C. splendens* on neighbouring rivers. Of particular interest is the expansion from the river Aln (presumably) to the river Till without any known occupancy of the river Breamish, which lies between the two.

Habitat characteristics

The results indicate that the presence of bankside vegetation, extensive emergent channel vegetation and fringing reed banks are the most important habitat factors for the occurrence of adults, so supporting the views of various studies (Rozenweig, 1991; Raab *et. al.*, 1996; Schutte, 1997; Jeffries, 2001; Ward & Mill, 2005, 2008). Such vegetation is used by males to guard and defend their territory (Corbet, 2008), and for shelter from adverse weather e.g. high winds (Ward & Mill, 2005). It is also important in reproduction, with females laying eggs endophytically into a wide range of emergent vegetation (Siva-Jothy, 1995) and larvae found amongst the root systems of such vegetation (Gibbons, 1986).

Agriculture and excessive cattle grazing, that reduce this bankside vegetation, do not produce suitable habitat for *C. splendens* (Schutte, 1997; Ward & Mill, 2005) and the present study demonstrates that *C. splendens* has a predilection for river habitat surrounded by rough/unimproved pasture, which allows vegetation to grow (Plate 1). The absence of *C. splendens* from the river Glen, which is grazed along almost its entire length, and so is virtually devoid of bankside vegetation, emphasises this relationship.

The degree of shading within a habitat is an area of contention in regards to its influence over site selection by *C. splendens*, with studies by Jeffries (2001), Corbet (2008) and Ward & Mill (2008) suggesting a preference for exposed sites (i.e. with little overhanging vegetation such as trees and shrubs), whilst Hofman (2005) indicated a tendency for it to choose shaded sites with plentiful overhanging vegetation. However, data from the present study suggests instead that there is no clear relationship between habitat shading (i.e. tree and shrub density) and site selection, and that this habitat variable does not appear to have any influence. This was an unexpected result, as previous studies have reported that various aspects of breeding behaviour require an exposed environment free of trees and shrubs (Ward & Mill, 2005). Such vegetation creates a visual barrier, blocking a males vantage point from which to protect its territory (Ward & Mill, 2005); it also creates shade, so minimising the sunlight exposure this species prefers, and suppresses other vegetation that would provide suitable perching and oviposition sites (Corbet, 1962).

Conclusion

It appears that the provision of suitable habitat along the Northumberland rivers has enabled this recent range expansion. However, there is much variation across the county. Thus the rivers Lyne and Breamish lack suitable vegetation, at least at the sites visited. Indeed the river Breamish runs through the uplands of Northumberland, where climatic limitations restrict land use to extensive livestock rearing (Swan, 1993), which limits the growth of suitable flora. Thus it is likely that there is no suitable habitat along the entire length of this river and hence it is unlikely that *C. splendens* will ever establish territory here. This is confirmed by its presence on rivers located immediately to the north and south.

The rivers Glen and Till lie within north Northumberland and are separated from the south by moorland and the Cheviot Hills, which has been suggested could provide a barrier to northward movements (Jeffries, 2001; Ward & Mill, 2005). However, *C. splendens* is now present along the river Till. Furthermore, there are suitable sites on this river that are currently unoccupied, signifying potential range expansion along its length. This, combined with sightings in south-west Scotland (Batty, 2007), suggests that this species has yet to reach its northern range limit in Northumberland.

References

Batty, P. 2007. Changes in Scottish dragonflies. *Dragonfly News* **51**: 20-21.

Brooks, S., Parr, A. & Mill, P. J. 2007. Dragonflies as climate change indicators. British Wildlife, **19:** 85-93

Cham, S., Nelson, B. Parr, A., Prentice, S. Smallshire, D. & Taylor, P. 2014. Atlas of Dragonflies in Britain and Ireland. The British Dragonfly Society and The Biological Records Centre, Wallingford. 280pp.

Clarke, D. 1999. The outpost populations of the Banded Demoiselle *Calopteryx splendens* (Harris) in the Solway Firth Area, Cumbria: historical perspective and recent developments. *Journal of the British Dragonfly Society* **15:** 33-38.

Corbet, P. 1962. *A Biology of Dragonflies*, Witherby: London.

Corbet, P., Brooks, S. 2008. *Dragonflies,* London: HarperCollins Publishers. 454 pp.

Gibbons, B. 1986. *Hamlyn Guide Dragonflies and Damselflies of Britain and Northern Europe*. London: Hamlyn Limited 144 pp..

Hassall, C. 2009. Variation in wing spot size and asymmetry of the Banded Demoiselle *Calopteryx splendens* (Harris, 1780). *Journal of the British Dragonfly Society* **25:** 7-15.

Hofmann, A. & Mason, C. 2005. Habitat characteristics and the distribution of Odonata in a lowland river catchment in eastern England. *Hydrobiologia* **539:** 137-147.

Jeffries, M. 2001. The Northumbrian frontier of the Banded Demoiselle *Calopteryx splendens* (Harris). *Journal of the British Dragonfly Society* **17:** 55-58.

Jeffries, M., Eales, H. & Storey, E. 2005. Distribution and habitat of the Banded Demoiselle *Calopteryx splendens* (Harris) in Northumberland. *Journal of the British Dragonfly Society* **21:** 1-5.

Merritt, R., Moore, N. W. & Eversham, B .C. 1996. *Atlas of the dragonflies of Britain and Ireland*. Huntingdon, HMSO.

Mill, P., Brooks, S. & Parr, A. 2010. dragonflies (Odonata) in Britain and Ireland. In: Silent

Summer: The State of Wildlife in Britain and Ireland (ed. Maclean, N.) Cambridge University Press, Cambridge. 471-494.

Perrin, V. 1999. Observations on the distribution, ecology and behaviour of the Hairy Dragonfly *Brachytron pratense* (Muller). *Journal of the British Dragonfly Society* **15:** 39-45.

Raab, R., Chovanec, A. & Wiener, A. 1996. Aspects of habitat selection by adult dragonflies at a newly created pond in Vienna, Austria. *Odonatologica* **25:** 387-390.

Rozenweig, M. 1991. Habitat selection and population interactions: the search for mechanism', *American Naturalist* **137:** 5-28.

Schutte, G. 1997. Mobility of the Rheobiont Damselfly *Calopteryx splendens* (Harris) in fragmented habitats (Zygoptera: Calopterygidae). *Odonatologica* **26:** 317-327.

Siva-Jothy, M., Gibbons, D. & Pain, D. 1995. Female oviposition-site preference and egg hatching success in the damselfly *Calopteryx splendens xanthostoma*. *Behavioural Ecology and Sociobiology* **37:** 39-44.

Storey, G. 2003. *Distribution and colonisation of the Banded Demoiselle (Harris) on the rivers Pont, Wansbeck, Blyth and Coquet in Northumberland*. B.Sc Thesis, Division of Environmental Management, Northumbria University, Newcastle upon Tyne.

Swan, G. 1993. *Flora of Northumberland*, 1st Edition, Newcastle upon Tyne: The Natural History Society of Northumbria. pp 24-27.

Ward, L. & Mill, P. 2004. Distribution of the Banded Demoiselle *Calopteryx splendens* (Harris) in northern England: an example of range expansion. *Journal of the British Dragonfly Society* **20:** 61-69.

Ward, L. & Mill, P. 2005. Habitat factors influencing the presence of adult *Calopteryx splendens* (Odonata: Zygoptera). *European Journal of Entomology* **102:** 47-51.

Ward, L. & Mill, P. 2008. Substrate selection in larval *Calopteryx splendens* (Harris) (Zygoptera: Calopreygidae). *Odonatologica* **37:** 69-77.

Website

Environment Agency. 2003. *River Habitat Survey in Britain and Ireland.* http://www.irpi.to.cnr.it/documenti/RHS%20manual%202003.pdf (Accessed: 25 February 2011).

Received 12 June, 2014, revised and accepted 12 October, 2014

Reintroduction and establishment of *Coenagrion mercuriale* (Charpentier) (Southern Damselfly) on Venn Ottery Common, Devon

David J. Thompson[1,3], Ameeka L. Thompson[1], Lesley Kerry[2] & Peter Gotham[2]

[1]Department of Evolution, Ecology & Behaviour, Institute of Integrative Biology, University of Liverpool, Liverpool, L69 7ZB
[2]Mount Pleasant, Stoneyford, Colaton Raleigh, Sidmouth, Devon, EX10 0HZ
[3]Corresponding author

Summary

The rationale and mechanics of a programme to re-introduce *Coenagrion mercuriale* (Charpentier) (Southern Damselfly) to Venn Ottery Common, a Devon Wildlife Trust reserve, is described. The donor sites were in the most genetically diverse area in the UK, Beaulieu Heath in the New Forest. Five hundred animals (100 males and 400 females) were collected and transported over the course of eight days in June 2009 (following a preliminary attempt in 2007). The recipient site was monitored regularly from May 2009 and numbers recorded in regular transect counts rose to 98 in July 2013. The key to the success of the re-introduction was prior knowledge of the habitat requirements of the study species and sustained preparation and maintenance of the recipient site.

Introduction

Coenagrion mercuriale (Charpentier) (Southern Damselfly) is one of the UK's rarest odonates. It is protected under Schedule 5 of the amended Wildlife and Countryside Act of 1981 and is classified as Rare (category 3) in the UK's Red Data Book. It occurs in Western Europe and North Africa and reaches the north-western edge of its range in the UK. It features in the Red Lists of all European countries in which it occurs and is listed in Appendix II of the Berne Convention and Annex II of the EU Habitats Directive. The Southern Damselfly Steering Group was established in 1997 under the chairmanship of Tim Sykes of the UK Environment Agency. Its aim was to co-ordinate an action plan for the species and to encourage conservation-oriented research. One of its stated aims was to re-establish *C. mercuriale* in sites from which it had been lost, provided that management plans were in place for its long-term persistence in such sites.

This paper describes the first such re-introduction project.

C. mercuriale was last recorded on Venn Ottery Common on the East Devon Pebblebeds in 1988. The probable reasons for its disappearance from the site were poor understanding of its ecological requirements, leading to unfavourable management. Specifically, there was insufficient grazing around its favoured runnels, leading to the development of large overhanging tussocks of *Molinia caerulea* (Purple Moor Grass). In addition, scrub encroachment higher up the site lead to a reduction in the amount of water entering these runnels. The one stream that did carry an adequate water supply flowed too quickly to be suitable for C*. mercuriale* larvae. These problems were acknowledged by local conservationists, including Lesley Kerry and Peter Gotham, and by the Devon Wildlife Trust (DWT). The site had been grazed by cattle since 1990 and prior to that by ponies. It is currently grazed by Exmoor ponies. In addition, the DWT had been opening up and diverting the main stream from a gully to run across the site, as at present. The site had been a candidate for the reintroduction of *C. mercuriale* since 1998 but it was clear that more work was needed before the site could be expected to hold a sustainable population again.

Rationale

Prior to the re-introduction programme, *Coenagrion mercuriale* occurred on two sites on the East Devon Pebblebeds, Colaton Raleigh Common and Aylesbeare Common (Fig. 1), though there were historical records from other Devon sites, notably Hense Moor (last recorded in 1965) and from two nearby Blackdown Hills sites, Southey Moor and Gotleigh Moor (last records from both were in 1959).

Previous work on *C. mercuriale* showed that it had poor dispersal ability as an adult (Purse *et al*., 2003; Rouquette & Thompson, 2007) and that isolated sites such as those on the East Devon Pebblebeds had relatively low genetic diversity, potentially rendering them liable to inbreeding depression (Watts *et al*., 2004, 2005, 2006). A third East Devon Pebblebeds site (Fig. 1) would increase the possibility of establishing a metapopulation structure in the area and increase the likelihood of an exchange of genetic material between sites. In addition, if animals could be brought in from the most genetically diverse site in the UK (Thompson & Watts, 2010) (Beaulieu Heath, New Forest), then the whole East Devon gene pool might be augmented. This proposition was put to Natural England, which granted a licence for the proposed re-introduction project to take place. It is fair to say that re-introductions merely to augment genetic diversity are not universally acceptable to the UK's conservation bodies. For example, the Countryside Council for Wales were not in favour of licensing

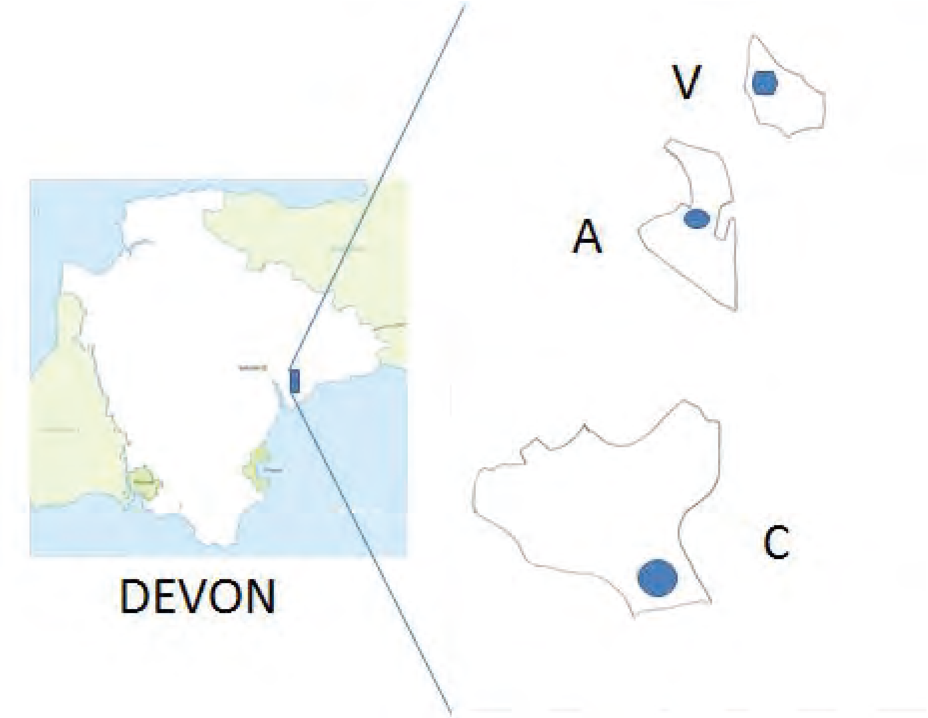

Figure 1. Relative positions of the three East Devon Pebblebed Heath sites that hold populations of *Coenagrion mercuriale*; V= Venn Ottery Common, A= Aylesbeare Common, C= Colaton Raleigh Common. The blue closed shapes indicate the approximate locations of the *C. mercuriale* colonies within each site. The distance between the centres of the Venn Ottery Common and Aylesbeare Common sites is 1.63 km; that between Aylesbeare Common and Venn Ottery Common is 3.81 km.

genetic augmentation to the UK's most genetically depauperate site (Nant Isaf, Anglesey), on the grounds that re-introduction could always take place at a later date if the present population were to go extinct. This is a defensible position, but not one with which we agree.

Preliminary attempt

The original plan was to introduce animals from Beaulieu Heath to Venn Ottery Common in 2007. A meeting that involved representatives from Natural England, Devon Wildlife Trust and three of the present authors (DJT, LK and PG) took place on site on 31 May 2007 and the project was given the go ahead. On 10 June 2007, 57 mature adults of *Coenagrion mercuriale* were brought from Beaulieu Heath to Venn Ottery in what was proposed to be the first of several reintroduction trips. However, there had been a dramatic change in the water level on the recipient site in a relatively short period (10 days) and those present (DJT, LK and PG) were of the opinion that the water supply to the site could no longer be considered to be reliable. The animals brought to the site were released in any case but the main reintroduction programme was halted until such time as the water supply could be relied upon.

Between the summers of 2007 and 2009 renewed efforts were made by LK, PG and DWT to secure the water supply. These efforts were made on four fronts. First, willow and birch trees were taken out at the north end of the site in the hope that the water they would have transpired would pass down the shallow runnels in which *C. mercuriale* was expected to breed. Second, a mixed herd of cross-bred cattle, was brought in to graze the site, especially the clumps of *Molinia caerulea* that still overhung some of the runnels, a technique used successfully in the expansion of the *C. mercuriale* population on nearby Aylesbeare Common (Kerry, 2001). Third, Devon Wildlife Trust constructed 14 dams at the western end of the site on the fast-flowing stream in the expectation that, if it could be slowed down further, it would produce ideal breeding habitat for *C. mercuriale*. Fourth, growth of *Potamogeton polygonifolius* (Bog Pondweed), a favoured oviposition plant for Southern Damselfly (Purse & Thompson, 2009), was encouraged.

Reintroduction

The re-introduction took place over eight days in June 2009. Adults of *Coenagrion mercuriale* were removed from various sites at Beaulieu Heath in the New Forest in Hampshire (Table 1). On the first two dates (22 and 24 June), only females that had previously laid a clutch of eggs were taken from the donor sites. These were distinguishable by the muddy tips of their abdomens, indicating that they had already oviposited. On subsequent trips, collections in the New Forest were made relatively early in the day, so that any females that had begun to lay a clutch of eggs would not have laid the full clutch. Both of these strategies were designed to increase the level of genetic diversity transferred from the New Forest to Venn Ottery Common. Thus a female would either have to re-mate with another male, thus increasing the level of genetic diversity in her offspring, or oviposit alone at Venn Ottery, using sperm stored from previous matings.

All adults were caught using standard kite nets. Animals were transferred from the kite nets into cylindrical, soft mesh, transparent butterfly cages in which they were transported. These cages measured 42cm in height, with a radius of 17.5cm. The maximum number transferred on a given day was 152 on 24 June in three separate cages. Of the 500 adults transported from the New Forest to

Table 1. The locations and dates (in 2009) from which 500 adult *Coenagrion mercuriale* were taken from the New Forest in Hampshire and relocated to Venn Ottery Common in Devon.

Date	British National Grid Reference	Location (all Beaulieu Heath)	Males	Females
22 June	SZ35909962	Peaked Hill West	13	82
24 June	SU34840004	Deep Moor	50	102
25 June	SZ36049895	Shipton Bottom	16	54
28 June	SZ36049895 SZ36189939	Shipton Bottom + Peaked Hill East	17	116
29 June	SZ35909962	Peaked Hill West	4	46
Total			100	400

Venn Ottery Common, a three hour car journey, only three individuals did not survive the journey. The remaining individuals all flew from the transfer cages shortly after the lids were unzipped.

The release points on Venn Ottery Common were close either to the newly dammed stream or to the original shallow runnels. Animals were released from more than one site each day to allow them to choose for themselves the most suitable breeding sites. Most individuals simply flew into surrounding vegetation as they would have done in the New Forest in late afternoon, though others began mating and some females began to oviposit alone.

Monitoring

The site has been monitored regularly by LK and PG since the preliminary re-introduction attempt of 2007. The first adults seen on the site were on 30 May 2009. Numbers of individuals encountered during a standard fixed route around the site were recorded (Table 2).

The habitats preferred by *Coenagrion mercuriale* on Venn Ottery Common include shallow runnels that have been opened up by grazing (Plate 1) and the

Table 2. Numbers of adult *Coenagrion mercuriale* recorded during fixed transect walks at Venn Ottery Common. The recorders were LK and PG. All walks began after 11.00 and were completed before 15.00 hours.

Date	Males	Females	Pairs	Total
2009				
30 May	2			2
1 June	5		4	13
2 June	10	1	3	17
3 June	11		3	17
5 June	11	1	8	28
7 June	9	1		10
13 June	7			7
14 June	15	2	3	23
22 June	11	1	2	16
2010				
2 June				0
24 June				0
28 June				0
2011				
20 May				0
31 May	8	1		9
3 June	2		1	4
4 June	21		8	37
14 June	9		3	15
16 June	11	2		13
23 June	1			1
27 June	18	4	2	26
2 July	25	1	8	42
2011 (cont.)				
8 July	18	4		22
14 July	16	2	4	26
27 July	6		1	8
3 August	4			4
2012				
8 July		1		1
11 July				0
17 July		1		1
22 July	1			1
2013				
8 June	7		1	9
19 June	25	2	8	43
29 June	44	3	9	65
6 July	43	4	23	93
9 July	31	5	31	98
14 July	25	2	14	55
19 July	9	1	2	14
2014				
20 June	11	1	1	14
1 July	13		2	17
17 July	5		1	7
22 July	5		1	7

habitat upstream of the 14 dams built across the fast-flowing stream, where there is a good growth of *Potamogeton polygonifolius* (Plate 2), a preferred oviposition plant, as noted above.

The re-introduction programme was successful. Some of those individuals released in 2007 were able to breed on the site and all of the data relating to 2009 (Table 2) refer to individuals that completed their life cycles on Venn Ottery Common and not those brought from the New Forest. A maximum count of 28 on 5 June, followed by counts of 23 and 16 on 14 and 22 June respectively indicate that the population may have been sustainable even before the main re-introduction attempt of 2009. Counts on 22 June were made prior to the

Plate 1. One of the shallow runnels preferred by *Coenagrion mercuriale* that has been opened up by an improved grazing regime. Photograph by Lesley Kerry.

Plate 2. A view from upstream of one of the 14 dams put in place to slow down the fast flowing stream at the western end of the site. The vertical posts that hold the dam board in place are visible at the top of the plate. One of the preferred oviposition plants for *Coenagrion mercuriale*, *Potamogeton polygonifolius*, grows well in the pools created in front of the dam. Photograph by Lesley Kerry.

release of New Forest animals on that date.

By 2011 the Venn Ottery population was even healthier than in 2009, with a high count of 37 on 4 June and the maximum count of 42 on 2 July. Given the mean mature adult lifespan of around five days for *C. mercuriale* at nearby Aylesbeare Common (Purse & Thompson, 2005), it is encouraging to note a 28-day gap between the two highest counts for 2011. This indicates a strong population throughout a month-long flying season, with a relatively high count (26) after a further 12 days (i.e. 14 July).

In 2013 the five highest counts at Venn Ottery Common were recorded, with peaks of 93 and 98 on the 6 and 9 of July respectively. These counts were more than double those of the peak counts in 2011, indicating further that the population was firmly re-established.

The Southern Damselfly has a semi-voltine life cycle in the UK (Purse & Thompson, 2002) and so, in the early years, almost all individuals were encountered in odd-numbered years. Three individuals (one male and two different female morphs) were found in 2012 but by 2014 the peak count had risen to 17 (Fig. 2) (see Thompson *et al*., 2015).

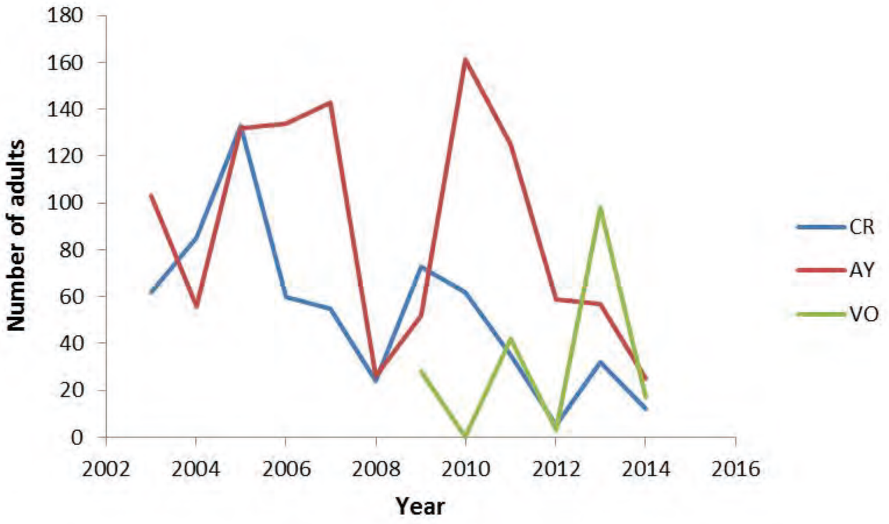

Figure 2. Maximum counts for adult *Coenagrion mercuriale* at the three East Devon Pebblebed sites from 2003 to 2014; CR= Colaton Raleigh Common; AY= Aylesbeare Common; VO= Venn Ottery Common.

Discussion

The re-introduction programme has been an undoubted success. It is likely that any population that gives a transect count of 98 on one day probably has an actual population size over the course of the season of more than a thousand (Allen & Thompson, 2014). However, it is dangerous to be complacent. The maximum population counts for *Coenagrion mercuriale* at the three East Pebblebed sites over the past 11 years shows that both the Aylesbeare and Colaton Raleigh Common populations fluctuated wildly, with the Colaton Raleigh population seemingly declining (Fig. 2). Each of these populations requires active management, with the monitoring giving advanced warning that more action may be required.

Continued grazing is certainly necessary on all three sites. Venn Ottery Common is currently grazed by four Exmoor ponies, probably a minimum requirement. There have been some early warning signs that close management is required at Venn Ottery. Some of the pools in front of the dams that were put in place to slow down the fast-flowing stream (see Plate 2), and which were so effective, have silted up and are in danger of becoming less effective. New dams are planned. As this site is closely monitored, the future for the *C. mercuriale* population on Venn Ottery Common looks secure.

Acknowledgements

This work was carried out under licence from Natural England. The Forestry Commission gave permission to remove animals from the donor site in the New Forest and Devon Wildlife Trust supported the introduction to their own site at Venn Ottery Common. We would like to thank those DWT staff involved in the site restoration work, especially Ian Chadwick, not least for the construction of the dams. Funding was provided by the British Dragonfly Society and the Environment Agency.

References

Allen, K.A. & Thompson, D.J. 2014. Population size and survival estimates for the rare damselflies *Coenagrion mercuriale* and *Ischnura pumilio*. *Insect Conservation & Diversity* **7:** 241-251.

Kerry, L. 2001. Habitat management for the Southern Damselfly, *Coenagrion mercuriale* (Charpentier) on Aylesbeare Common, Devon. *Journal of the British Dragonfly Society* **17:** 45-48.

Purse, B.V., Hopkins, G. W., Day, K.J. & Thompson, D.J. 2003. Dispersal characteristics and management of a rare damselfly. *Journal of Applied Ecology* **40:** 716-728.

Purse, B.V. & Thompson, D.J. 2002. Voltinism and larval growth patterns in *Coenagrion mercuriale* (Odonata: Coenagrionidae) at its northern range margin. *European Journal of Entomology* **99:** 11-18.

Purse, B.V. & Thompson, D.J. 2005. Lifetime mating success in a marginal population of a damselfly, *Coenagrion mercuriale*. *Animal Behaviour* **69:** 1303-1315.

Purse, B.V. & Thompson, D.J. 2009. Oviposition site selection by *Coenagrion mercuriale* (Odonata: Coenagrionidae). *International Journal of Odonatology* **12:** 257-273.

Rouquette, J.R. & Thompson, D.J. 2007. Patterns of movement and dispersal in an endangered damselfly with implications for its management. *Journal of Applied Ecology* **44:** 692-701.

Thompson, D.J. & Watts, P.C. 2010. Dragonflies and damselflies. In: Newton, A.C. (ed.) *Biodiversity in the New Forest*. Pisces Publications, Newbury. Ch. 4: 36-45.

Thompson, D.J., Kerry, L., Sims, A. M. & Watts, P.C. 2015. Rapid cohort splitting in *Coenagrion mercuriale* (Charpentier) (Southern Damselfly) following its re-introduction to Venn Ottery Common, Devon. *Journal of the British Dragonfly Society* **31:**24-29.

Watts, P.C., Kemp, S.J., Saccheri, I.J. & Thompson, D.J. 2005. Conservation implications of genetic variation between spatially and temporally distinct colonies of the damselfly *Coenagrion mercuriale*. *Ecological Entomology* **30:** 541-547.

Watts, P.C., Rouquette, J.R., Saccheri, I.J., Kemp, S.J. & Thompson, D.J. 2004. Molecular and ecological evidence for small-scale isolation by distance in the endangered damselfly, *Coenagrion mercuriale*. *Molecular Ecology* **13:** 2931-2944.

Watts, P.C., Saccheri, I.J., Kemp, S.J. & Thompson, D.J. 2006. Population structure and the impact of regional and local habitat isolation upon genetic diversity of the endangered damselfly *Coenagrion mercuriale* (Odonata: Zygoptera). *Freshwater Biology* **51:** 193-205.

Received 29 July 2014, accepted 8 August 2014

Rapid cohort splitting in *Coenagrion mercuriale* (Charpentier) (Southern Damselfly) following its re-introduction to Venn Ottery Common, Devon

David J. Thompson[1], Lesley Kerry[2], Angela M. Sims[3] & Phillip C. Watts[4]

[1,5]Department of Evolution, Ecology & Behaviour, Institute of Integrative Biology, University of Liverpool, Liverpool, L69 7ZB
[2]Mount Pleasant, Stoneyford, Colaton Raleigh, Sidmouth, Devon, EX10 0HZ
[3]Section of Ecology & Evolutionary Biology, Department of Biology & Environmental Sciences, University of Jyväskylä, PO Box 35, 40014 Finland
[4] Department of Biology, University of Oulu, PO Box 3000, FI–90014 Oulu, Finland
[5] Corresponding author

Summary

The rapid occurrence of cohort splitting in a population of *Coenagrion mercuriale* (Southern Damselfly), recently re-introduced to Venn Ottery Common, an East Devon Pebblebed site, is described. Evidence of cohort splitting, rather than immigration from one of the other East Devon Pebblebed sites, was confirmed by analysis of 14 microsatellite loci from DNA extracted from a leg of one of the 'odd-year' cohort. This individual carried alleles not previously recorded in any Devon population.

Introduction

Coenagrion mercuriale (Charpentier) (Southern Damselfly) (Plates 1, 2) has a two-year life cycle in the UK (Purse & Thompson, 2002). In those populations in which there has been regular monitoring, notably in Aylesbeare Common on the East Devon Pebblebeds (Fig. 1) and Dry Sandford Pit in Oxfordshire, there has been evidence of a strong and a weak year class. Both of these populations have been closely monitored, following management that has led to large population increases (Kerry, 2001). The populations in the alternate year classes would appear outwardly to behave as two separate populations, each with its own dynamics.

Watts & Thompson (2012) compared the genetic signatures of nine UK populations of *C. mercuriale* (including Aylesbeare Common and Dry Sandford Pit) in consecutive years (2002, 2003) at 14 microsatellite loci. The results were particularly clear. There were low levels of genetic divergence between

Plate 1. Adult male *Coenagrion mercuriale*. Photograph by Phillip Watts.

Plate 2. Andromorph female *Coenagrion mercuriale*. Photograph by Phillip Watts.

sympatric cohorts, indicating that those individuals that jumped cohorts recruited (i.e. reproduced) successfully to a different cohort. Genetic diversity at each site was maintained in each year class and, indeed, was maintained in alternate year cohorts regardless of the level of diversity. The mean allelic richness values of 14 microsatellite loci from Aylesbeare Common and Colaton Raleigh Common (also an East Devon Pebblebed site) were 2.30 and 2.74 respectively, whereas those of various sites at Beaulieu Heath in the New Forest were between 4.70 and 4.80 (Watts *et al*., 2005). Thus the Devon sites were genetically depauperate and hence the recent reintroduction of individuals

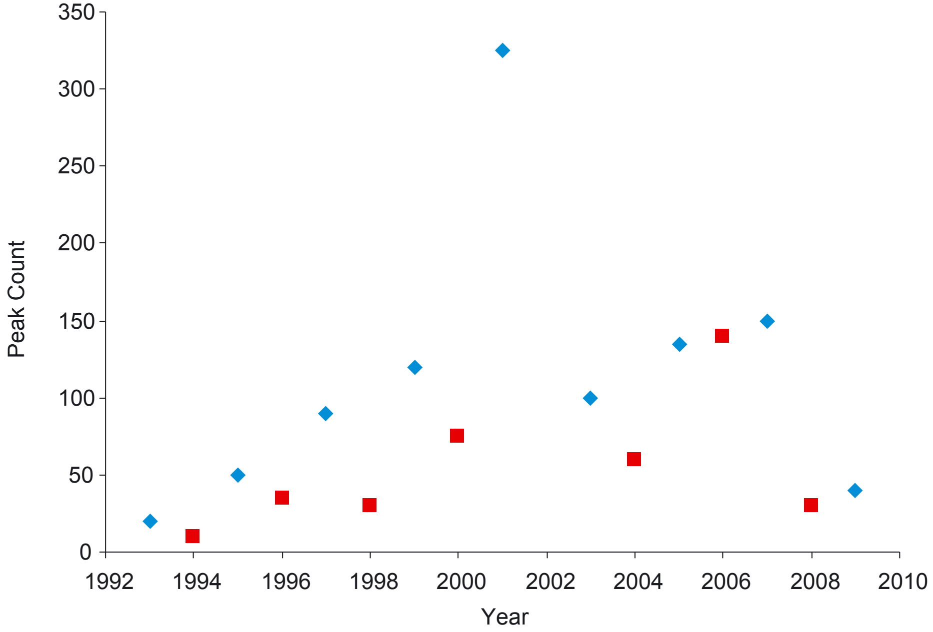

Figure 1. Peak counts of *Coenagrion mercuriale* at Aylesbeare Common, Devon, indicating the strength of the ‘odd year’ year-class in the early years of population growth compared with that of the ‘even year’ year-class (see Purse & Thompson, 1992). ◆, odd-numbered years; ■, even-numbered years. Note that there is no peak count for 2002.

of *C. mercuriale* from Beaulieu Heath to the East Devon Pebblebed site at Venn Ottery Common, a Devon Wildlife Trust reserve (Thompson et al., 2015), would bring with them more genetic diversity, i.e. greater allelic richness, to the East Devon Pebblebeds.

Any factor that creates variation in development times may partition a population into discrete subpopulations – or cohorts. In all UK populations of *Coenagrion mercuriale* there are ‘odd’ and ‘even’ year cohorts which, most likely, all originated from colonisers in one year (be they odd or even). What has never been clear is how rapidly cohort splitting can occur. In other words how strict is the two-year life cycle? The opportunity arose to investigate this phenomenon with the above mentioned re-introduction of *C. mercuriale* to Venn Ottery Common (Thompson *et al*., 2015). During this re-introduction, 57 *C mercuriale* were taken from Beaulieu Heath, New Forest to Venn Ottery Common in 2007. A larger re-introduction involving 500 individuals took place in June 2009.

Method

As noted above, individuals of *Coenagrion mercuriale* were only re-introduced to Venn Ottery Common in ‘odd’ years (i.e. 2007 and 2009) and Venn Ottery Common has been monitored for *C. mercuriale* from May 2009 each year up to the present time (Thompson *et al*., 2015).

The first animals recorded in an even year were one male and two (different) females in 2012 (see below). It was unclear initially whether these even-year animals were derived from the 2007 or 2009 re-introductions (i.e. cohort splitters) or were immigrants from one of the two other East Devon Pebblebed sites for *C. mercuriale* (Aylesbeare Common and Colaton Raleigh Common). For this reason the left middle tibia of one of the females was removed for genetic analysis (by microsatellite genotyping). Full details of the molecular biology protocols used to genotype this individual at 14 microsatellite loci have been described by Watts *et al*. (2004a, b). To determine the most likely population of origin of the sampled female, we used the assignment index calculator. Briefly, this software calculates a probability (an assignment index) that any genotype would originate from potential donor populations on the basis of their allele frequencies and the assumptions of Hardy-Weinberg equilibrium conditions and unlinked loci – individuals are assigned to a population on the basis of having the highest probability of assignment to that population; full details of the calculations are as described by Paetkau *et al*. (1995). The potential source populations used represented genotyped *Coenagrion mercuriale* from (1) Dartmoor (*n*=99 individuals), (2) East Devon Pebblebeds – the nearest sites to Venn Ottery Common (*n*=68), (3) Dorset (*n*=143), (4) Itchen Valley (*n*=366), (5) New Forest – the donor sites for the re-introduction (*n*=1,135) and (6) Oxford (*n*=50).

Results

One of the two females observed at Venn Ottery Common in July 2012 was an andromorph. Andromorph females have not previously been recorded on either of the other East Devon Pebblebed sites, strongly suggesting that it was derived from the introduced New Forest stock.

In addition, analysis of microsatellite genotyping at 14 loci, showed that the New Forest was the most likely source of that same andromorph female (Assignment Index probability $p=7.9\times10^{-11}$), with the next most likely source being the Itchen Valley (Assignment Index probability, $p=8.7\times10^{-12}$). The local (i.e. East Devon) populations were an unlikely source for the sampled female, with a very low Assignment Index probability ($p=2.7\times10^{-21}$).

Discussion

The origin of at least one of the three animals recorded on Venn Ottery Common in 2012 is undoubtedly from the stock of animals brought from Beaulieu Heath, New Forest in either 2007 or 2009. This indicates that cohort splitting occurred surprisingly quickly. It is unclear whether some individuals were able to pass through their life cycle in just one year, or whether some drifted into a three-year life cycle. The former seems more likely as the population density of damselfly larvae in the runnels and streams would be lower than in the New Forest and so food intake is likely to be higher, leading to a reduction in the development time (Pickup & Thompson, 1990).

Acknowledgements

This work was carried out under licence from Natural England. Funding was provided by the British Dragonfly Society, the Natural Environment Research Council (NER/A/S/2000/01322) and the Environment Agency.

References

Kerry, L. 2001. Habitat management for the Southern Damselfly, *Coenagrion mercuriale* (Charpentier) on Aylesbeare Common, Devon. *Journal of the British Dragonfly Society* **17:** 45-48.

Paetkau, D., Calvert, W., Sterling, I. & Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* **4:** 347-354.

Pickup, J. & Thompson, D.J. 1990. The effects of temperature and prey density on the development rates and growth of damselfly larvae (Odonata: Zygoptera). *Ecological Entomology* **15:** 187-200.

Purse, B.V. & Thompson, D.J. 2002. Voltinism and larval growth patterns in *Coenagrion mercuriale* (Odonata: Coenagrionidae) at its northern range margin. *European Journal of Entomology* **99:** 11-18.

Thompson, D.J., Thompson, A.L., Kerry, L. & Gotham, P. 2015. Reintroduction and establishment of *Coenagrion mercuriale* (Charpentier) (Southern Damselfly) on Venn Ottery Common, Devon. *Journal of the British Dragonfly Society* **31:** 14-23.

Watts, P.C., Hong-Wu, J., Westgarth, C., Thompson, D.J. & Kemp, S.J. 2004a. A panel of microsatellite loci for the Southern Damselfly, *Coenagrion mercuriale* (Odonata: Coenagrionidae). *Conservation Genetics* **5:** 117-119.

Watts, P.C., Kemp, S.J., Saccheri, I.J. & Thompson, D.J. 2005. Conservation implications of genetic variation between spatially and temporally distinct colonies of the damselfly *Coenagrion mercuriale*. *Ecological Entomology* **30:** 541-547.

Watts, P.C. & Thompson, D.J. 2012. Developmental plasticity as a cohesive evolutionary process between alternate-year insect cohorts. *Heredity* **108:** 236-241.

Watts, P.C., Thompson, D.J. & Kemp, S.J. 2004b. Cross-species amplification of microsatellite loci in some European zygopteran species (Odonata: Coenagrionidae). *International Journal of Odonatology* **7:** 87-96.

Received and accepted 8 August 2014

A Review of the Odonata of the Channel Islands

[1]Adrian J. Parr and [2]Roger Long

[1]10 Orchard Way, Barrow, Bury St Edmunds, Suffolk IP29 5BX
[2]Ozarda, Les Hamonnets, St John, Jersey JE3 4FP

Summary

In all, some 37 species of Odonata – comprising 12 zygopterans (damselflies) and 25 anisopterans (true dragonflies) - have been recorded from the Channel Islands, and records of these species are reviewed. A number of species formerly considered to be resident are now known to be locally extinct, largely as the result of the loss of suitable habitat. A number of species have, by contrast, only started to appear in the Islands within the last twenty years, probably part of the pan-European range changes resulting from climate change.

Introduction

The Channel Islands – of which Jersey, Guernsey and Alderney comprise the most significant islands, but which also include others such as Sark, Herm, Brecqhou and Jethou (Fig. 1) – have historically been linked to England since at least 1204 but are more intimately part of the French faunistic zone. This has lead to some debate as to how best to publish information on their wildlife. Coupled with the relatively low number of active recorders for many animal and plant groups, this has often led to a shortage of readily-accessible information on the Islands' wildlife, particularly outside of the Islands themselves. Dragonflies are no exception to this phenomenon. With major shifts in the distribution of British and European dragonflies now taking place, there is a growing need to bring the Islands' dragonfly fauna to a wider audience, and the present paper attempts to give an overview of the current situation.

History of dragonfly recording in the Channel Islands

Information on the dragonfly fauna of some of the larger islands was first published in 1862 (Ansted & Latham, 1862) but, more importantly, around the end of the nineteenth century by William Luff (e.g. Luff, 1892, 1900). Further information then became available during the late 1930s and 1940s, when Roderick Dobson started a study of the dragonflies of Jersey. During the 1940-

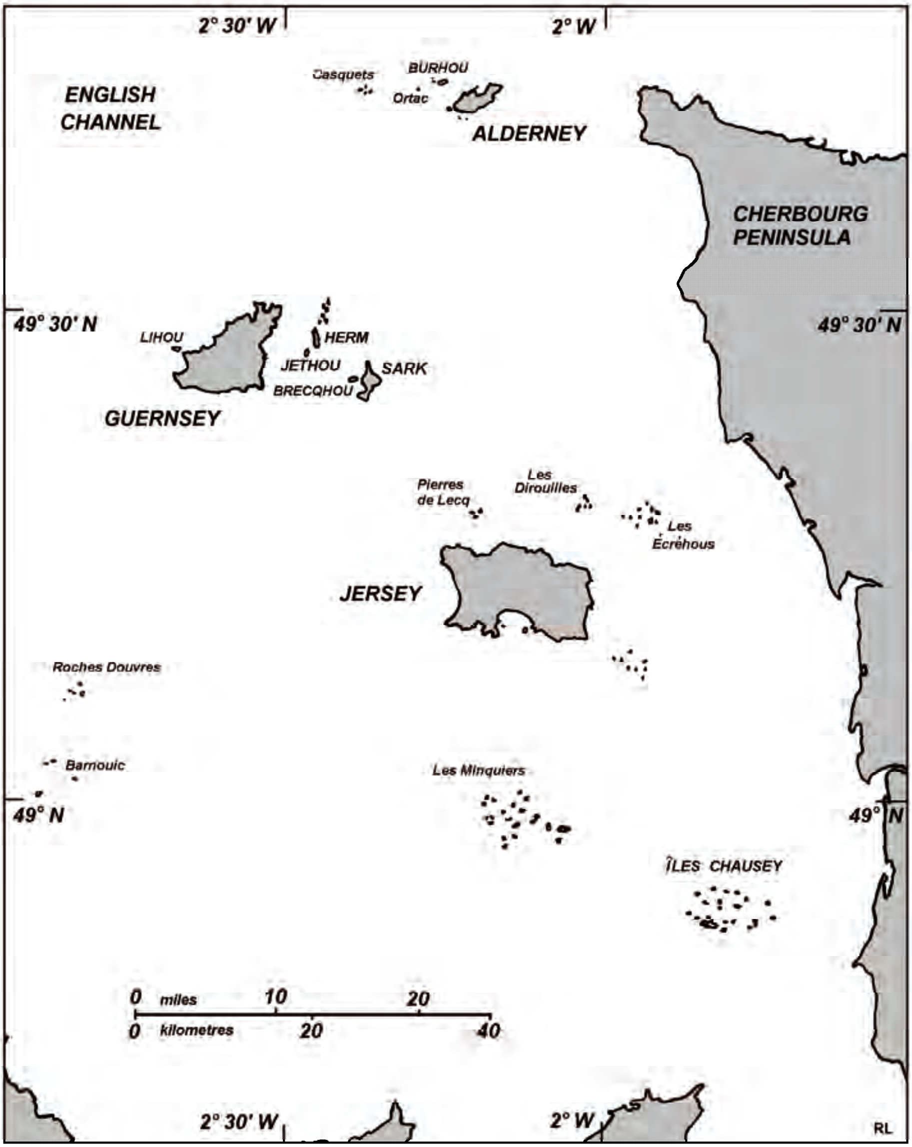

Figure 1. The location of the Channel Islands in relation to the English Channel and the Cherbourg Peninsula, France.

45 German occupation, Dobson also established a junior group of the Société Jersiaise, the star member of which was to be a young Walter Le Quesne. Dobson and Le Quesne studied dragonflies together, with Le Quesne going on to write up many of the results (e.g. Le Quesne, 1941, 1946). From this period on, entomological reports in journals such as the *Annual Bulletin of the Société Jersiaise* and the *Report and Transactions of La Société Guernesiaise* not infrequently contain dragonfly-related snippets, but another major milestone was in 1980, when Jean Belle published an article on the Odonata of Guernsey and the other Sarnian Islands (i.e. islands in the Bailiwick of Guernsey) such as Alderney (Belle, 1980). Jill Silsby later described the results of a visit to Jersey during July 1988 (Silsby & Silsby, 1988), which was supplemented with further information from Le Quesne, who had retired to live in Jersey in 1985 after a long period away. Importantly, Margaret Long together with one of the present authors (RL) – two more people initially enthused by Dobson – have also published much information on the dragonflies of the Channel Islands, and Jersey in particular, over the last third of the twentieth century and into the twenty-first, lately having been greatly assisted by Richard Perchard. Since about 1995 onwards, interest in dragonflies in the Channel Islands has become slightly more widespread, and there are now regular, if scattered, notes in the literature as well as some less-formally published information (e.g. photographs available on the internet). This paper sets out to pull together much of the diverse information that is available on the Odonata of the Channel Islands, in the hope that it will not only help bring the Islands' dragonflies to a wider audience, but also perhaps stimulate further interest. It should be noted that considerable changes (often involving a deterioration or loss of sites) have occurred to the Islands' ponds and wetlands over the last century and historic records thus do not always fit closely with the current status of many species. In particular, several species that were probably resident a hundred years ago have now been lost. Of the larger islands, the dragonfly fauna of Guernsey now seems especially limited by the lesser availability of suitable habitat.

Species accounts

The following species have been recorded over the years from one or other of the Channel Islands:

Zygoptera

***Chalcolestes viridis* (Vander Linden) - Willow Emerald Damselfly -** Resident. The species' local stronghold is in Jersey, from where it was first reported in 1944 (Le Quesne, 1946). Following a period of very few records during the mid-1960s to mid-1980s, when it was once feared that the species might have died out, though it was most probably just under-recorded, reports then began once again in 1989 (Le Quesne, 1990). In the modern era, the species is clearly well-established in the island with numerous widespread, regular, sightings; a particularly striking observation was of a gathering of well over a hundred individuals found amassed on a willow bush in early September 2001 (Long, 2001). There are two records from Alderney, the most recent being in 2012 (Wedd, pers. comm.), and a single male was recorded from Guernsey during July 2003 (Medland, pers. comm.).

Lestes barbarus **(Fab.) - Southern Emerald Damselfly -** Vagrant, transient resident/recent colonist (Plate 1). Two females were reported from Jersey during autumn 1945 (Le Quesne, 1946), after which further records were not forthcoming from the island until 1995 (Long, 1996). In the years thereafter, there were to be many more records, with regular sightings at two sites (Noirmont Warren and L'Ouaisné Pond (Plate 2)) up to 2009, strongly suggesting the presence of established colonies. A lack of records during 2010-2012 was probably due to the great difficulty in gaining adequate access, as up to a dozen were then seen on two occasions at one of the regular sites in 2013, with over 50 present there in July 2014. In Alderney, the species was recorded at the end of the nineteenth century in numbers suggestive of an established colony (Luff, 1901), but the only later record was when Dobson took two males and two females at Mannez Pond on 5 June 1965 while visiting the island.

Plate 1. *Lestes barbarus*, male. Jersey, 9 August 2006. Photograph by R. Perchard.

Plate 2. L'Ouaisné Pond, St Brelade, Jersey. Photograph by R. Long.

Sympecma fusca **(Vander Linden) - Winter Damselfly -** Vagrant, may have bred. Two immatures were noted from La Hague Reservoir, St Peter, Jersey, on 2 August 1945, with another individual found a week later (Le Quesne, 1946). This perhaps suggests transient local breeding. The only other record from the island, and indeed from the Channel Islands, is one found over a small reservoir at St Catherine, Jersey, on 8 July 1992 (Long & Long, 1993).

Calopteryx splendens **(Harris) - Banded Demoiselle -** Migrant. The Channel Islands lack the broad, slower-flowing rivers and streams favoured by *Calopteryx splendens*, so that the species is not resident. It was listed for Jersey by Ansted & Latham (1862), and further occasional individuals have been encountered in Jersey and Alderney since 1941, presumably being immigrants from France; one was even noted from Jersey arriving in off the sea during 2007 (Long & Long, 2008). There is but one record from Guernsey, that being of a male photographed during 2010 (Medland, pers. comm.). Records tend to come late in the species' flight period, often in August. This is perhaps due to a post-breeding dispersal phase, though local weather conditions might also be important.

Calopteryx virgo **(L.) - Beautiful Demoiselle -** Resident. This is the typical demoiselle of shady streams in the Channel Islands, and was recorded from the region as early as the mid-nineteenth century (Ansted & Latham, 1862). The species can be locally common, though its occurrence is limited by the availability of suitable unpolluted habitat. In Jersey, records from the earliest dates right up until the late twentieth century were centred on small valleys in the east of the island but, during the last decade, it has steadily spread to more valleys, working progressively westwards. Records from Guernsey declined during the twentieth century, probably due to habitat loss, and the species is now very rare and erratic in the island; *Calopteryx virgo* is apparently unrecorded from Alderney.

***Coenagrion puella* (L.) - Azure Damselfly -** Resident. First reported in the nineteenth century (Ansted & Latham, 1862), the species is generally common, though dependent on the availability of suitable habitat. It is recorded from Jersey, Guernsey and Alderney. Almost all records from Guernsey date from pre-2000, though singles were noted at four sites during 2014 (Medland, pers. comm.).

***Coenagrion pulchellum* (Vander Linden) - Variable Damselfly -** Status uncertain, probably former resident. The species was reported as common at the Grande Mare, Guernsey, by Luff (1892), though, with a later reduction in the water-table at this site having made the area unfavourable, there have been no subsequent records from the island. Reports from Jersey during 1940 and 1941 (Le Quesne, 1941) are now known to be in error, the damselflies having later been correctly identified as *Coenagrion scitulum* Dainty Damselfly (Le Quesne, 1951). However, Le Quesne (1946) did report additional individuals from two sites in Jersey during June 1945.

***Coenagrion scitulum* (Rambur) - Dainty Damselfly -** Vagrant and transient(?) resident. (Plate 3). The species was recorded from Guernsey in 1956 (Shayer, 1957) but there have been no further records from the island. In Jersey, two individuals were reported during 1940 and a further individual was noted from a different site during 1941, though it took some while for the true identify of these damselflies to be established (see Perchard & Long, 2009). Sightings then ceased and the species went unrecorded for many years. During 2009, individuals were, however, to be observed during June/July at two sites in the same general area as the older Jersey sightings (Perchard & Long, 2009). Breeding clearly took place and, at the main site (Plate 4), records continued for several more years. A lack of sightings during 2012–14 may, however, suggest that the colony has now been lost. *Coenagrion scitulum* is known to currently be expanding its range in north-west Europe, and the recent Jersey records appear to be part of this phenomenon (Swaegers *et al*., 2013).

***Enallagma cyathigerum* (Charp.) - Common Blue Damselfly -** Resident. First reported from Jersey by Luff (1909). During the 1940s Le Quesne (1941, 1946) found the species to be strongly centred on just one pond at Portelet Common. In more recent times there has been a much wider scatter of records

Plate 3. *Coenagrion scitulum*, female. Jersey, 24 June 2009. Photograph by R. Perchard.

Plate 4. Meadow in Grouville, Jersey; the larger of the two sites where *Coenagrion scitulum* was recently re-found. Photograph by R. Perchard.

from Jersey and records have also been forthcoming both from Alderney, starting in 1981 (Long, 1989), and from Guernsey (Austin, 2004). Over the last few years, Wedd (pers. comm.) notes the species as now ‘very common’ in Alderney, whilst Medland (pers. comm.) describes it as widespread, but at low density, in Guernsey. Perhaps this species is becoming more common in the Channel Islands as the nature of water-bodies in the region has evolved.

***Erythromma viridulum* (Charp.) - Small Red-eyed Damselfly -** Transient resident and potential colonist. The species was first reported from the Channel Islands in the extensive grounds of a hotel west of St Peter Port, Guernsey, during 2003 (Austin, 2004) (Plate 5), with significant numbers also being seen in the island during 2004. Few records were received from Guernsey over the period 2005-2013 but 2014 saw several further sightings, with oviposition being noted at two sites (Medland, pers. comm.). In Jersey the first record of *Erythromma viridulum* came during July 2004, when 50+ individuals were seen at Jersey Zoo (Long & Long, 2005). Sightings persisted at this site until 2008, strongly suggestive of local breeding taking place, though the colony has seemingly now disappeared. These records from the Channel Islands are clearly part of the well-documented range expansion currently taking place in north-west Europe (Cham *et al*., 2014).

***Ischnura elegans* (Vander Linden) - Blue-tailed Damselfly -** Resident. An abundant breeding species, long known from the Islands (Luff, 1892, 1904). It is reported from Jersey, Guernsey, Alderney and Sark.

***Pyrrhosoma nymphula* (Sulzer) - Large Red Damselfly -** Resident. This species was common in the past in Jersey (Le Quesne, 1946) and in Guernsey (Luff, 1892), though there have been fewer recent reports, perhaps as a result of habitat loss and also under-reporting. Certainly it has long since vanished from La Grande Mare, Guernsey, as a result of habitat changes, and the species was reported by Belle (1980) as now threatened in Guernsey. In contrast, the species was not noted from Alderney until 2010, but is now increasing fast, being found principally at Mannez Pond (Wedd, pers. comm.).

Anisoptera

***Aeshna affinis* Vander Linden - Southern Migrant Hawker -** Migrant and possible resident. (Plate 6). The first record for the Channel Islands was made at Rosel Manor, Jersey (Plate 7), on 17 July 1998 (Long, 2000). The next record followed from the island on 8 August 2004 (Long & Long, 2005) and a run of sightings from several localities during the next few years may suggest that the species had become established. The lack of observations in very recent years is probably attributable to much reduced coverage and its present status is not

Plate 5. Ornamental pond at St Pierre Park Hotel, Guernsey. Photograph by J. Medland.

able to be assessed. Sightings are clearly part of the ongoing range expansion in north-western Europe (see e.g. Cham *et al*. (2014) for details of the British situation).

Aeshna cyanea **(Müller) - Southern Hawker -** Resident. This species was first reported from the region by Luff (1892), based on a specimen from Guernsey, though Belle (1980) gives no later records for the island. In Jersey, Le Quesne (1946) noted it as common in the 1940s and there have been regular and widespread later records, whilst in Alderney, Wedd (pers. comm.) mentions about three sightings per year in modern times, though it certainly breeds. It seems that the species is a somewhat patchily distributed resident.

Aeshna grandis **(L.) - Brown Hawker -** Migrant. This species was listed from Jersey by Ansted & Latham (1862), but perhaps through confusion or in error, as several other hawker dragonflies now common in the Channel Islands were not included, and there were to be essentially no further reports until the first confirmed record of one at Grands Vaux, Jersey, on 27 July 1993. The early years of the twenty-first century have, however, seen sporadic sightings from

Plate 6. *Aeshna affinis*, male. Jersey, 17 July 1998. Photograph by R. Perchard.

Plate 7. One of two ponds in Rosel Manor Grounds, Jersey, where Roderick Dobson made many of his earliest records. Photograph by R. Long.

Jersey, including one at Queen's Valley Dam on 31 August 2000 (Long, 2001), and also from Guernsey and Alderney. It is likely that the species is a migrant from France.

Aeshna mixta **Latreille - Migrant Hawker -** Resident and migrant. *Aeshna mixta* is a common and widespread species in the Channel Islands, with records dating back to the late nineteenth century (Luff, 1892, 1901, 1909). The species has been recorded from Jersey, Guernsey, Alderney, Sark and Herm; reports from the latter two islands probably refer to migrants/wanderers, as suitable breeding habitat in these islands is limited. Indeed, the species may currently also only be a migrant to Guernsey (Medland, pers. comm.).

Anaciaeshna isoceles **Müller - Norfolk Hawker -** Vagrant or former transitory resident. The species was reported from Jersey in the 1940s, both at St Ouen's Pond (Plate 8) and at another site about a mile away (Le Quesne, 1946). It might be a vagrant, or perhaps a now extinct resident.

Anax ephippiger **(Burmeister) - Vagrant Emperor -** Vagrant. A female was photographed on the south coast of Guernsey on 29 November 2014 (Medland, pers. comm.). Reports of single brown dragonflies from Jersey on 17 February 1998 (Long & Long, 1999) and from Guernsey during May 2011 probably also refer to this Afro-tropical migrant species, which has been noted in Great Britain at all times of year, even during mid-winter (Cham *et al*., 2014). Early 1998

Plate 8. St Ouen's Pond, Jersey. Photograph by R. Long.

saw several records from southern England of unidentified dragonflies similarly thought to be *Anax ephippige*r (Parr, 1998), whilst April-May 2011 saw a major influx of the species into many countries of north-west Europe (Parr, 2011).

Anax imperator **Leach - Emperor Dragonfly -** Resident. A common breeding species, noted from Jersey, Guernsey and Alderney. Records go back to the late nineteenth century (Luff, 1892).

Anax parthenope **(Selys) - Lesser Emperor -** Vagrant. Within the last two decades, there have been occasional records from Jersey (e.g. Long & Long, 1999) and from Guernsey (e.g. Austin, 2004). These fit within the recent range expansion of the species being seen in north-west Europe (Parr *et al*., 2004).

Brachytron pratense **(Müller) - Hairy Dragonfly -** Former resident(?). There is an historic record of one male captured many years ago in Guernsey (Luff, 1892), while in Jersey the species was noted as common at St Ouen's Pond (Plate 8) during spring 1945, with larvae found at a second site (Le Quesne, 1946). This implies that the species was then breeding in Jersey, but there are apparently no recent records.

Cordulegaster boltonii **(Donovan) - Golden-ringed Dragonfly -** Resident. In Jersey there have been occasional but widespread records over a long time interval, the species apparently being a scarce resident. In Guernsey it used also to be present, though not common (Luff, 1892). It is, however, apparently now absent from this island, probably as a result of habitat loss (Belle, 1980). The first record for Alderney was as recently as 30 June 2014 (D. Wedd, pers. comm.); since there is little suitable breeding habitat in the island, this individual was presumably a migrant/wanderer.

Cordulia aenea **(L.) - Downy Emerald -** Former(?) resident. The species has been recorded solely from Jersey, where it is mentioned as early as the mid-nineteenth century (Ansted & Latham, 1862). Still noted as breeding by Le Quesne (1946), there have been no recent records, though Silsby & Silsby (1988) report a 'possible' in 1988. Perhaps the species has now been lost.

Crocothemis erythraea **(Brullé) - Scarlet Darter -** Migrant and transient(?) resident. *Crocothemis erythraea* was noted in good numbers from St Ouen's Pond in Jersey (Plate 8) during the mid 1940s by Le Quesne (1946, 1948), with egg laying having been observed and successful breeding likely taking place; this was during a period of warmer than average annual temperatures. Records then ceased, though in recent years, as temperatures have risen once more, further sightings have resumed. These include individuals both in Jersey (e.g. Long & Long, 2007) and Guernsey (e.g. Austin, 2005, Parr, 2007) and indeed sightings from one or other of these islands now occur nearly annually.

***Libellula depressa* L. - Broad-bodied Chaser -** Migrant. In Jersey there have been intermittent records since the 1940s (e.g. Le Quesne, 1946; Dobson, 1961; Long & Long, 1993), though usually only isolated individuals are involved. However, good numbers were seen in the spring of 1998 (perhaps suggestive of successful local breeding). In Guernsey there have been a few sightings over the last two decades (e.g. Austin, 2004), while in Alderney the species is described as very uncommon, with none seen in the last few years (Wedd, pers. comm.).

***Libellula fulva* Müller - Scarce Chaser -** Vagrant. A few individuals have been reported from Jersey. A female was seen during June 1944 (Le Quesne, 1946), with other records on 11 June 1997 (Long & Long, 1998) and on 6 April 2004 (Long & Long, 2005). This last date is surprisingly early in the year.

***Libellula quadrimaculata* L. - Four-spotted Chaser -** Migrant and transient resident. (Plate 9). *Libellula quadrimaculata* has been noted from Jersey, Guernsey and Alderney. The species can go unreported for several years and then suddenly appear in numbers. Such immigrations include ‘thousands’ seen over Jersey on 1 June 1963 (Long & Long, 1964), with only a handful seen in 1964, though nowadays movements seem to be of a much smaller magnitude. Le Quesne (1946) found the species breeding freely at Mont Mado, Jersey, in 1943-45 after having not seen the species in the immediately preceding years. This was presumably a recently-established transient colony following an influx, and similar events probably still occur in the present day. The most recent record from the Islands is of one at Grouville Marsh, Jersey, on 25 June 2009.

***Orthetrum brunneum* (Fonscolombe) - Southern Skimmer -** Vagrant. A male was taken at La Grande Mare, Guernsey, during July 2001 (Long, 2002). This individual was present amongst a group of three or four male skimmers, the identity of the others not being determined.

***Orthetrum cancellatum* (L.) - Black-tailed Skimmer -** Resident. This is the typical skimmer of the Channel Islands. It was first reported at St Ouen’s Pond, Jersey (Plate 8), during 1945 (Le Quesne, 1946), then, after a period with few further observations, sightings in Alderney during 1988 (Long, 1989) and in Jersey during 1995 (Long, 1996) marked the start of an upturn in records. The species is now seen quite regularly and has in recent years been noted from Jersey, Guernsey and Alderney, though records from Guernsey show signs of a decline over the last few years (Medland, pers. comm.).

***Orthetrum coerulescens* (Fab.) - Keeled Skimmer -** Vagrant or former

Plate 9. *Libellula quadrimaculata*. Jersey, 25 June 2009. Photograph by M. Dryden.

resident. There is an old record of two taken at the Grande Mare in Guernsey in the nineteenth century (Luff, 1892). The habitat in this area is no longer suitable for the species.

Sympetrum danae **(Sulzer) - Black Darter -** Vagrant. One was taken in Guernsey during 1890 (Luff, 1892) and there are two old records for the island shown by Merritt *et al*. (1996). A 'possible' was observed in Jersey some 20 years ago but views were too brief to allow its identification to be confirmed.

Sympetrum flaveolum **(L.) - Yellow-winged Darter -** Migrant. This species has been reported on several occasions in the past, e.g. from Guernsey and Alderney around the turn of the twentieth century (Luff, 1892, 1901) and from Jersey in the 1940s (Le Quesne, 1946). These records broadly correlate with periods of major migratory movements seen elsewhere in north-western Europe (Cham *et al*., 2014). It was reported from Herm during 1955 (Shayer, 1956), again during a period of major migration. Modern records include sightings from Grouville, Jersey, during the famous European darter invasion year of 1995 (Long, 1996) and the most recent sighting refers to an individual from Alderney in 2012 (Wedd, pers. comm.).

Sympetrum fonscolombii **(Selys) - Red-veined Darter -** Migrant, has bred. This species was occasionally reported from the Islands in the past, with old records from Alderney at the end of the nineteenth century (Luff, 1900) and from

Jersey on several occasions during the 1940s (Le Quesne, 1946). Successful breeding is known to have taken place during 1945, when an influx starting in mid-May led to the emergence of a locally-bred second generation from August of that year (Le Quesne, 1946). More recently, sightings have become more widespread and more frequent, as has happened elsewhere in north-western Europe (Cham *et al*., 2014). Individuals were seen at La Grande Mare, Guernsey, in 2004 (Austin, 2005), and the most recent record from the island was in May 2009, coincident with a huge influx of *Vanessa cardui* (Painted Lady) (Medland, pers. comm.). In Alderney, *Sympetrum fonscolombii* is now seen quite frequently, with breeding probably having taken place at Mannez regularly since 2007 (Wedd, pers. comm.). However, whether this is a stable breeding colony is unclear, as certainly individuals emerging in autumn are known to be highly dispersive (Cham *et al*., 2014).

***Sympetrum meridionale* (Selys) - Southern Darter -** Vagrant. A female was found near Rozel Manor, Jersey, on 5 August 1948 (Moore, 1949). This species is currently expanding its range in north-western Europe and occurs as close as the Manche region of France, so future sightings may well be forthcoming. Livory (2000) notes that the species has been recorded from Chausey, the island group to the south of the Channel Islands that has always been part of France (Fig. 1).

***Sympetrum sanguineum* (Müller) - Ruddy Darter -** Migrant. This species appears to be no more than a migrant to the region. There were a number of reports from Jersey during the 1940s and early 1950s (Le Quesne, 1946, 1992), but subsequent years saw no further records until one on 5 August 1991 (Le Quesne, 1992). This was followed by a period during the mid 1990s when records were more or less annual, but recent sightings have faded away again somewhat. Two or three were, however, identified from a group of up to six darters *Sympetrum* sp. on Les Écréhous, a small reef between north-east Jersey and France (Fig. 1), on 26 July 2014; conditions for migration were very good at this time. In Alderney, *S. sanguineum* has occurred at Mannez but not since 2009 (Wedd, pers. comm.).

***Sympetrum striolatum* (Charp.) - Common Darter -** Resident (and likely migrant). This is a common and widespread breeding species in Jersey and Alderney. Although noted from Guernsey as early as the nineteenth century (Luff, 1892), the species may have temporarily declined here in the mid-twentieth century as a result of habitat loss – individuals, for instance, not having been seen by Belle (1980). More recently, however, Medland (pers. comm.) described the species as now being widespread in the island. In addition to records from the main islands, the species has also been reported from Sark (Austin, 1999) and Brecqhou (Austin, 2003).

Table 1. Summary of the status of the Odonata of the Channel Islands. (Note that the former status of some species is not fully clear; for further details, see text.)

- **Resident (13)**
  - *Chalcolestes viridis*
  - *Lestes barbarus*
  - *Calopteryx virgo*
  - *Coenagrion puella*
  - *Enallagma cyathigerum*
  - *Ischnura elegans*
  - *Pyrrhosoma nymphula*
  - *Aeshna cyanea*
  - *Aeshna mixta* (& migrant)
  - *Anax imperator*
  - *Cordulegaster boltonii*
  - *Orthetrum cancellatum*
  - *Sympetrum striolatum* (& likely migrant)
- **Transient resident (2)**
  - *Coenagrion scitulum*
  - *Erythromma viridulum*
- **Likely former resident, now locally extinct (3)**
  - *Coenagrion pulchellum* (original status uncertain)
  - *Brachytron pratense*
  - *Cordulia aenea*
- **Migrant (9)**
  - *Calopteryx splendens*
  - *Aeshna affinis* (& possible resident)
  - *Aeshna grandis*
  - *Crocothemis erythraea* (& possible transient resident)
  - *Libellula depressa*
  - *Libellula quadrimaculata* (& transient resident)
  - *Sympetrum flaveolum*
  - *Sympetrum fonscolombii* (has bred)
  - *Sympetrum sanguineum*
- **Vagrant * (9)**
  - *Sympecma fusca*
  - *Anax ephippiger*
  - *Anax parthenope*
  - *Libellula fulva*
  - *Orthetrum brunneum*
  - *Orthetrum coerulescens* (or former resident)
  - *Sympetrum danae*
  - *Sympetrum meridionale*
  - *Sympetrum vulgatum*
- **Status uncertain (1)**
  - *Anaciaeshna isoceles*

***** The distinction between Migrant and Vagrant is somewhat arbitrary; the term ‘Migrant’ has been used where there are more than four records of a species.

Sympetrum vulgatum **(L.) - Vagrant Darter -** Vagrant. Some three or four records were made from diverse areas of Jersey during the 1940s (Le Quesne, 1946), though Le Quesne (1941) cautioned that some records were perhaps not categorically proven. There have been no subsequent reports, though the species is easily overlooked.

Conclusions

The dragonfly fauna of the Channel Islands comprises some 37 species including migrants/vagrants (Table 1), a figure that is strongly limited by the availability of suitable habitat, particularly given the relatively small size of even the more major islands. A number of species have not been seen for many years, including some that are believed to have once been resident (with the exact status of many others being unclear). Habitat degradation or loss, mainly though drainage and lowering of the water-table or through pollution, is probably the principal factor involved here. On the plus side, a number of species have, however, started to appear only in recent times. Large-scale European range changes, driven by factors such as climate change, probably lie behind much of this phenomenon, though increased recorder effort and awareness might also be involved in some instances (this increase in coverage is particularly noticeable in Alderney).

Acknowledgements

The authors thank Julian Medland, Richard Perchard and David Wedd for commenting on early versions of the manuscript and for providing access to their unpublished records. Their help is very much appreciated. The Guernsey Biological Records Centre also provided much useful information, and visitors to the Channel Islands might wish to consider submitting records to the Centre via their website at http://www.biologicalrecordscentre.gov.gg or to the recently established Jersey Biodiversity Centre at http://www.jerseybiodiversitycentre.org.je.

References

Ansted, D.T. & Latham, R.G. 1862. *The Channel Islands*. W.H. Allen & Co., London. 604pp.

Austin, R.A. 1999. Entomology Section Report for 1998. *Report and Transactions of La Société Guernesiaise* **23:** 371-384.

Austin, R.A. 2003. Entomology Section report for 2002. *Report and Transactions of La*

Société Guernesiaise **25:** 256-268.

Austin, R.A. 2004. Entomology Section report for 2003. *Report and Transactions of La Société Guernesiaise* **25:** 426-436.

Austin, R.A. 2005. Entomology Section Report for 2004. *Report and Transactions of La Société Guernesiaise* **25:** 610-621.

Belle, J. 1980. Survey of the dragonfly fauna of the Sarnian islands. *Report and Transactions of La Société Guernesiaise* **20:** 465-481.

Cham, S., Nelson, B., Prentice, S., Parr, A., Smallshire, D. & Taylor, P. 2014. *Atlas of Dragonflies in Britain and Ireland*. Field Studies Council, Telford. 280pp.

Dobson, R. 1961. Entomological Report for 1960, *Annual Bulletin of the Société Jersiaise* **18:** 20-27.

Le Quesne, W.J. 1941. The dragonflies of Jersey. *Bulletin Annuel de la Société Jersiaise* **14:** 72-75.

Le Quesne, W.J. 1946. The dragonflies of Jersey. *Bulletin Annuel de la Société Jersiaise* **14:** 213-216.

Le Quesne, W.J. 1948. Entomological Report, 1947. *Bulletin Annuel de la Société Jersiaise* **14:** 357-359.

Le Quesne, W.J. 1951. Entomological Report for 1950. *Annual Bulletin of the Société Jersiaise* **15:** 297.

Le Quesne, W.J. 1990. Entomological Section Report for 1989. *Annual Bulletin of the Société Jersiaise* **25:** 220-223.

Le Quesne, W.J. 1992. Entomology Section Report for 1991. *Annual Bulletin of the Société Jersiaise* **25:** 598-604.

Livory, A. 2000. Faune de Chausey. Compléments, nouveautés. *L'Argiope* **29:** 22-26.

Long, M.L. & Long, R. 1964. Entomological report for 1963. *Annual Bulletin of the Société Jersiaise* **18:** 374-377.

Long, M.L. & Long, R. 1998. Entomology report for 1997. *Annual Bulletin of the Société Jersiaise* **27:** 195-198.

Long, R. 1989. Dragonflies in Alderney. *Report and Transactions of La Société Guernesiaise* **22:** 370-371.

Long, R. 1996. Entomology Section Report for 1995. *Annual Bulletin of the Société Jersiaise* **26:** 471-475.

Long, R. 2000. Southern Migrant Hawker *Aeshna affinis* in Jersey, Channel Islands. *Atropos* **9:** 81.

Long, R. 2001. Entomology Section Report for 2000. *Annual Bulletin of the Société Jersiaise* **28:** 43-46.

Long, R. 2002. Southern Skimmer *Orthetrum brunneum* (Fonsc.) on Guernsey. *Atropos* **15:** 10.

Long, R. & Long, M.L. 1993. Entomology Section report for 1992. *Annual Bulletin of the Société Jersiaise* **26:** 38-40.

Long, R. & Long, M.L. 1999. Entomology report for 1998. *Annual Bulletin of the Société Jersiaise* **27:** 371-374.

Long, R. & Long, M.L. 2005. Entomology Section report for 2004. *Annual Bulletin of the*

Société Jersiaise **29:** 22-26.

Long, R. & Long, M.L. 2007. Entomology Section report for 2006. *Annual Bulletin of the Société Jersiaise* **29:** 240-245.

Long, R. & Long, M.L. 2008. Entomology Section report for 2007. *Annual Bulletin of the Société Jersiaise* **29:** 356-359.

Luff, W.A. 1892. A list of the Neuroptera inhabiting the island of Guernsey. *Report and Transactions of the Guernsey Society of Natural Science* **2:** 155-160.

Luff, W.A. 1900. The insects of Alderney. *Report and Transactions of the Guernsey Society of Natural Science* **3:** 388-408.

Luff, W.A. 1901. Additions to the list of Alderney Insects. *Report and Transactions of the Guernsey Society of Natural Science* **4:** 29-31.

Luff, W.A. 1904. Report of the Entomological Section. *Report and Transactions of the Guernsey Society of Natural Science* **4:** 197-199.

Luff, W.A. 1909. The insects of Jersey. *Report and Transactions of the Guernsey Society of Natural Science* **5:** 482-511.

Merrit, R., Moore, N.W. & Eversham, B.C. 1996. *Atlas of the dragonflies of Britain and Ireland*. (ITE research publication no. 9). HMSO, London.

Moore, B.P. 1949. *Sympetrum meridionale* Selys new to the C. I. *Entomologist's Monthly Magazine* **85:** 23.

Parr, A.J. 1998. Winter dragonfly sightings in Britain during early 1998. *Atropos* **5:** 13-16.

Parr, A.J. 2007. Migrant dragonflies in 2006. *Atropos* **30:** 26-35.

Parr, A.J. 2011. The Vagrant Emperor *Anax ephippiger* in Britain and Europe during early 2011. *Journal of the British Dragonfly Society* **27:** 80-87.

Parr, A.J., De Knijf, G. & Wasscher, M. 2004. Recent appearances of the Lesser Emperor *Anax parthenope* (Sélys) in north-western Europe. *Journal of the British Dragonfly Society* **20:** 5-16.

Perchard, R. & Long, R. 2009. The rediscovery of Dainty Damselfly *Coenagrion scitulum* (Ramb.) in Jersey. *Atropos* **38:** 3-5.

Shayer, C.J. 1956. Report of the Entomological Section, 1955. *Report and Transactions of La Société Guernesiaise* **16:** 18-20.

Shayer, C.J. 1957. Entomological report, 1956. *Report and Transactions of La Société Guernesiaise* **16:** 126-127.

Silsby, J.D. & Silsby, R.I. 1988. Dragonflies in Jersey. *Journal of the British Dragonfly Society* **4:** 31-36.

Swaegers, J., Mergeay, J., Therry, L., Larmuseau, M.H.D., Bonte, D. & Stoks, R. 2013. Rapid range expansion increases genetic differentiation while causing limited reduction in genetic diversity in a damselfly. *Heredity* **111:** 422-429.

Received and accepted 27 October 2014

Spatial distribution modelling of the colonisation of *Erythromma viridulum* (Charpentier) (Small Red-eyed Damselfly) in the UK

Rebecca Trippier[1], Steve Brooks[2] & Nick Isaac[3]

[1]Department of Geography, University College London, London, WC1E 6BT
[2]Life Sciences, Natural History Museum, London SW7 5BD
[3]Centre for Ecology and Hydrology, Wallingford, Oxfordshire OX10 8BB

Summary

Northward shifts of many UK Odonata and increased occurrences of migrants have been well documented over the last few decades. *Erythromma viridulum* has greatly expanded its European range and is the first damselfly to have colonised the UK since records began. Since its arrival in 1999, the species has spread rapidly in a north westerly direction by approximately 36.5km per year as it has occupied climatically suitable space. In recent years the rate of northward expansion has decreased, however western expansion and range infilling has continued.

Introduction

Poleward expansion in the distributional range of dragonflies, particularly of Mediterranean species, has been widely observed across Europe in recent decades and is attributed to a response to rising summer temperatures enabling the colonisation of latitudes with previously unsuitable climates (De Knijf & Anselin, 2010; Kalkman *et al.*, 2010). In Britain, Hickling *et al.* (2005) concluded that 34 of 37 resident species had undergone northward shifts over the last 40 years, although northerly distributed species and habitat specialists had shown a range contraction. The small red-eyed damselfly, *Erythromma viridulum*, a species rapidly expanding its range across Europe, recently began breeding in Britain (Dewick & Gerussi, 1999) and is the first damselfly to establish breeding populations in this country since recording began (Hassall *et al.*, 2014). The species is believed to have arrived naturally from continental Europe, where it has recently expanded its range across the Netherlands, Germany and France (Keat, 2007; Ketelaar, 2002; Wasscher, 1999).

The first record of *E. viridulum* was in Essex in 1999, when several individuals were seen. Further colonies were reported in Essex and the Isle of Wight the following year (Dewick & Gerussi, 1999; Cham, 2000). Subsequently, large waves of immigration have been recorded on the Norfolk, Suffolk and Essex coasts and inland expansion in a north-westerly direction has radiated from the population stronghold in Essex (Keat, 2007; Cham, 2004). *E. viridulum* has been observed in many diverse freshwater habitats, although it favours eutrophic lakes and ponds with large amounts of submerged macrophytes, especially hornworts, *Ceratophylum* spp. (Ketelaar, 2002; Brooks, 2004). Its distribution and expansion across Britain from 2001 to 2012 are shown in Figure 1.

In this study we investigate the species' movement across the UK since its arrival in 1999 and whether expansion has slowed in recent years (Dewick & Gerussi, 1999; Cham *et al.*, 2014). Species distribution models (SDMs) were used to estimate the most suitable environmental and climatic conditions for *E. viridulum* in the UK and to explore how these factors influenced its expansion.

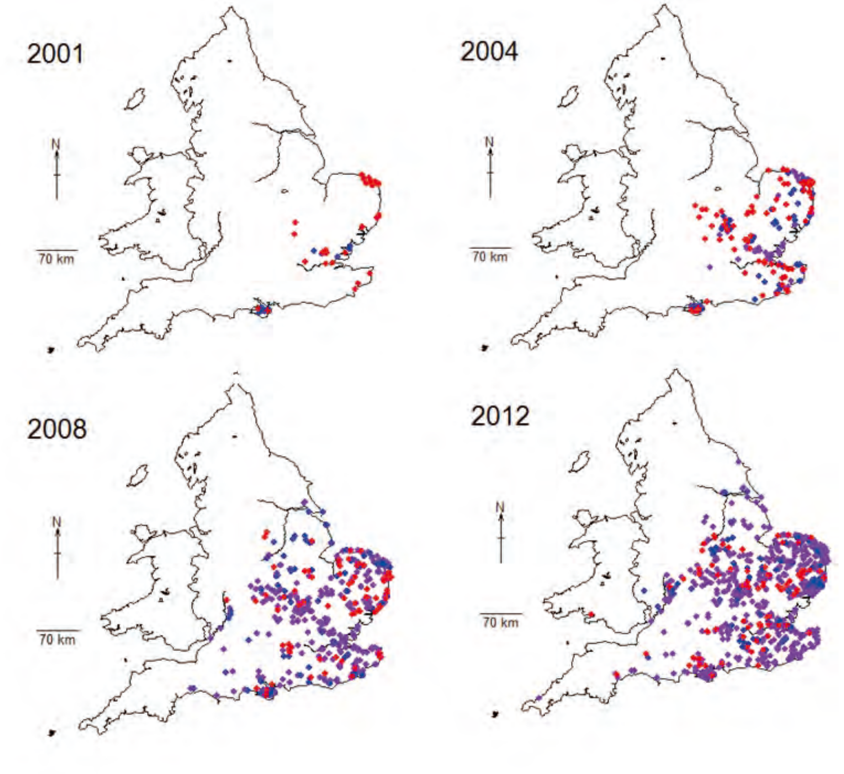

Figure 1. UK distribution of *Erythromma viridulum* in 2001, 2004, 2008 and 2012 at a monad scale (1x1km). 🟪, sites with records from years prior to the stated year; 🟦, sites with records from the previous year; 🟥, sites with records from the current year. Based on data from the BDS Dragonfly Recording Network.

Specifically, we tested the role of climatic suitability and isolation distance in shaping the spread of *E. viridulum* across the UK and how these have changed over time.

Materials and Methods

The data used in this study were obtained from the Dragonfly Recording Network (DRN), which is coordinated by the British Dragonfly Society (BDS). Presence records of *E. viridulum* from 1999 to 2012 were collated within 1x1km grid cells (monads) and 10x10 km grid cells (hectads). Monad scale data were used to describe the patterns of change, while hectad scale data were used for modelling. This is appropriate since all hectads in England were surveyed by the DRN (Cham *et al.*, 2014), whereas most monads were not.

The distributional data were collated with environmental data to create correlative species distribution models. The environmental data incorporated into the model included lake density obtained from the Ordnance Survey OpenData Strategi® cartographic style sheets, which are annually updated national datasets (Ordnance Survey, 2014). The regional lake data of water bodies equal to or greater than 0.25 x 0.25 km^2 were digitised with a coordinate resolution of 1m. The data were then converted to lake density within each 1x1 km square of UK grid cells and were incorporated into the model, together with elevation data at a 1km resolution acquired from NEXTMap® Britain (Getmapping plc, 2014). UK mean annual temperatures and precipitation data for the period 1971 to 2012 were obtained at 5km resolution from the Met office UKCP09 datasets (Met Office, 2014; Perry & Hollis, 2005). These data were collated and converted to a 10x10 km (hectad) scale to match the resolution of the DRN dataset.

Species Distributional modelling

Suitability was determined through modelling the distributional data for the species against the environmental data, which included lake density, mean annual UK temperature, precipitation and elevation. Using the Biomod2 package in the statistical software ‘R’ (Thuiller *et al.*, 2013), six different species distribution (presence/absence) models (SDMs) were run 10 times to predict their environmental responses based upon comparisons between their distribution and environmental gradients. Each of these individual SDMs gave a prediction of the likelihood for the species to be present in a given grid cell. However, since *E. viridulum* is expanding in the UK, our models violate the assumption that the species’ distribution is in equilibrium and therefore that populations are stable. We parameterized the SDMs using the full UK distribution (2000 - 2012) in order to minimise the impact of this assumption but the SDMs nonetheless under-estimate the true climatic envelope of this species.

The Biomod2 package was used to combine the predictability values from each of the six SDMs to create an ensemble model, which averages their predictability scores, and then compares this with the individual SDMs to generate an overall meta-model projection for grid cell suitability (Thuiller *et al.*, 2013). This averaged out uncertainties associated with a single modelling approach, producing an overall Position Weight Matrix (PWM) score for each cell. The PWMs provide a measure of the pattern occurring in the predictability of the species being within each cell, and so representing their suitability to the environmental conditions of each cell. This assumes that their distribution at sites relates to the suitability of the site to the species, with more records at a site representing greater suitability than sites with fewer records. Grid cell suitability was mapped using the ‘ggmap’ package (Kahle, 2013).

The mean model was cross-validated through random sampling, run using 80% of the data and cross-validated against the remaining 20%. Model performance was assessed using True Skill Statistic (TSS) and Receiver Operating Characteristic (ROC) statistics. These metrics were extracted together with the relative importance of each contributing variable towards the modelled suitability scores of each grid cell.

Statistical analysis

Grid cell suitability over time was evaluated, using Pearson’s correlation, against the year in which *E. viridulum* was first present in each cell. The minimum distance to each newly occupied cell from a previously occupied cell was calculated and collated to determine the average distances travelled by the species in a given year to new colonisation sites. This was estimated by calculating the difference of a cell’s northing and easting from those of all cells previously occupied. This was then placed into a Pythagoras equation to calculate the distance, where ‘A’ is a new cell and ‘B’ is a previously occupied cell:

$$\text{Easting}_{\text{diff}} = \text{A[Easting]} - \text{B[Easting]}$$

$$\text{Northing}_{\text{diff}} = \text{A[Northing]} - \text{B[Northing]}$$

$$\text{Distance} = \sqrt{}(\text{Easting}_{\text{diff}}{}^{2} + \text{Northing}_{\text{diff}}{}^{2})$$

These distances were analysed to see how the pattern of dispersal of *E. viridulum* may have varied during the study period. This was then compared against regional climate data from the central England database HadCET

(Parker *et al.*, 1992). A general linear model (GLM) was used to observe how suitability and distances to new cells affects whether a cell has been occupied and how distance and suitability may change over time.

Results

E. viridulum has undergone rapid expansion in its UK distribution and has continued to occupy new monad cells annually since its arrival in the UK. The species has spread northwards and westwards, increasing occupancy from 15 monads in 2000 to 947 monads in 2012. Between 2000 and 2012, the distribution expanded on average 72.85 new monads per year (Fig. 2). The highest concentration of occupied cells were present in south east England, particularly in Bedfordshire, Essex, Norfolk and the Thames Valley.

However, the expansion has not been uniform over this period. Thus the number of newly occupied monads between 2000 and 2006 increased at a rate of 67.07 monads per year with the peak number of newly occupied cells occurring in 2006, with 106 monads occupied that year, suggesting a year of high dispersal. The rate of occupation between 2007 and 2012 was 89.34 monads per year, greater than that of the initial expansion. This is not apparent at the hectad-level, where new colonisations appear to decrease after a peak of 53 hectads in 2006, suggesting recent range infilling of monads within the same hectad or previously occupied hectads. This slowing of range expansion since 2006 suggests that the distribution of *E. viridulum* in the UK may be approaching equilibrium, and that our under-estimate of niche space predictions from the DSM are fairly mild.

The leading edge of the distributional range of *E. viridulum* was mapped using the mean latitude of the five most northerly and five most westerly monads. This was used to estimate the rate of expansion (Fig. 3). Since 2000, the range has shifted by approximately 36.61km northwards and 36.44km westwards per year. Initially, the rate of northward expansion was faster than westward expansion (Fig. 4). However, this has now decreased and western shifts have become the predominant movement. On average, the rate of northward expansion decreased during the study period by 4.09km per year, and overall advancement, taking account of both longitude and latitude distances decreased by 1.43km per year. However, western expansion continued to increase from 2000 to 2012 by an average of 1.22km per year, with maximum increases in distance occurring between 2009 and 2010.

The suitability of all UK grid cells based upon the species' distributional responses to the environmental variables was examined using a high-performance species distribution ensemble model, which has a True Skill Statistic (TSS) score of 0.851

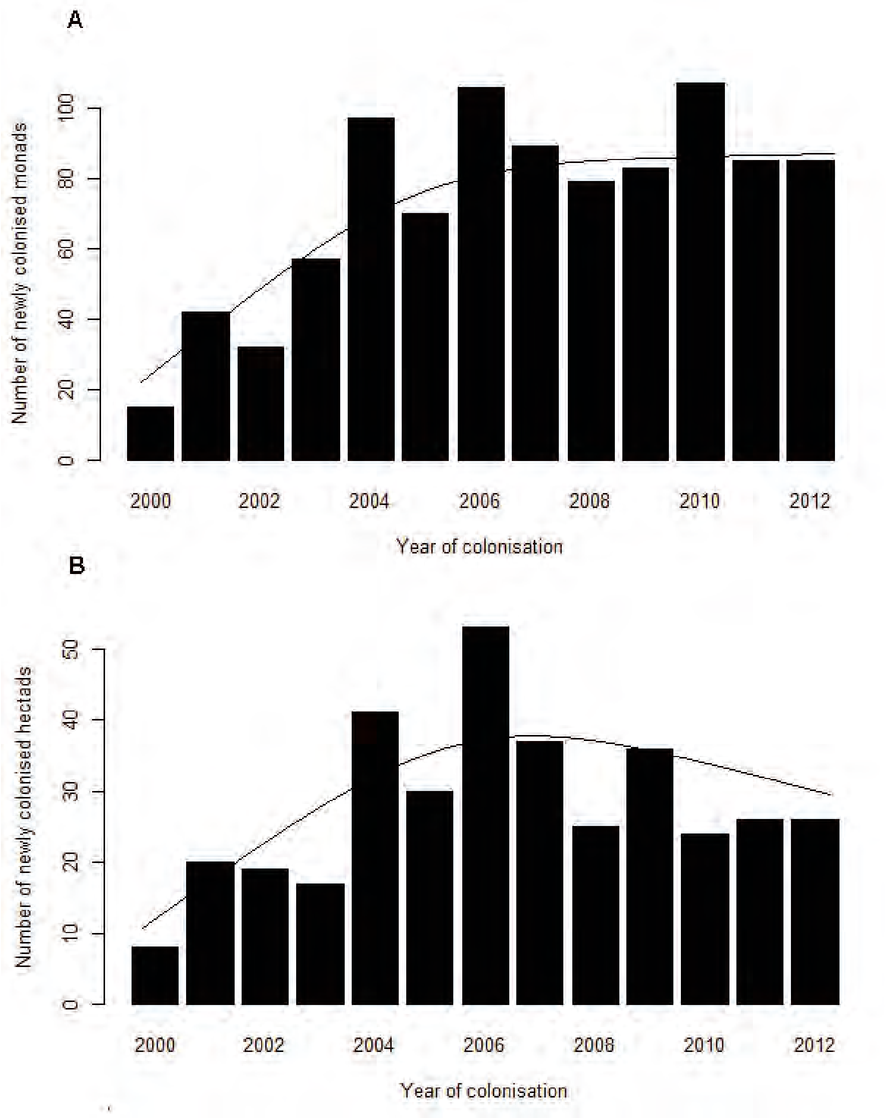

Figure 2. The number of cells newly occupied by *Erythromma viridulum*, recorded each year (A) at a monad spatial-scale, (B) at a hectad spatial-scale.

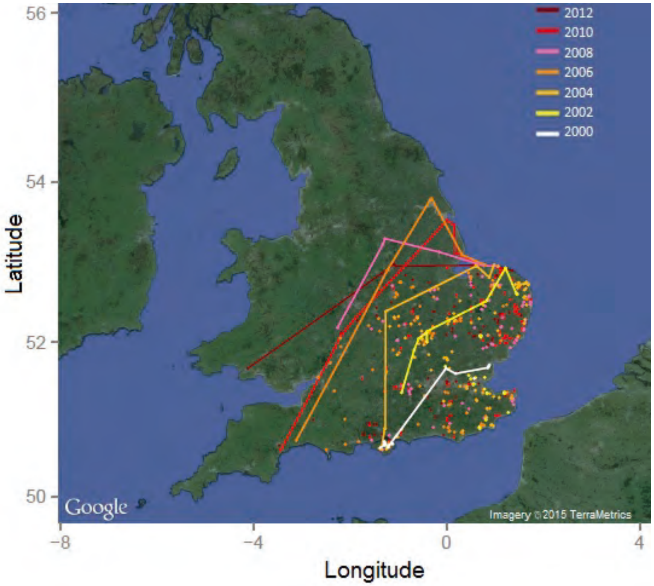

Figure 3. The leading edge of the distributional range of *Erythromma viridulum* from 2000 to 2012, at the monad spatial scale.

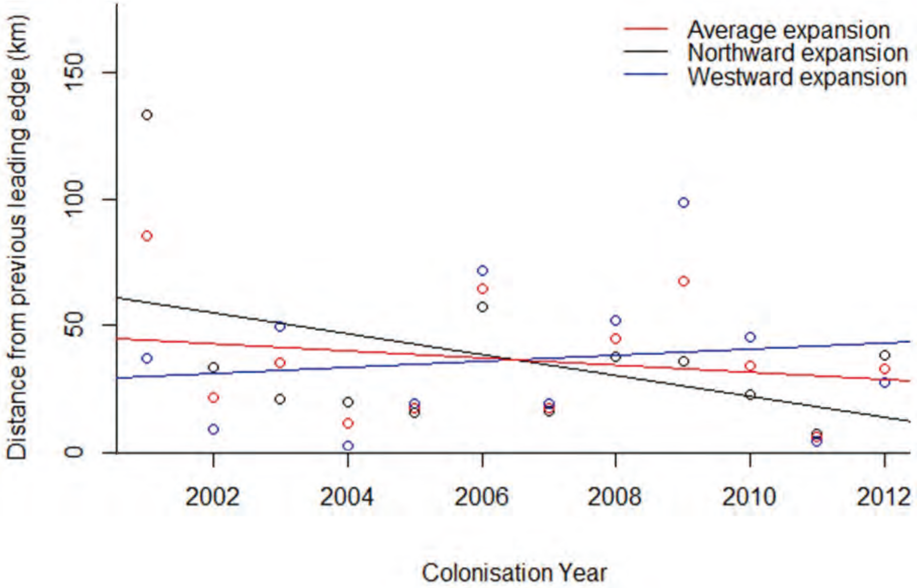

Figure 4. The yearly distances advanced by *Erythromma viridulum* from the previous leading edge northwards, westwards and the average, at the monad spatial scale.

(Sensitivity = <1, Specificity = <1). The TSS Score measures the predictability power of the model through analysing the net success rate for predicting the presence or absence of the species at sites. The results (Fig. 5) show suitability measured on a scale of Position Weight Matrix (PWM), the sum of log-likelihoods of their presence based upon the modelled variables and species distribution. Most highly suitable areas were located towards south east England and the Isle of Wight, where the current distribution is concentrated. The average suitability of newly occupied sites was 720 ± 4.60 PWM, varying greatly between 115 and 890 PWM (IQR = 187). Model analysis showed suitability to be more heavily influenced by climatic factors than by elevation and lake density (Table 1). Some areas beyond the periphery of the current distribution, including South-West England, Yorkshire and North Wales-English borders appear suitable but are currently unoccupied. This may be due to physical barriers in these regions restricting colonisation, such as the Peak District and the Mendip Hills, and may also reflect dispersal potential and colonisation rates of the species.

Table 1. The relative importance of climatic and physical factors in determining the suitability of sites for *Erythromma viridulum* at a 10 km (hectad) resolution.

Environmental variable	Mean temperature	Mean rainfall	Elevation	Lake density
Relative importance in determining suitability	0.509	0.523	0.042	0.035)

The suitability of newly occupied cells varied and cells occupied earlier showed a higher suitability than those occupied more recently 9 (Fig. 6). The mean PWM of newly occupied hectads from 2000 to 2002 was 806.2 ± 9.78. Only highly suitable sites were initially occupied (Range = 236.00, SD = 89.16, Variance = 7949.34). Cells occupied in 2012 had a wider range (Range = 746.00, SD = 214.20, Variance = 45880.32) and, on average, lower suitability scores (mean: 704.5 ± 8.68 PWM) compared with earlier colonisations. A Pearson's correlation test showed a significant negative relationship between the suitability of newly occupied cells against time (correlation coefficient = -0.17, P < 2.2 x 10-16).

Distances between previously occupied and newly occupied hectads were highly variable but, in general, the results indicated that the greatest distances were in 2001 (Range = 133.64, SD = 52.25). Apparent colonisation distances in this year are likely over-estimates, reflecting under-sampling and a lack of awareness of the species' presence in the UK. The maximum distance to newly occupied cells was 164.44km (Fig.7). However, the majority of newly

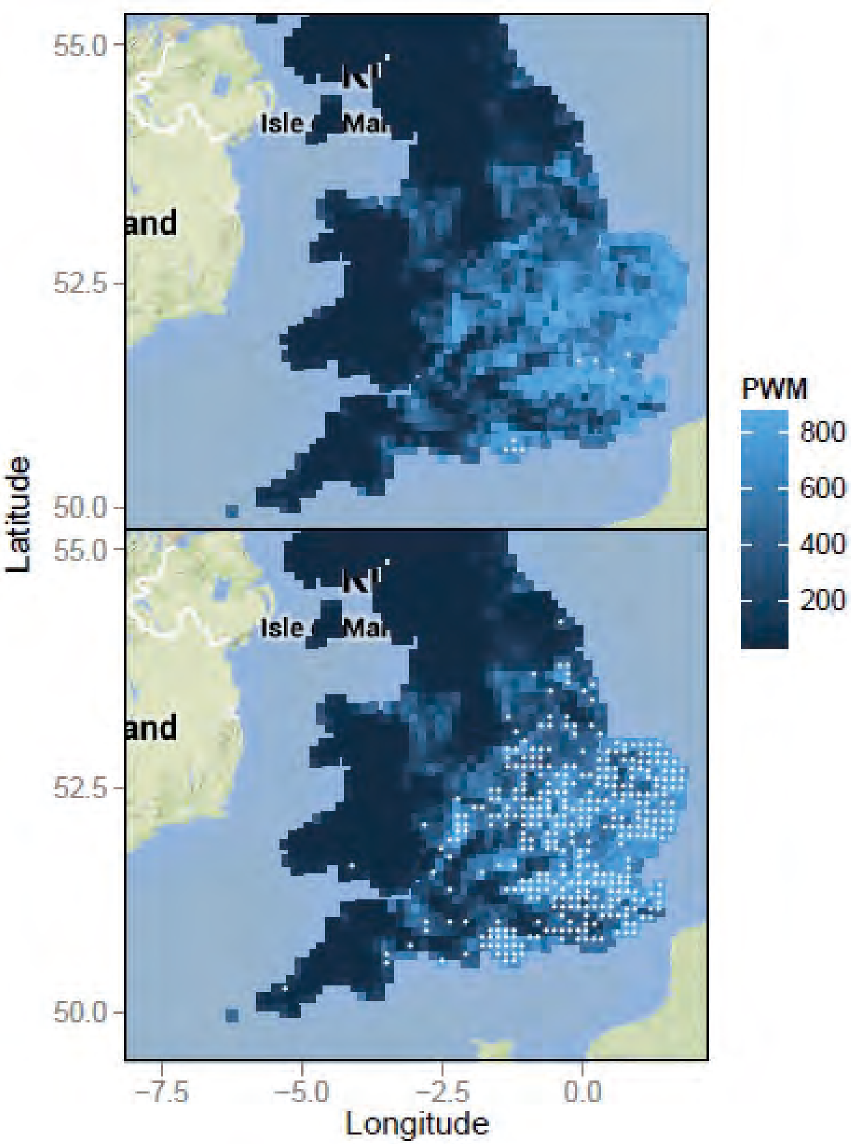

Figure 5. Suitability scores (PWM) mapped against the distribution of *Erythromma viridulum* in 2000 (top) and 2012 (bottom) at a 10 km (hectad) resolution. High scores, displayed by pale colours, indicate the most suitable grid squares.

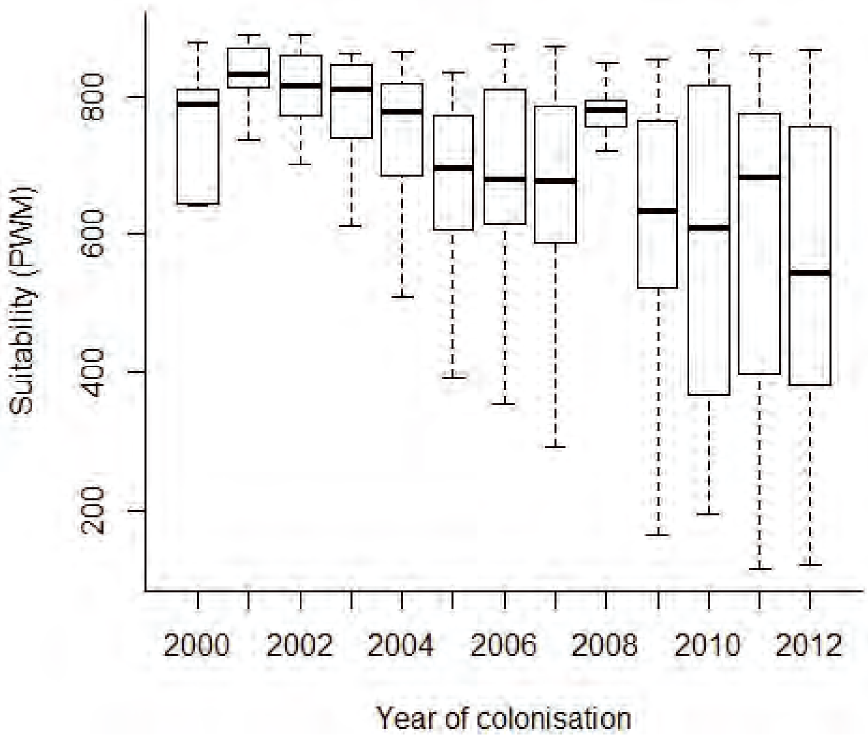

Figure 6. The suitability scores (PWM) of each hectad at a 10 km (hectad) resolution for each year of colonisation from 2000 to 2012. The boxes represent the interquartile ranges (i.e. with 50% of the data falling within them); the solid horizontal line in each box is the mean suitability score for a given year; the dashed lines indicate the range of values.

occupied cells were from nearby cells, supporting earlier results suggesting the main movement being range infilling (mean distance of 11.68± 0.71 km; sd = 21.54km). Correlation tests with HadCET temperature records for Central England showed no statistically significant relationships between temperature and distance. This indicates that dispersal distance is dependent upon a number of factors and complex interactions, not solely upon seasonal temperatures.

GLMs and ANOVA demonstrated cell suitability was significantly higher in colonised cells than uncolonised (F = 0.011, P <2 x 10^{-16}), whereas cells being colonised had a weaker relationship with distance (F = 0.19, P = 0.04). This suggests that highly suitable cells were more likely to be colonised early; however, both distance between cell occupation and suitability of occupied cells declined over time. Suitability significantly declined by 21.08 PWM per year during the study period (F = 23.60, P <2.2 x 10^{-16}) and the minimum dispersal distances decreased significantly by 2.60km per year, indicating declining rates

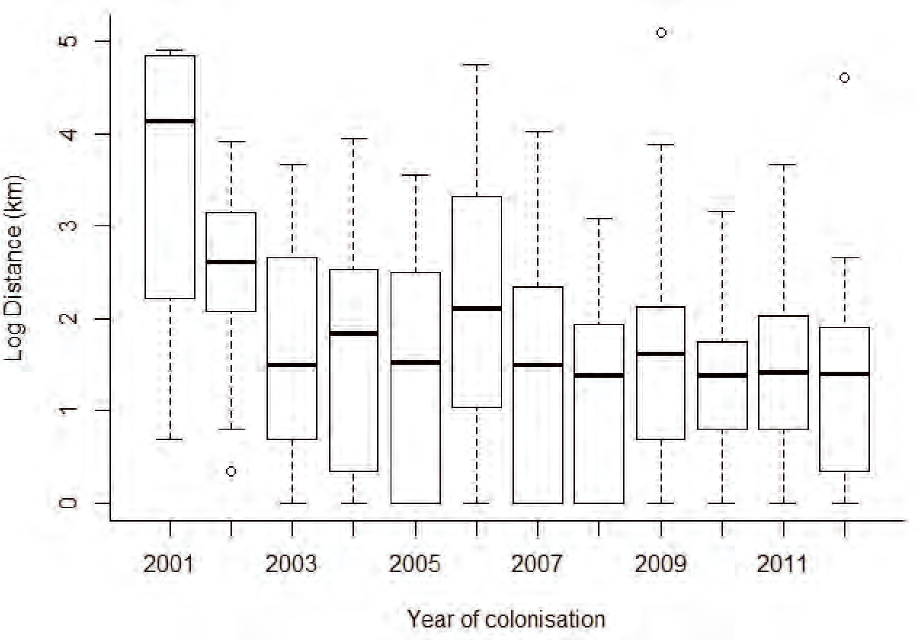

Figure 7. The distances of cells newly colonised by *Erythromma viridulum* from previously colonised cells at a 1 km (monad) resolution. The boxes represent the interquartile ranges (i.e. with 50% of the data falling within them); the solid horizontal line in each box is the mean distance for a given year; the dashed lines indicate the range of distances; o, outliers.

of range expansion ($F = 98.61$, $P < 2.2 \times 10^{-16}$).

Discussion

Analysis of the UK range expansion of *Erythromma viridulum* has shown that northward spread has slowed since the initial period of high expansion between 2000 and 2006, when peak numbers of new sites were colonised in south east England. This indicates the high suitability of the region, which may reflect the presence of a large number of wetlands and lake habitats (Ordnance Survey, 2014) and a suitable climate. *E. viridulum* is highly associated with *Ceratophyllum* species, probably due to the structure and life-cycle of the plant providing refuge for larvae. The distribution of *E. viridulum* may also reflect the distribution of *Ceratophylum demersum* in the UK, which is also restricted to southern England (Fig. 8) (National Biodiversity Network, 2012). Watts *et al.* (2010) postulated their rapid expansion was assisted through exploiting waterways, as they spread along river systems such as the Thames, Severn and Humber.

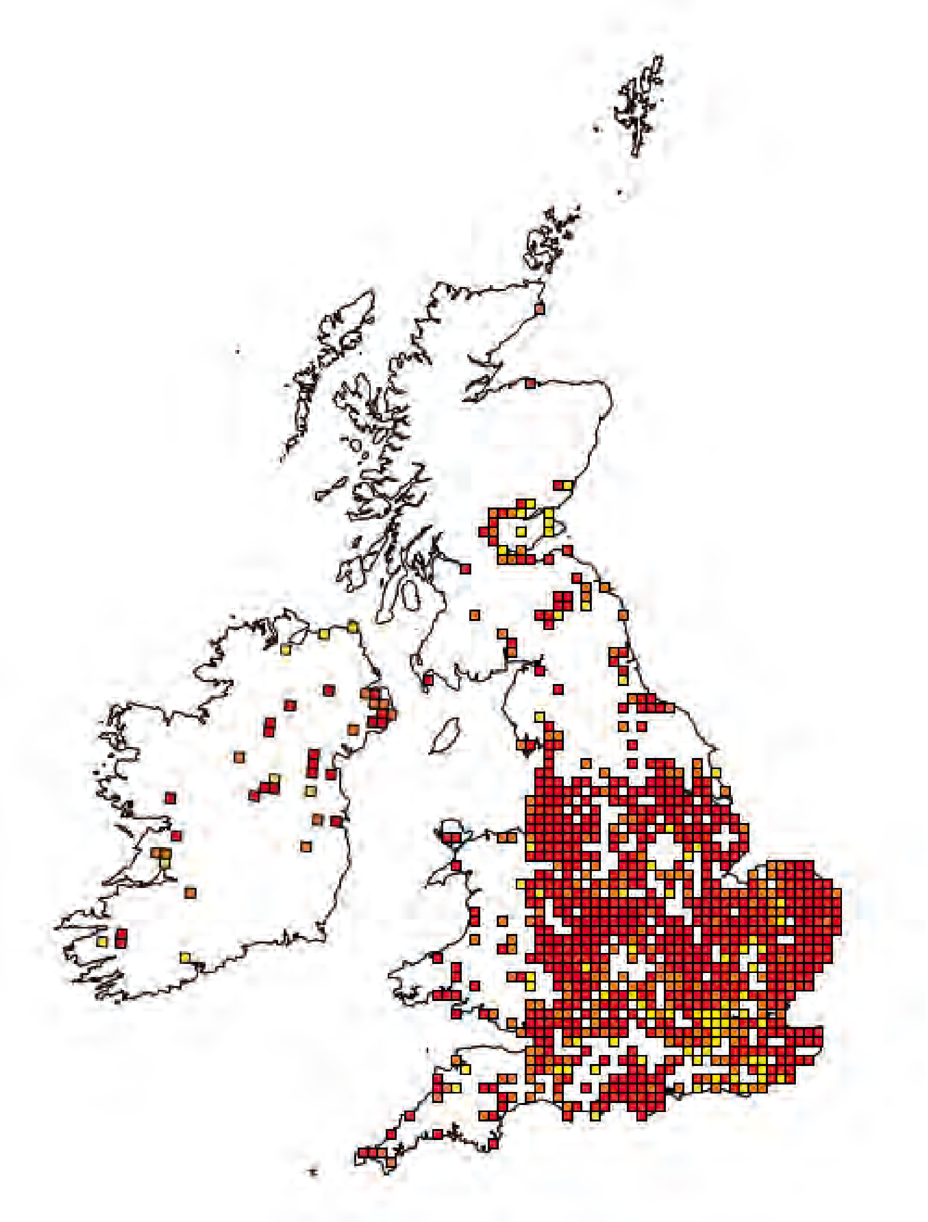

Figure 8. The distribution of *Ceratophyllum demersum* in the UK at a 10 km (hectad) resolution. 🟥 , present 1990-2013; 🟧 , present 1970-1989; 🟨 present before 1970. (National Biodiversity Network, 2012). Crown copyright and database rights 2011 Ordnance Survey [100017955]

Early expansion of *E.viridulum* occurred mostly from the population established in Essex, with the Isle of White population appearing to remain fairly static until 2004, when individuals began to establish across to the nearest mainland. In recent years, *E. viridulum* has continued its western expansion across the UK. The overall rate of range expansion has slowed, demonstrated by the decline in the number of new hectads occupied, although the number of new monads occupied each year remained fairly constant. Over the study period, the species has progressively occupied cells at shorter distances from those previously occupied and cells with lower suitability scores, as highly suitable cells become depleted over time. There has been an increase in range infilling, increasing the population density in regions in which the species is well-established. The slowed expansion is also reflected in the decline in average expansion of the leading northern and western edges during the study period by 1.43km, in particular the northward expansion, which has declined by 4.09km per year. The average rate of range expansion between 2000 and 2012 was 36.61km per year, which is consistent with the estimates of Hassall *et al.* (2014). The grid cell suitabilities were modelled on the assumption that *E. viridulum* is in equilibrium with the environment*;* however, the species is still currently expanding its range. This may result in an under-estimation of grid cell suitability and so more UK cells may be suitable for the species in North-West England. The suitability model could be improved by incorporating more environmental variables and habitat associations, such as distribution of *C. demersum*, modelling at the monad scale, and including sampling effort and spatial auto-correlation.

Continued westward expansion suggests the species is still filling suitable climatic niches, and it is highly likely that the north-west boundary of the species' UK distribution will continue to shift as the species occupies cells which are apparently already suitable. Some regions towards the periphery of the distribution, such as the lowlands near Shrewsbury and the Welsh border, appear highly suitable for the species but are currently unoccupied. This may be due to physical barriers restricting movement. However, this is likely to be temporary as the species has demonstrated strong dispersal capabilities across Europe. Based upon recent expansion rates, the species is likely to reach the Welsh border region within the next year or so. In comparison with other UK species analysed by Hickling *et al.* (2005), *E. viridulum* seems to be expanding at a much faster rate. However, Hickling *et al.* (2005) conducted their analysis on species that had already reached equilibrium in Britain, unlike *E. viridulum* which appears to be still expanding. We predict *E. viridulum* will approach an 'equilibrium' distribution, filling sites within its climatic niche in Britain, and then be likely to continue to expand northwards in response to climate change at a rate similar to that seen in other UK Odonates. However, since the species is the first breeding migrant to have colonised the UK and has a Mediterranean origin, its response to climate change may be highly variable.

Acknowledgements

We are grateful to Gary Powney, Tom August, Louise Barwell (CEH), Jonathan Holmes and Naomi Arnold, University College London, for all the support and advice throughout the project. Thank you to all of the BDS volunteers and staff for collecting the valuable data. We also thank Chris Hassall and an anonymous referee for their constructive suggestions for improvements to the manuscript.

References

Brooks, S. 2004. *Field guide to the dragonflies and damselflies of Great Britain and Ireland*, Revised ed. British Wildlife Publishing, Hook, Hampshire. 160 pp.

Cham, S., Nelson, B., Parr, A., Prentice, S., Smallshire, D. & Taylor, P. (eds) 2014. *Atlas of Dragonflies in Britain and Ireland.* Biological Records Centre and the British Dragonfly Society, Field Studies Council, Telford.

Cham, S. 2004. Oviposition behaviour of the two British species of red-eyed damselflies *Erythromma najas* (Hansemann) and *E. viridulum* (Charpentier). *Journal of British Dragonfly Society* **20:** 37-41.

Cham, S. 2000. The status of small red-eyed damselfly *Erythromma viridulum* (Charpentier) in the British Isles. *Atropos* **12:** 7-9.

De Knijf, G. & Anselin, A. 2010. When south goes north: Mediterranean dragonflies (Odonata) conquer Flanders (North-Belgium). In: Ott, J. (ed.) Monitoring climatic change with dragonflies. *BioRisk* **5:** 141-153.

Dewick, S. & Gerussi, R. 1999. Small red-eyed damselfly, *Erythromma viridulum* (Charpentier) found breeding in Essex – The first British records. *Atropos* **9:** 3-4.

Hassall, C., Keat, S., Thompson, D.J. & Watts, P.C. 2014. Bergmann's rule is maintained during a rapid range expansion in a damselfly. *Global Change Biology* **20:** 475-482.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. 2005. A northward shift of range margins in British Odonata. *Global Change Biology* **11:** 502-506.

Kalkman, V.J., Boudot, J.-P., Bernard, R., Conze, K-J., De Knijf, G., Dyatlova, E., Ferreira, S., Jović, M., Ott, J., Riservato, E. & Sahlén, G. 2010. *European Red List of Dragonflies*. Publications Office of the European Union, Luxembourg. 38 pp.

Keat, S. 2007. *Range expansion, population structure and life history of the small red-eyed damselfly, Erythromma viridulum (Charpentier, 1840) at its northwest margin*. Unpublished PhD thesis, University of Liverpool.

Ketelaar, R. 2002. The recent expansion of the small red-eyed damselfly *Erythromma viridulum* (Charpentier) in the Netherlands. *Journal of the British Dragonfly Society* **18:** 1-8.

Parker, D.E., Legg, T.P. & Folland, C.K. 1992. A new daily central England temperature series, 1772-1991. *International Journal of Climatology* **12:** 317-342.

Perry, M. & Hollis, D. 2005. The generation of monthly gridded datasets for a range of climatic variables over the UK. *International Journal of Climatology* **25:** 1041-1054.

Wasscher, M. 1999. Identification of small red-eyed damselfly, *Erythromma viridulum*, (Charp.). *Atropos* **7:** 7-9.

Watts, P.C., Keat, S. & Thompson, D.J. 2010. Patterns of spatial genetic structure and diversity at the onset of a rapid range expansion: colonisation of the UK by the small red-eyed damselfly, *Erythromma viridulum*. *Biological Invasions* **12:** 3887-3903.

Web sites

Getmapping plc. 2014. *Products: NEXTMap*. http://www2.getmapping. com/ Products/ NEXTMap [Accessed 14/06/14].

Kahle, D. 2013. *Package 'ggmap': A package for spatial visualisation with google maps and openstreet map.* http://cran.r-project.org/web/packages/ggmap/ ggmap.pdf [Accessed 20/06/14].

Met Office, 2014. Met Office: UKCP09: Download data sets. http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/index.html [Accessed 14/06/14].

National Biodiversity Network 2012. *Grid map for Ceratophyllum demersum L.* http://data.nbn.org.uk/Taxa/NBNSYS0000002761/Grid_Map [Accessed 11/08/14].

Ordnance Survey. 2014. *Mapping data and geographic information from Ordnance Survey*.https://www.ordnancesurvey.co.uk/opendatadownload/products.html [Accessed 15/06/14].

Thuiller, W., Georges, D. & Engler, R. 2013. *Package 'biomod2'.* http://cran.r-project.org/web/packages/biomod2/biomod2.pdf [Accessed 14/06/14].

Received 10 November 2014, revised and accepted 19 December 2014