Journal of the British Dragonfly Society

Volume 26   Number 1   April 2010

CONTENTS

BDS

British Dragonfly Society

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
e-mail: gpmill@supanet.com

Secretary:
H.G. Curry
23 Bowker Way
Whittlesey
Peterborough, PE7 1PY
e-mail: bdssecretary@dragonflysoc.org.uk

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

Membership Secretary
L. Curry
23 Bowker Way
Whittlesey
Peterborough, PE7 1PY
e-mail: membership@dragonflysoc.org.uk

Back numbers of the Journal can be purchased from the Librarian / Archivist at £2.75 per copy to members or £5.50 per copy to non-members.

Species Reviews: The third species review appears in this issue. Others 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 subscription £15.00
Overseas subscription £20.00
All subscriptions are due 1 April each year.

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

BDS Website: www.dragonflysoc.org.uk

Cover Illustration: Male *Pyrrhosoma nymphula*. Photograph by Steve Cham

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

SCIENTIFIC AND ENGLISH NAMES OF BRITISH ODONATA

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

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

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

Registered Charity No. 800196

Robert John Tillyard (1881-1937) F.R.S. – an account of his life and legacy with special reference to Odonatology

Richard A. Baker

Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK.

Summary

R. J. Tillyard had a short but remarkable life into which he packed so much scientific work. Trained as a mathematician at Cambridge, he soon left England for Australia to teach at the grammar school in Sydney before embarking on a career in scientific research and then scientific administration in Australia and New Zealand. However his first love was in natural history and in particular dragonflies. He published about 180 scientific papers; also five books, his best known being "*The Biology of Dragonflies*". He was elected a Fellow of the Royal Society in 1925.

Introduction

One hundred years ago Tillyard was publishing widely on odonates and this therefore is a suitable time to look again at his life and work. Most dragonfly specialists will remember his name as the author of the classic work: "*The Biology of Dragonflies*" published in 1917 (Tillyard, 1917) but few will know that he was an outstanding entomologist or be aware of his interesting and varied career. The fact that he was an internationally recognised naturalist may raise the question – but who was he?

Robert, also called Robin, was born in Norwich, Norfolk on the 31 January 1881. His father, John Joseph Tillyard, was a solicitor and his mother was Mary Ann Frances Wilson. Coming from East

Figure 1. Photograph of R. J. Tillyard with his signature, (from Evans,1946). Reproduced with kind permission of the Linnean Society of New South Wales.

Anglia, mostly a rural county particularly in his day, it would not be surprising to hear that from an early age he was interested in natural history. However, there are few clues to his boyhood interests. It is known that he was interested in and collected butterflies and received book prizes on natural history. He entered Dover College in Kent as a scholar in 1895, during the headship of the Reverend W. C. Compton, and began to show real promise in mathematics. He became a prefect and Head of the Sixth Form in 1898, "quite a prestigious post" (Stephen Jones pers. comm., 2009). Such was the breadth of his ability, that he won scholarships at both Oxford and Cambridge. He chose Cambridge and read mathematics, entering Queens' College as a Foundation scholar in 1899, graduating in 1903 (later an M.A. in 1907); he followed this by a further year studying oriental languages and theology. Early plans for a career in the army or the church were abandoned, choosing science instead.

He was classed as a 'Senior Optime' (Second Class degree) in Part 1 of the Mathematics Tripos in 1903. "Mathematics was ...by far the most prestigious course at Cambridge at the time...and seen as a prerequisite for any sort of serious science" (Reverend Jonathan Holmes pers. comm., 2009). In 1920 he was awarded an honorary fellowship by his college, an award and honour given only to distinguished alumni.

Tillyard suffered poor health from boyhood and was especially troubled by rheumatism. Seeking a climate that might improve his health, he emigrated to Sydney, Australia in 1904 where he taught science and mathematics at Sydney Grammar School from 1904 to 1913. Here he became fully involved in school life. He was editor of the school magazine, *The Sydneian*, organized the dramatics, helped with the Old Boys' Association and was President of the Debating Society. However, the attractions of natural history and especially zoology led him to resign from school teaching in 1913 and return to research, this time at the University of Sydney.

Unfortunately his health was never good but he worked on despite being in pain. Apart from rheumatism, he suffered a number of setbacks from accidents. A railway accident in 1914 crippled his back and broke an arm, a cycling accident in New Zealand broke his left arm and a car accident in California broke some of his ribs. He died on January 13th 1937 just short of his 56th birthday from injuries received in an accident involving a skidding motor car,

Described as a man of many interests and, "gleaming with excitement and interest"... his personality ranged from mercurial to deep periods of depression" (Evans, 1963). He was also something of a showman and egocentric and loved an audience (Evans, 1963) and this stimulated him. He found it difficult to relax as his mind was full of new ideas. He was also a deeply religious man. In the

magazine of the school where he taught, it was said of him that, "His own energy never flagged, his enthusiasm was never dulled" (H.S.D. *The Sydneian*, April 1937). His wife wrote that, despite all his physical pain and disappointment, "the most remarkable thing about him was his happiness" (Imms, 1938).

Professional life - other posts held in Australia and New Zealand

Following his teaching career at Sydney Grammar School and the research carried out under the Macleay Fellowship, Tillyard became head of Biology at the Cawthron Institute (1919) based in Nelson, New Zealand. This proved to be the happiest period of his life. The climate suited him and his eight years there were very productive, publishing his second insect book, "The Insects of Australia and New Zealand" (Tillyard, 1926). He visited England and the USA before taking up his appointment in Nelson.

In 1928 Tillyard became the Australian Governments' chief entomologist in the Division of Economic Entomology at the Commonwealth Council for Scientific and Industrial Research (CSIR). Initially he had doubts about accepting the post and was described as "temperamentally unsuited to administrative work" (Evans, 1963). During 1929 he visited England looking for young entomologists whom he could recruit to work at the CSIR (later CSIRO). Amongst them he found Herbert Womersley, who moved to Australia and became an international authority on mites. However, this proved to be an unhappy period for Tillyard and an unsuitable appointment in many ways. He had no real understanding of ecology and lacked the training and interest in applied entomology (Evans, 1963). Although he had been successful in introducing an insect parasite to control the Apple Woolly Aphis, his work on biological control was not regarded as wholly successful (Evans, 1963). He resigned from this position in 1935.

Work on dragonflies

Tillyard's first published paper on dragonflies was in 1905 (Tillyard, 1905), although in the same year, the journal *Nature* ([Anon.] **72**, 1905: 552) collated "Notices of Societies and Academies" and reported a summary of the lecture given by Tillyard to the New South Wales Linnean Society, "On dimorphism in the female of *Ischnura heterostricta*, Burm. (Neuroptera: Odonata)". Further summaries of lectures given by him to the society were to follow ([Anon.] *Nature* **73**, 1905-1906: 24). These were the first indications of his developing interest in dragonflies and were published very soon after his arrival in Australia. It is of interest to note that one of his last contributions also appeared in Nature (and other papers appeared after his death). His "Letter to the Editor" of Nature, from Canberra, dated October 25th 1936, was published in *Nature* (Tillyard, 1937a) and discussed the ancestors of the Diptera. An obituary notice appeared in the

same volume (Imms, 1937) as well as the report of a lecture, The Cawthron Lecture, given by him in 1935, "Tracing the dawn of life further backwards" (Tillyard, 1936a.) Imms (1938) later provided a comprehensive obituary.

Within a year of arriving in Australia Tillyard had recorded several species of dragonfly new to science and traveled as far as North Queensland in pursuit of his interest. Most of his papers on these trips were published in the *Linnean Society of New South Wales*, though some important ones (e.g. Tillyard, 1916) are to be found in the *Journal of the Linnean Society*, London. Between 1905 and 1912 he published around 27 papers on dragonflies and "entomology had become his dominant occupation" (Evans, 1963).

Tillyard married in 1909 and bought a house at Hornsby on the outskirts of Sydney. His wife was a friend from his Cambridge days. Patricia "Pattie" Craske (1880-1971), a Newnham College graduate in Natural Sciences, was to become an important figure as a community leader and served on many boards and councils in Australia (Clarke, 1990), and a large part of Tillyard's success was due to her. She gave him her full support, managed all family affairs and brought up four daughters. She also illustrated some of his articles. Indeed it is thought that his "debt to her was incalculable" (Evans, 1963). He named a dragonfly species after her, *Phyllopetalia patricia* (Tillyard, 1910).

Tillyard worked in the zoology department at Sydney University (1913-1920), first as a research scholar and then as Macleay Fellow under the guidance of Professor of Zoology, W. A. Haswell. He was awarded the B.Sc. degree in zoology by research, believed to be the first student from that university to receive such an award. By the time the degree was conferred, Tillyard had published several papers on dragonflies. He had earlier applied for the Australian Linnean Macleay Fellowship in order to do full time research in entomology but required a science degree first. The Fellowship was awarded in 1915 and was tenable for five years. He became a demonstrator and lecturer in zoology in the department (1918-1920) and was awarded the higher doctorate (D.Sc.) in 1918 and a medal for his thesis on dragonflies entitled "On the caudal gills of the larvae".

During his Macleay Fellowship period he published 29 papers, however he had now broadened his interests, and only 11 dealt with dragonflies. As well as being an expert odonatologist, Tillyard was an expert on several other groups of insects including lace-wings and ant-lions (Neuroptera), scorpion-flies (Mecoptera) and caddis flies (Trichoptera). Tillyard also studied insect palaeontology and his professional work led him to studies on biological control. Described by Hale Carpenter (1936-1937) as a "skilled field worker", Tillyard was fundamentally a taxonomist but embraced much more, being interested

in the biology, life histories, evolution of wing venation and fossil record as well as the distribution of the Anisoptera and their systematics. The respiratory mechanisms of dragonflies fascinated him and he paid particular attention to the gills (Tillyard, 1915). He was an authority on the wing venation of Odonates and with the aid of palaeontology, established a complete phylogeny based on the venation of dragonflies (Hale Carpenter, 1936-1937).

In all he published around 180 papers and four books on insects but his first love was dragonflies. His classic work, *The Biology of Dragonflies* was published in 1917. Much of the material for the book was collected and studied while Tillyard was a schoolmaster. One reviewer described it as "a comprehensive summary… every chapter bears the mark of the author's own personality and frequently of his own research" (F.W.C. *The Sydneian*, September 1917 No. 233: 25-26). Another reviewer (Campion, 1917) wrote that the book was, "a lucid, well-arranged, and authoritative statement of all the most recent information upon every aspect of the subject. Nothing of importance has been omitted, and nothing has been treated of undue length". Incorporating much of his own research, made available to the public for the first time, as well as a review of previous work, the book includes chapters on the stages in the life cycle, the imago, the various systems such as the respiratory system and the nervous system, embryology, colouration, geological record and bio-geography. Campion (1917) points out that Tillyard's wife helped with the illustrations. However the book does not go without some criticism as the reviewer found that the chapter on "zoo-geographical distribution will probably be considered the least satisfactory" (Campion, 1917) and he described as "highly debatable", Tillyard's interpretation of wing venation relating to classification.

"Surprisingly, he made no use of his mathematical talents in his research" (Waterhouse and Norris, 1990). The nearest known incident to this was described by a close friend and colleague, "when he measured the speed of the flight of a dragonfly with a stop watch" (Evans, 1963).

Tillyard's other main interest was in fossil dragonflies and other fossil insects and he became an international authority. The fossil dragonflies of Britain were first studied in detail by the Reverend Peter Bellinger Brodie (1815-1897) and form the basis of the national collections acquired by the British Museum (now the Natural History Museum) in 1898 (Tillyard, 1933). Tillyard studied the type specimens on a visit to England and he was supplied with other material and photographs sent from England. The fossils were classified mainly on their wing venation and Tillyard described 17 new species from the Brodie collections.

Tillyard's two monographs on the subject were masterly accounts of the Liassic fossil dragonflies of Britain (Tillyard, 1925) and other fossil insects (Tillyard,

1933). He also worked for many years in Australia on fossils and the origins of the arthropods, in collaboration with the geologist and academic, Sir Tannatt William Edgeworth David (1858-1934) and together they published several accounts including a book (David and Tillyard, 1936). They named and described a group known as the Arthrocephala, the members of which had four moveable head segments each bearing appendages.

Even after his death, important contributions on the insects found in the Permian rocks of Kansas (summarized in *Nature* [Anon.] **140**, 1937: 116, 1018, 1104) were being published. These were published in full both before and after his death in the *American Journal of Science* (Tillyard, 1936b, 1937b).

Tillyard's dragonfly collections

Watson (1969), who published widely on Australian Odonates over many years, lists the dragonflies described by Tillyard and traces the type specimens. Watson stated in the introduction to his 1969 paper, "Of all workers on Australian dragonflies – that is, dragonflies from Australia, New Zealand, New Guinea, and the nearer Pacific Islands – the late Dr. R. J. Tillyard contributed most of our knowledge of the fauna. Thus between 1906 and 1925, Tillyard described more than a hundred Australian forms, only slightly less than half the known fauna".

After Tillyard died, parts of his dragonfly collection, including all specimens labeled as type were deposited in the Natural History Museum, London (Watson, 1969), then referred to as The British Museum (Natural History). The specimens are incorporated into the main collection and there is no separate Tillyard named collection. The other part of his material is now in the Australian National Collection, Canberra and the remainder is scattered throughout the sub continent, including The Australian Museum, Sydney, The South Australian Museum, Adelaide, The Tasmanian Museum, Hobart, New Zealand (Watson, 1969). The type holdings in the Natural History Museum, London are discussed by Kimmins (1968, 1969).

Of the Australian National Collections at CSIRO in Canberra, only 5% is data-based (Beth Mantle pers. comm.) but there are spreadsheets listing specimens with Tillyard as the collector of his many primary types. The Australian Museum collections in Sydney also contain many of Tillyard's odonates (David Britton pers. comm.) but again this collection is incompletely databased.

Assessment of his scientific work

According to Hale Carpenter (1936-1937) Tillyard's entomological work fell into five categories, general entomology, morphological and phylogenetic contributions, palaeontology, evolution of insects and economic entomology. It is very clear that he made important contributions to odonatology in several fields including morphology, taxonomy, physiology, life histories, evolution and systematics as well as fossil dragonflies and he embraced whole areas of zoology in the study of these insects. He was a pioneer in Australian entomology, and internationally at the forefront of the subject. Through his teaching and writing he stimulated many to take up the study of dragonflies and brought Odonatology to the attention of a worldwide audience.

Membership of societies, fellowships and medals

Tillyard was elected a Fellow of the Linnean Society of London in 1915, his certificate of recommendation being signed by C. Hedley, W. A. Haswell and A. A. Lawson. In 1917 this Society awarded him the Crisp medal for work on dragonflies, the subject title being, "On the rectal breathing apparatus of some anisopteroid larvae" (Evans, 1946).This award and medal (now the Trail-Crisp award and medal of the Linnean Society of London) was instituted in 1910 from money presented by Sir Frank Crisp (1843-1919) to encourage microscopical research. Confined to Fellows, it is based on papers contributed to the Society's publications.

 A Fellowship of the Royal Society of London followed, conferred in 1925. The citation showing his supporters, including the important entomologists of the day - Newstead, Nuttall, Poulton and Shipley amongst others, state he was "distinguished for his knowledge of recent and fossil forms of the Class Insecta… [and the]… author of eighty-five original papers" (Certificate of a candidate for Election, Royal Society of London, elected May 7, 1925). He was also a Fellow of the Royal Society of New Zealand (1924) and became an honorary member in 1935. He also received several other medals and awards.

Acknowledgements

(archivist, University of Sydney), Beth Mantle (CSIRO, Australian National Insect Collection, Canberra), Dave Britton (Australian Museum, Sydney), Steve Brooks and David Goodger (Natural History Museum, London) and David Pryce (Stirling University).

Books in chronological order

Tillyard, R. J. 1917. *The biology of dragonflies* (Odonata or Paraneuroptera). Cambridge University Press. 396pp.

Tillyard, R. J. 1925. *Fossil Insects No.1 The British Liassic dragonflies* (Odonata). By order of the Trustees of the British Museum, London. Oxford University Press, 39pp.

Tillyard, R. J. 1926. *The insects of Australia and New Zealand*. Angus and Robertson, Sydney 560pp.

Tillyard, R. J. 1933. *Fossil Insects No. 3 The panorpoid complex in the British Rhaetic and Lias.* By order of the Trustees of the British Museum, London. Oxford University Press 79pp.

David, E. and Tillyard, R. J. 1936. *Memoir on fossils of the late Pre-Cambrian (Newer Proterozoic) from the Adelaide series, South Australia.* **xi**. Angus and Robertson, Sydney in conjunction with the Royal Society of New South Wales.

Tillyard's papers number around 180. Only those cited in the text are listed (see 'References').

Main obituaries and works about Tillyard and his scientific achievements

Evans, J. W. 1946. Robin John Tillyard 1881-1937 *Proceedings of the Linnean Society of New South Wales.* **71:** 252-256.

Evans, J. W. 1963. *The life and work of R. J. Tillyard (1881-1937).* The John Murtagh Macrossan lectures 1962. University of Queensland Press. 32pp.

Hale Carpenter, G. D. 1936-1937. Robin John Tillyard. *Proceedings of the Linnean Society of London.* (1936-37) 212-218.

Imms, A. D. 1937. Obituary R. J. Tillyard. *Nature* **139:** 182-183.

Imms, A. D. 1938. Robin John Tillyard. *Obituary Notices of Fellows of the Royal Society* **2:** 339-345. Royal Society, London.

Waterhouse, D. F. and Norris, K. R. 1990. Tillyard, Robin John (1881-1937). *Australian Dictionary of Biography* **12:** 232-233.

References

Campion, H. 1917. Review of *The biology of dragon-flies* by R. J. Tillyard. *The Entomologist's Monthly Magazine* L111 New series **3:** 212-215.

Clarke, P. 1990. Tillyard, Pattie (1880- 1971). *Australian Dictionary of Biography*, **12:** 232. Melbourne University Press, Australia.

Kimmins, D. E. 1968. A list of the type-specimens of Libellulidae and Corduliidae (Odonata) in the British Museum (Natural History). *Bulletin of the British Museum of*

Natural History (Entomology) **22:** 277-305.

Kimmins, D. E. 1969. A list of the type specimens of Odonata in the British Museum (Natural History). Part 2. *Bulletin of the British Museum of Natural History (Entomology)* **23:** 289-314.

Tillyard, R. J. 1905 On the supposed numerical preponderance of males in Odonata. *Proceedings of the Linnean Society of New South Wales*, Sydney **30:** 344-349.

Tillyard, R. J. 1910. Studies in the life-histories of Australian Odonata. No. 3. Notes on a new species of *Phyllopetalia* with descriptions of nymph and imago. *Proceedings of the Linnean Society of New South Wales* **34**(1909)**:** 697-708.

Tillyard, R. J. 1915. On the physiology of the rectal gills in the larvae of Anisopterid dragonflies. *Proceedings of the Linnean Society of New South Wales* **xl:** 422-437.

Tillyard, R. J. 1916. Life-histories and descriptions of Australian Aeschninae; with a description of a new form of *Telephlebia* by Herbert Campion. *Journal of the Linnean Society (Zoology)* **33:** 1-83.

Tillyard, R. J. 1936a *Tracing the Dawn of Life Further Backwards*. Cawthron Lecture No. 15. 1935. The Cawthron Institute, Nelson, New Zealand.

Tillyard, R. J. 1936b. Kansas Permian insects. *American Journal of Science* **32:** 435-453.

Tillyard, R. J. 1937a. Letter to the Editor, from Canberra, The ancestors of the Diptera. *Nature* **139:** 66-67.

Tillyard, R. J. 1937b. Survey of the fossil insects from the Permian rocks of Kansas. *American Journal of Science* **33:** 81-110.

Watson, J. A. L. 1969. Australasian dragonflies described by R. J. Tillyard, with the location of types and the designation of lectotypes. *Journal of the Australian Entomological Society* **8:** 153-160.

Websites

Australian Dictionary of Biography- on line edition. Tillyard, Robert John (1881-1937). http://www.adb.onlineanu.edu.au/biogs/A120258b.htm

Robert John Tillyard from Wikipedia. http://en.wikipedia.org/wiki/Robert_John_Tillyard

Variations in the key features of exuviae of the Variable Damselfly *Coenagrion pulchellum* (Vander Linden) and the use of a score matrix to determine identification

Steve Cham

24 Bedford Avenue. Silsoe, Bedfordshire, MK45 4ER

Summary

The identification of exuviae of the Variable Damselfly *Coenagrion pulchellum* can be determined in the majority of cases by examination of the caudal lamellae and the setae on the prementum. These can however, be highly variable and some specimens are similar to the Azure Damselfly *C. puella* and pose difficulties for separation. A combination of characters when used in a score matrix will aid identification of borderline specimens.

Introduction

As its name suggests the Variable Damselfly *Coenagrion pulchellum* poses challenges for identification, not only of the adult stages but also of larvae and exuviae. Various attempts have been made to separate the larvae and exuviae of this species from the closely related Azure Damselfly *C. puella*, yet many of the characters used have not been robust enough to be applicable to all populations (Brooks, 1997; Smallshire & Swash, 2004). The objective here is to seek readily accessible identification characters to facilitate reliable separation of the two species. The following is based on a study of the exuviae of *C. pulchellum.*

Material and methods

Larvae were collected from three widely separated populations of *C. pulchellum*: at the Tennant Canal in South Wales, Meadow Lane Gravel Pits at St Ives Cambridgeshire and Upton Fen in Norfolk. At each site this species occurs in significant numbers, although *C. puella* is also known to occur. At sites where the species are sympatric, collection of sufficient specimens was made to ensure that the target species was included.

Larvae were bred through to emergence in small plastic tanks (140x79x60mm) containing aquatic vegetation, and fed with water fleas and bloodworms. A wigwam of wooden chopsticks placed in the tank provided a suitable emergence support and also facilitated convenient removal of exuviae. On emergence the

newly emerged teneral adult was identified from the hind margin of the prothorax, which readily separates *C. pulchellum* from *C. puella*. The associated exuviae were collected and labelled with confirmed identification. Some of the emerging adults (approximately 45%) proved to be *C. puella* and exuviae of these were not examined further.

Exuviae proven to be *C. pulchellum* were examined for key characters under a Leica M420 stereomicroscope giving actual viewing magnifications between 6 and 60X. The caudal lamellae were removed with fine forceps from their point of attachment to the abdomen. They were separated by soaking in warm water with a drop of washing up liquid to act as a wetting agent. The three caudal lamellae were arranged on a glass microscope slide and photographed for reproduction at 3x life size (Plates 1-15) using a Canon 5D digital SLR camera fitted with a Canon MP-E 65mm macro lens and twin flash illumination. The labial mask was removed by applying slight pressure at its base with a mounted needle and fine forceps, and placed on a glass microscope slide. No attempt was made to press the mask. All prementa were photographed for reproduction at 5x life size on the slide (Plates 16-31).

All images of caudal lamellae and labial masks were directly transmitted from camera to computer for examination on-screen and measurement using Adobe Photoshop CS software. Each image was named with a unique identifier for each exuvia. To obtain key ratios for caudal lamellae, measurements were made at high magnification from the on-screen images (using the info palette in Photoshop CS). Images of the prementa were overlaid with lines at predefined angles, in increments of 5°, to measure the included angle of the rows of premental setae (see plate 31 for further details). This enabled the angle to be measured at high magnification. A count of the number of premental setae and their arrangement were also made.

The exuviae of three known *C. puella* were used as controls.

Observations

Fifteen exuviae of confirmed *C. pulchellum* were examined for a number of characters of the body, caudal lamellae and head. Some of the characters, such as setae on the labial palps, stout setae on margins of caudal lamellae and stout setae above the lateral carina, considered by Crick (2009) to be highly variable and of no value in the identification of *C. puella*, were not included.

Body

Overall pigmentation of whole body

The colouration of 26% of the exuviae could be described as dark brown pigmentation whereas others were light brown coloured, similar to the exuviae of other species. Dark pigmentation is suggestive of, but not diagnostic for, *C. pulchellum* (Brooks, 1997; Smallshire & Swash, 2004). It should be noted that the exuviae from green larvae of *C. puella* appeared light brown.

Sex. Sex was determined by assessing the presence of an ovipositor (female) or two spines (male) on the underside of S9.

Caudal lamellae

Tip profile The rounded profile of the tip of the caudal lamellae is an often-quoted character of *C. pulchellum* in available keys (Askew, 1988; Brooks, 1997; Gardner, 1954). In this sample the tip profile ranged from very rounded (R), through rounded (M) to slightly pointed (P). The description of this feature is highly subjective, thus making comparisons between results from different workers problematic. For each exuvia the tip of all three caudal lamellae was allocated to one of the above profiles. However, this feature is a continuous spectrum from pointed to round with some profiles difficult to discern whether they were very rounded or medium rounded (Fig. 1). Furthermore, the tips often became folded over and great care needed to be taken to ensure that they were fully flat when taking profile measurements. The lamellae can be flattened readily in a
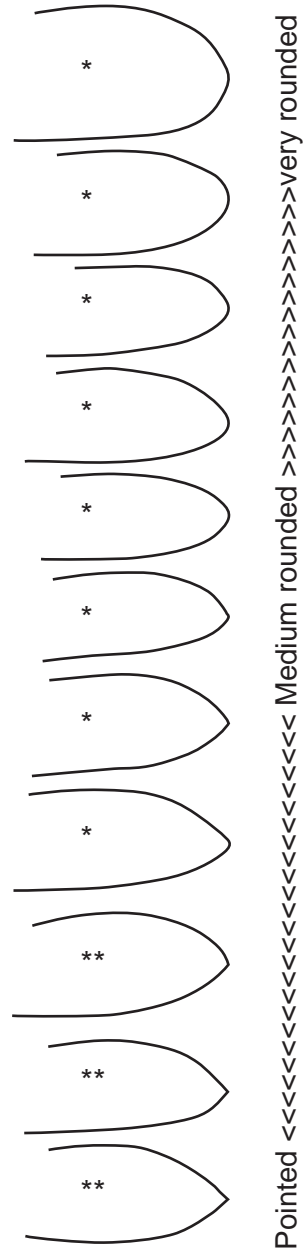
Figure 1: Caudal lamellae tip profiles drawn from *C. pulchellum* (*) and *C. puella* (**).

Plate 1 Caudal lamellae from Exuvia D (RRR)

Plate 2 Caudal lamellae from Exuvia G (PRM)

Plate 3 Caudal lamellae from Exuvia M (RRR)

Plate 4 Caudal lamellae from Exuvia J (MRP)

Plate 5 Caudal lamellae from Exuvia C (RPR)

Plate 6 Caudal lamellae from Exuvia A (RRR)

Plate 7 Caudal lamellae from Exuvia K (MRR)

Plate 8 Caudal lamellae from Exuvia B (RMR)

Plate 9 Caudal lamellae from Exuvia H (PPP)

Plate 10 Caudal lamellae from Exuvia O (PPP)

Plate 11 Caudal lamellae from Exuvia I (PMP)

Plate 12 Caudal lamellae from Exuvia F (MRP)

Plates 13,14,15 Caudal lamellae from
C.puella (PP*P, PPP, PPP)

N.B.* is underdeveloped

drop of water on a microscope slide by rolling a fine brush over them. By wicking away the water with filter paper and then drying they form a permanently flat preparation.

Pigmentation of nodal line The pigmentation of the nodal line ranged from highly pigmented (YY), through lightly pigmented (Y) to very slight or no pigmentation (N) (Plates 1-15). The angle of the node was oblique in most cases and not considered to be diagnostically useful.

Width of lamellae at node and length of lamellae from node to tip The ratio of width at node to length from node to tip ranged from 1.56 to 2.16 (Table 1 & Cham, 2009). At the higher ratios there is overlap with lower ratios from caudal lamellae of *C. puella* (Cham, 2009).

Number of twists of primary tracheae prior to the nodal line The number of twists of the primary tracheae was highly variable and the determination of the number sufficiently problematic not to warrant further consideration. Seidenbusch (1996) described 5-9 pre-nodal twists for *C. pulchellum*. In this study some caudal lamellae had no twists that were visible. This character is difficult to determine and requires high magnification, which induces further difficulties due to shallow depth of focus.

Head

Spotting on upper hind margin Dark pigmented spotting was observed on the head of all exuviae in the sample. The spotting was indistinguishable from that of C. puella.

Arrangement and number of setae on prementum The number of premental setae on either side of the central line ranged from 1 to 5 in a variety of combinations (Fig. 2). Other confirmed exuviae used for the production of a field guide (Cham, 2009) have been added to this sample.

Included angle of premental setae The included angle ranged from 90° to 107° (Plates 16-31). The included angle of the exuviae with a 1+ 5 arrangement was determined by overlaying the image against an image of an exuvia with a full complement of setae.

Antennal segments *C. pulchellum* and *C. puella* have the same number (seven) of antennal segments. However, antennal segments are often lost or damaged on exuviae and anyway are less useful in the identification of exuviae.
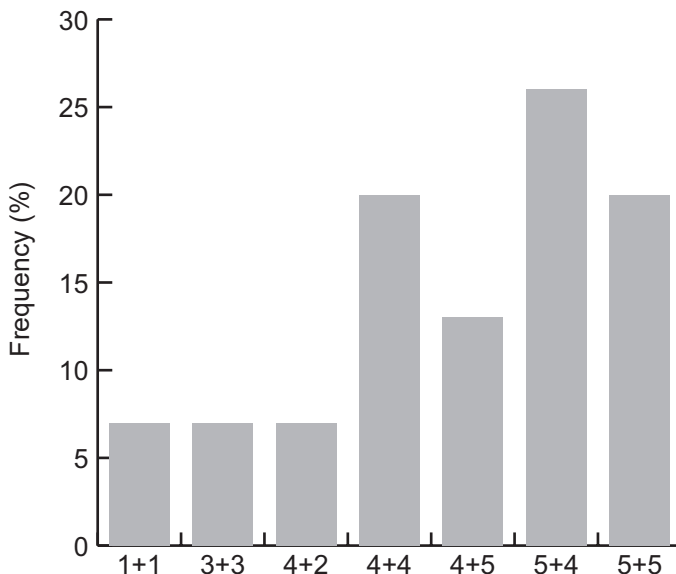
Figure 2. Frequency of different arrangements of the premental setae in *C. pulchellum*.
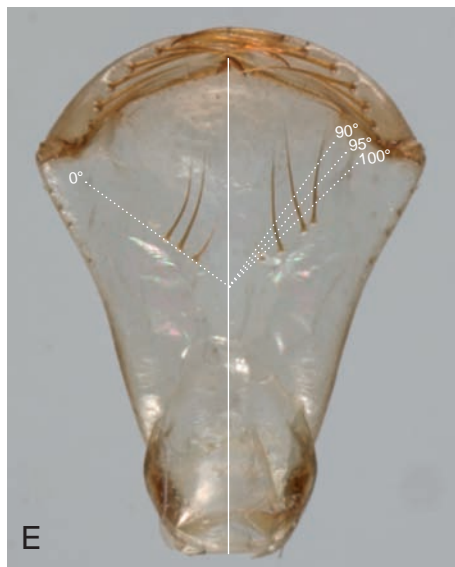
Plate 16 Prementum from Exuvia E
(3+4, 107°)
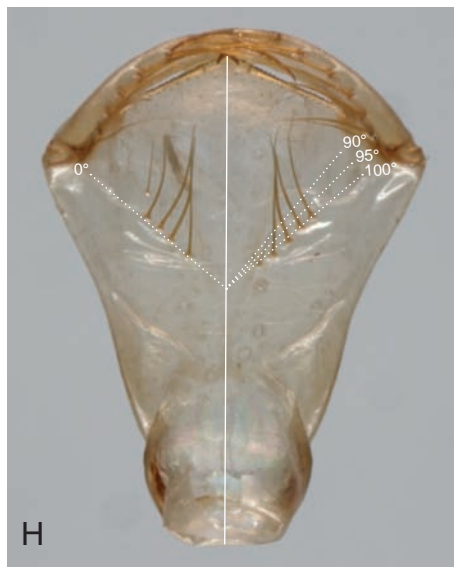
Plate 17 Prementum from Exuvia H
(5+5, 105°)
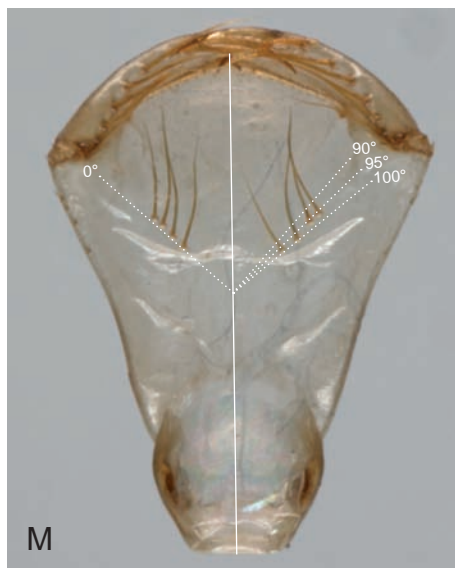
Plate 18 Prementum from Exuvia M
(4+4, 100°)
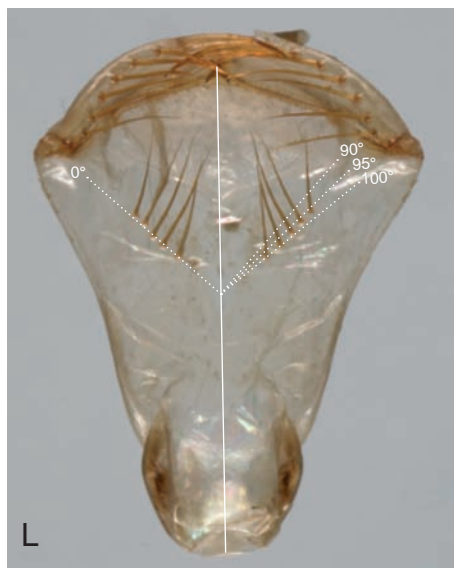
Plate 19 Prementum from Exuvia L
(5+5, 100°)

Plate 20 Prementum from Exuvia J
(1+5, 96°)
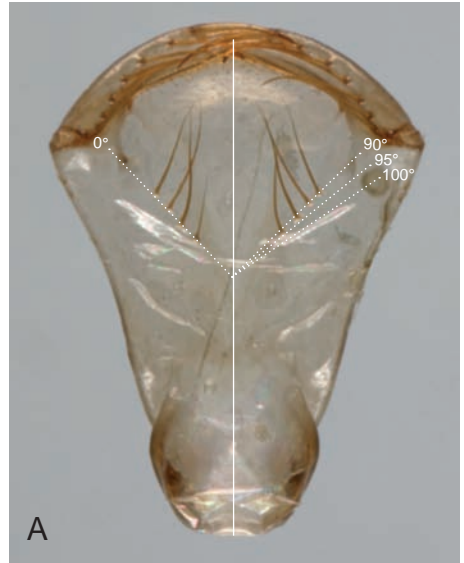
Plate 21 Prementum from Exuvia A
(4+4, 95°)
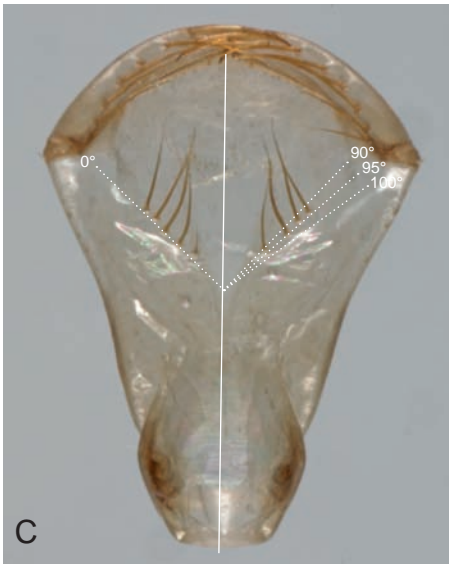
Plate 22 Prementum from Exuvia C
(5+4, 95°)
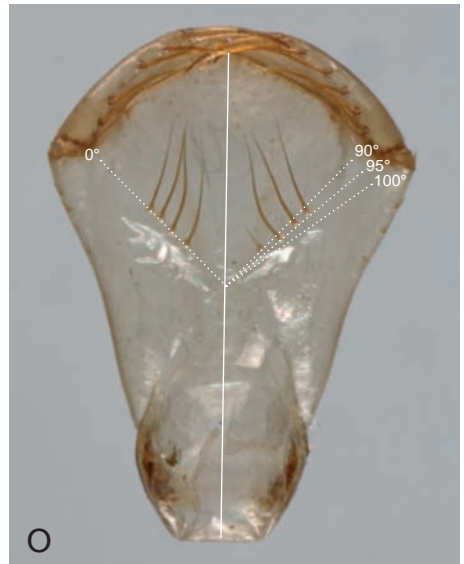
Plate 23 Prementum from Exuvia O
(4+4, 95°)

Plate 24 Prementum from Exuvia N
(5+5, 95°)
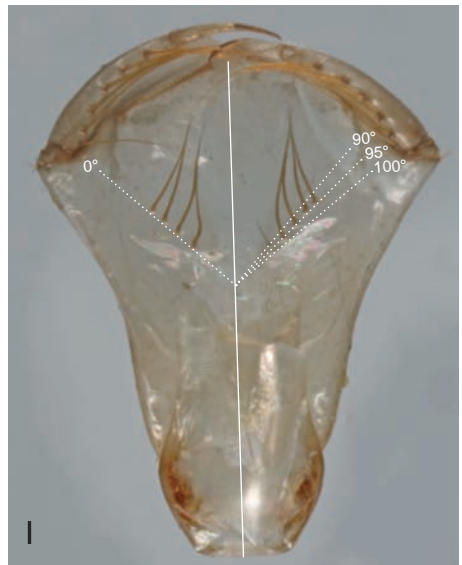
Plate 25 Prementum from Exuvia I
(4+5, 95°)
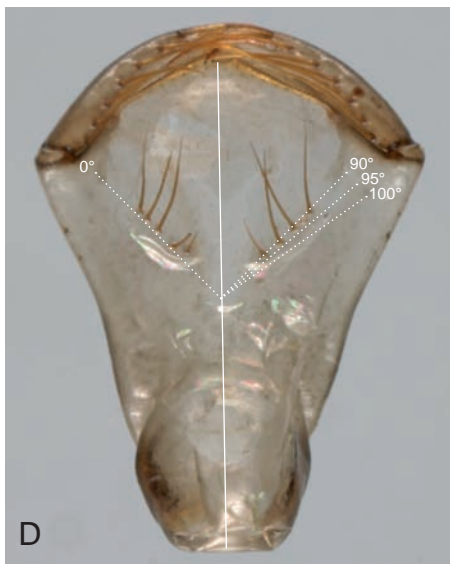
Plate 26 Prementum from Exuvia D
(5+5, 94°)

Plate 27 Prementum from Exuvia G
(4+4, 93°)

Plate 28 Prementum from Exuvia B
(5+4, 92°)
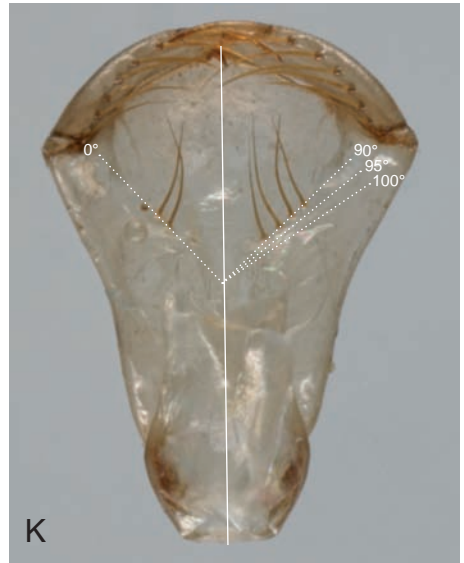
Plate 29 Prementum from Exuvia K
(3+4, 92°)
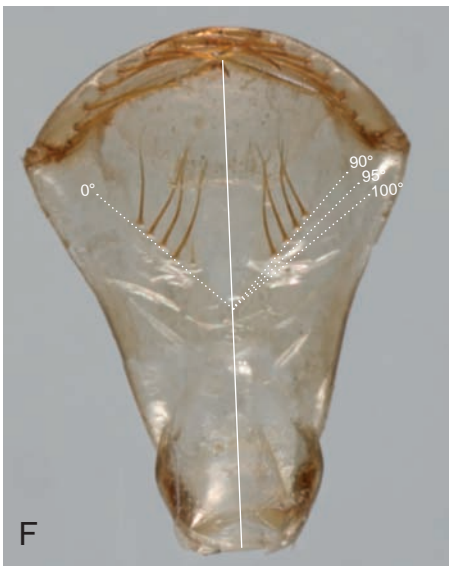
Plate 30 Prementum from Exuvia F
(5+4, 90°)
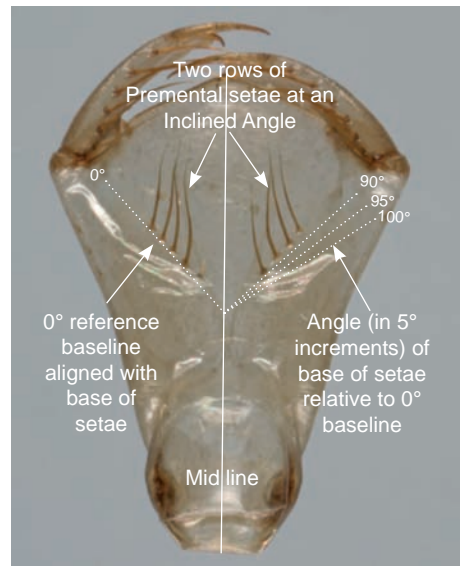
Plate 31 Prementum from *C.puella*
(5+4, <90°)

Score matrix

To enable four characteristics of the exuviae to be compared, a score matrix was set up in a spreadsheet. Values were entered in the appropriate columns with the relevant scores and totals automatically calculated, thus allowing comparison between specimens to be made quickly.

Caudal lamellae ratio The caudal lamellae ratio (Cham, 2009) was calculated and scored 3 if <=1.9, 2 if > 1.9 yet < 2.0 and 0 if >= 2.0. A score of 0 was given to the last category so that borderline specimens scored low

Caudal lamellae tip shape The tip shape of the caudal lamellae was assessed for each lamella (Fig. 1). R = very rounded, M = rounded point and P= pointed. Each R scored 3, each M scored 1 and pointed scored 0, giving a maximum of 9 for a specimen with RRR. Exuviae with one or more missing or underdeveloped lamellae would score low, as would noticeably pointed lamellae. It is intended that the photographs of caudal lamellae illustrated here will serve as reference from which further comparison can be made in the future.

Pigmentation of the node Pigmentation of the node was assessed and, if heavily pigmented, given a YY which scored 2, slightly pigmented Y scored 1 point and others 0.

The Included Angle of premental setae The Included Angle of premental setae was measured and scored - equal or less than $90°$ scored 0; greater than $90°$, but less than $95°$ scored 2; equal or greater than $95°$, but less than $100°$ scored 3 and greater or equal to $100°$ scored 5. The Included Angle is considered to be one of the more consistent characters for separating the two species (Seidenbusch 1996) and this is reflected in the allocation of scores here, notably 5 rather than 4 for an angle equal to or greater than $100°$. Crick (2009) has provided further analysis and support for the Included Angle in *C. puella* being $90°$ or less.

The resulting spreadsheet (Table 1) summed the four scores for each criterion and sorted by total score in descending values. Total scores greater than 5 were allocated to High confidence, between 3-5 allocated to Medium confidence and 2 and below to Low confidence. Three exuviae of *C. puella* were included here as a benchmark.

Assessment of the matrix

Using the score matrix a perfect *C. pulchellum* specimen could attract a maximum score of 19 if all criteria were met. The maximum score was only

High confidence scoring (6-20)

M:- scored 19. This specimen had all three lamellae rounded with strongly pigmented nodal lines and a high Included Angle of premental setae. (Plates 3,18).

D:- scored 16. This very dark specimen had three exceptionally large rounded lamellae with strongly pigmented nodes. The Included Angle however was borderline at 90°. (Plates1,26).

A:- scored 15. It had three rounded CL with pigmented nodes. Combined with an Included Angle of 100° it had the key characters of *C. pulchellum*. (Plates 6, 21).

K:- scored13. Two very rounded CL and one slightly rounded, pigmented nodes and an Included Angle of 92°. (Plates. 7,29).

J:- scored 12. It had one rounded middle CL with one outer less rounded and one pointed. It had strongly pigmented nodes. The Included Angle was 96°. (Plates 4, 20).

G:- scored 11. This exuvia scored in each category, particularly the characters of the CL. (Plates 2, 27).

C:- scored 11. It had two rounded CL and the middle one was pointed. The nodes were strongly pigmented. It had an Included Angle of 95°. (Plates 5, 22).

H:- scored 9. This exuviae had all pointed lamellae but with strongly pigmented nodes. It had a high Included Angle of 105°. (Plates 9,17).

B:- scored 9. It had two rounded CL and one less rounded. There was a lack of pigmented nodes. It had an Included Angle of 95°. (Plates 8, 28).

F:- scored 8. This had a relatively low Included Angle of 90°. It had a low CL ratio and one very rounded and one slightly rounded lamella. The third was pointed. The nodal lines were lightly pigmented. (Plates 12,30).

I:- scored 6. This exuvia was tricky due to the three pointed CL and a high ratio. It had heavily pigmented nodes. The included angle was 95°. (Plates 11, 25).

Medium confidence scoring (2 –5)

L:- scored 5 and was a very dark exuvia. This exuviae lacked CL and was therefore initially difficult to identify. The Included Angle was very high at >100° thus confirming identification as *C. pulchellum*. (Plate 19).

E:- scored 5. This exuvia lacked CL and was therefore initially difficult to identify. The Included Angle was very high at 107°, contributing to all of the score of 5 and thus confirming identification as *C. pulchellum*. (Plate 16).

O: scored 5. This exuvia had three pointed lamellae very similar in tip profile to *C. puella*. They lacked dark pigmentation of the nodes. The Included Angle of 95° was the defining character. (Plates 10, 23).

Table 1. Exuviae Score Matrix. CL, caudal lamella; Sc, score. All lettered specimens are confirmed *C. pulchellum*.

Specimen identifier	CL Ratio	Sc	CL tip shapes	Sc	Pigmented node	Sc	Included angle of premental setae	Sc	Total Score	Confidence of identification
M	1.84	3	RRR	9	YY	2	100	5	19	High
D	1.56	3	RRR	9	YY	2	94	2	16	High
A	1.98	2	RRR	9	Y	1	95	3	15	High
K	1.94	2	MRR	7	YY	2	92	2	13	High
J	1.78	3	MRP	4	YY	2	96	3	12	High
G	1.84	3	PRM	4	YY	2	93	2	11	High
C	2.09	0	RPR	6	YY	2	95	3	11	High
B	2.09	0	RMR	7	N	0	92	2	9	High
H	1.92	2	PPP	0	YY	2	105	5	9	High
F	1.82	3	MRP	4	Y	1	90	0	8	High
I	2.16	0	PMP	1	YY	2	95	3	6	High
L	NA	0	NA	0	NA	0	100	5	5	Medium
E	NA	0	NA	0	NA	0	107	5	5	Medium
O	1.93	2	PPP	0	N	0	95	3	5	Medium
N	NA	0	NA	0	NA	0	95	3	3	Medium
Puella 2	2.12	0	PPP	0	Y	1	86	0	1	Low
Puella 1	2.25	0	PPP	0	N	0	90	0	0	Low
Puella 3	2.13	0	PPP	0	N	0	87	0	0	Low

N:- scored 3. This exuvia lacked CL and was therefore difficult to identify. It was a light coloured specimen. It caused the greatest difficulty of all 15 specimens in confirming its identity as *C. pulchellum*. The Included Angle of 95° was the defining character. (Plate 24).

Low confidence scoring (0-2)

Puella 1,2,3: these three *C. puella*, selected at random, were included as a control. Two of them scored 0 as would be expected, whilst the third scored one due to light but faint pigmentation of the nodal lines. (Plates. 13,14,15, 31).

Discussion

C. puella is a common and widespread species with many populations sufficiently isolated from *C. pulchellum* to avoid any chance of misidentification of exuviae. In contrast *C. pulchellum* is less widespread and it often occurs together with *C. puella*. There appears to be no evidence of hybridisation between *C. puella* and

C. pulchellum (Lowe *et al.*, 2008). However, accurate identification of exuviae is not straightforward, especially in the field. To distinguish the two species from each other reliably requires robust features described from exuviae of confirmed identification. The latter can only be realised for *C. pulchellum* where the emergent adult has been seen with the exuvia from which it has just emerged. Collection from sites where *C. pulchellum* occurs exclusively has so far not been possible. If and when such a site is identified there is potential for further study.

A series of key characters have been examined for *C. puella* (Crick 2009) and for *C. pulchellum* (Carchini, 1983; Cham, 2009; Seidenbusch, 1996). Other authors make little or no attempt to separate the two (Gerken & Sternberg, 1999) or add a caution. Norling & Sahlén (1997) concluded that the exuviae of "These species cannot reliably be separated". Askew (1988) states that "This separation of *puella* and *pulchellum* follows Gardner 1954 and seems to be unreliable". It should also be noted that Seidenbusch (1996) does not describe the methods for determining how the exuviae were of known identification. Without such information the confidence level of identification is low. It should be noted that all of the characters examined here showed no differences between the two sexes.

The only ways to assess characters useful for the identification of exuviae of *C. pulchellum* is to breed larvae through to emergence or to search for newly emerged adults still in association with their exuviae. This in itself is labour intensive and requires large samples if sufficient exuviae of confirmed identification are to be collected.

Dark pigmentation can be suggestive of species but should not be used for identification alone. Dark brown larvae and exuviae from the three populations in this study all proved to be *C. pulchellum* and a dark exuvia increases the probability of it being *C. pulchellum*. However, care should be taken using colour, as it is all too easy to confuse pigmentation with staining from dark substrate. Should dark brown-pigmented specimens of *C. puella* be found in the future this would eliminate the potential usefulness of this character.

The spots on the upper hind margin of the head are not sufficiently different to those of *C. puella* to be of any use in separating the two species. Setae on the labial palps were not examined, as they have proved unreliable in *C. puella* (Crick, 2009). The stout setae above the lateral carinae of 2nd or any abdominal segment are highly variable and not diagnostic. Furthermore, exuviae often curl so making it difficult to observe all setae.

It is often reported that the caudal lamellae of *C. pulchellum* have a more

rounded tip than those from *C. puella*. The definition of 'rounded' and 'pointed' is subjective in descriptive terms. Comparison of the tip shape therefore needs to be compared against a reference series of tip profiles (Fig. 1) from known specimens if it is to be diagnostically useful. A pointed tip generally results in a relatively long lamella and therefore a high CL ratio. Whilst the middle lamella offers a standard for comparisons of the tip profile, the outer lamellae should also be examined. Some exuviae with a slightly pointed middle lamella were found to have very rounded outer lamellae. Several exuviae had lost their caudal lamellae and could not be included. Such specimens are often encountered in 'pond dipping' samples and their identification relies on the use of other characters. Care must also be taken with larvae and exuviae that have regrown or underdeveloped lamellae. Damaged lamellae in *C. puella* often regrow with a rounded tip (Cham, 2009), yet are usually shorter relative to others. Such lamellae should be disregarded in any comparative assessment.

The nodal line is highly variable. The pigmentation of this line varied from faint to heavily pigmented in specimens of *C. pulchellum*. Heavily pigmented nodal lines remain a character of *C. pulchellum*. Faintly pigmented nodal lines have been observed in a small number *C. puella*, including one in this study (Plate15).

The number and arrangement of premental setae is highly variable and not a useful character (Fig. 2). However, the Included Angle of the baselines of the premental setae appears to be a distinctive character and is sufficient to separate the majority of specimens, including those that have lost their caudal lamellae. The Included Angle was equal to or greater than 90° in all the C. pulchellum exuviae examined. Specimens with 95° or greater can confidently be identified as *C. pulchellum*. However, specimens where the angle is approximately 90° may overlap with specimens of *C. puella* at the upper end of the range of the latter. Crick (2009) reported that 36.4% of his *C. puella* sample had an included angle of 90°. However, more than 62% of his sample had an Included Angle of 85° or less and none had an angle greater than 90°. Care should be taken when making this measurement and it should be done on prementa that have not been distorted in any way. Seidenbusch (1996) proposed using prementa pressed between glass slides. This approach requires a reproducible amount of compression and may lead to user-induced variation when making measurements.

Single identification characters, unless sufficiently exaggerated, do not provide a high level of confidence. When combined with others in a score matrix (Table 1) the confidence level increases. The score matrix was constructed for 15 exuviae, including three where the caudal lamellae were missing. For each criterion 3-5 points were given if the ID character was exaggerated, 1-2 points were given if the ID character was noticeable and 0 points if it was not observable. After

the scores were added up a level of confidence was allocated to each exuvia: 0-2 low confidence, 3-5 medium confidence and >5 high confidence. Whilst this allocation is in itself subjective, it is a line in the sand and an attempt to flag borderline specimens of both species. It is hoped that the results presented here will encourage further critique and study by others to refine the methodology.

The use of digital photography has greatly enhanced the recording, measurement and storage of images relating to specimen identification. It enables a library of images to be built up and, if stored with full details and information of magnification/scale, then future comparisons with additional material of known identification can be made.

C. pulchellum remains a species whose larvae and exuviae will continue to pose problems for identification in the field. Some specimens can be identified with confidence whilst others with similarities to *C. puella* will need to be examined in more detail and a number of characters compared in a score matrix such as the one proposed here.

Conclusions

Whilst it is hoped that this approach is a helpful step along the path to better identification of exuviae of *C. pulchellum* it does not claim to be the complete answer to this perennial problem. It has been demonstrated that two or more characters need to be assessed to increase confidence in achieving identification of *C. pulchellum* specimens. Exuviae with pointed caudal lamellae are especially likely to be confused with *C. puella*, yet such specimens can be separated if the nodal line is heavily pigmented and the Included Angle of the premental setae exceeds 90°. Some specimens may remain difficult to identify although these should be few. There is clearly need for more research in this area, with larger sample sizes and statistical analysis of exuviae of confirmed identification. As more experience is gained from other populations this approach can be refined and its usability extended. From examining various features of the caudal lamellae and labial mask, confidence levels in identification can be attained for exuviae of *C. pulchellum*. It is urged that anyone finding newly emerged adults of *C. pulchellum* still in association with their exuviae should test the identification characters described here.

Acknowledgements

References

Askew, R. R. 1988. *The Dragonflies of Europe*. Harley Books, Colchester. 291pp.

Brooks, S. 1997. *Field Guide to the Dragonflies and Damselflies of Great Britain and Ireland*. British Wildlife Publishing. Hook, Hampshire. 160pp.

Carchini, G. 1983 A key to the Italian odonate larvae. – *Societas Internationalis Odonatologica Rapid Communications (Supplements)* **1:**1-101.

Cham, S. A. 2009. *Field Guide to the larvae and exuviae of British Dragonflies*. Volume 2: *Damselflies (Zygoptera)*. British Dragonfly Society, Peterborough. 75pp.

Crick, K 2009. Variations in key features of the final instar larvae and exuviae of the Azure Damselfly *Coenagrion puella* (Linnaeus) *Journal of the British Dragonfly Society* **25**: 16-26.

Gardner, A. E. 1954 A key to the larvae of British Odonata. Part 1. Zygoptera. *Entomologists Gazette* **5:** 157-71.

Gerken, B. and Sternberg, K. 1999. *The exuviae of European Dragonflies*. Huxaria Druckerei GmbH.

Lowe, C. D., Harvey, I. F., Thompson, D. J. and Watts, P. C. 2008. Strong genetic divergence indicates that congeneric damselflies *Coenagrion puella* and *C. pulchellum* (Odonata: Zygoptera: Coenagrionidae) do not hybridise. *Hydrobiologica* **605:** 55-63.

Norling, U. and Sahlén, G. 1997. *Odonata, Dragonflies and Damselflies*. In: Aquatic Insects of North Europe: A taxonomic handbook. Volume 2: Odonata and Diptera. (ed. A. Nilsson). Appolo Books. Stenstrup. 13-65.

Seidenbusch, R. 1996. Notes on the identification of the exuviae of *Coenagrion pulchellum* (Vander Linden) and *Coenagrion puella* (Linnaeus). *Journal of the British Dragonfly Society* **12:** 22-24.

Smallshire, D and Swash, A. 2004. *Britain's Dragonflies: A guide to the identification of the damselflies and dragonflies of Great Britain and Ireland*. WILDGuides. Old Basing, Hampshire. 168pp.

Remembering Encounters with Dragonflies from the 1930s to the Launching of the BDS in 1983.

Norman W. Moore

117 Boxworth End, Swavesey, Cambridge, CB24 4RA.

The history of research on dragonflies has been extensively reviewed by Corbet and Brooks (2008). The aim of this paper is to describe the problems experienced by an odonatologist during the 45-year period before the formation of the BDS in 1983.

I remember as a boy in the early 1930s being bitten by a Common Darter *Sympetrum striolatum* which I had caught. I did not know its name because at that time there was no popular book about dragonflies and I did not know about E.V. Lucas's "British Dragonflies" (1900) which, in any event, was not in print. The contrast between butterflies and dragonflies was striking and surprising.

In 1937 I came across Cynthia Longfield's book "The Dragonflies of the British Isles" (1937) in a bookshop in Hastings. I bought it and within a few months was writing to Cynthia at the Natural History Museum in London about dragonflies and she became a colleague and friend. In her book she listed the counties in which each species was known to occur and, as I explored the country for dragonflies, I was able to record counties from which Cynthia had no records. I had a large notebook in which I recorded all the localities of the species I observed and made observations and drawings of their behaviour. Shortly after, in 1939, I came across a second hand copy of E.V. Lucas's book in a shop and bought it. It was and is an outstanding book. It contains not only the original description of each species but also sections about synonymy, size, descriptions of male and female and immature adults, seasons and distribution in the British Isles as known at that time, and descriptions of larvae. Where relevant and when the information was available there are sections on the egg, "nymph", oviposition, habits, migration and differences between similar species. The book has excellent colour photographs and some clear illustrations of larvae.

After the publication of Lucas's book in 1900 no other books about dragonflies were published in English until Cynthia's book in 1937, except for a short chapter in R. J. Tillyard's book, 'The Biology of Dragonflies' (Tillyard, 1937). Cynthia's book contains drawings and diagrams by Dorothy Fitchew and photographs by W. H. T. Tams. It describes the British species, including details of their life history; also methods of collecting, preserving and rearing. All papers on dragonflies continued to be published in entomological and ecological journals

along with articles about other entomological subjects as had occurred since the mid 18th century.

In the early 1950s Philip Corbet and I began corresponding about British dragonflies. We first met when Philip was a PhD student at Cambridge and I was starting my career in the Nature Conservancy. We both studied dragonflies in the field; Philip's main interest concerned the factors governing the life history of dragonflies. Later he studied dragonflies in East Africa and emigrated to Canada and from there went on to New Zealand, returning to the U.K. in 1983. Throughout his long and distinguished career Philip published numerous papers on dragonfly biology culminating in his magnum opus "Dragonflies; behaviour and ecology of Odonata" (Corbet, 1999).

In 1960 Philip, Cynthia and I published 'Dragonflies' in The New Naturalist series. Apart from Cynthia and myself the only other active worker in the field in this country was Macan, who was carrying out long-term studies in the Lake District. He studied twenty generations of the Large Red Damselfly *Pyrrhosoma nymphula* (Sulzer) and the Common Blue Damselfly *Enallagma cyathigerum* (Charpentier) (Macan, 1974). Peter Miller and Peter Mill both started out as neuroscientists working in the 1960's on the neural control of respiration in adult and larval aeshnids respectively; both later turned their attention to ecology and behaviour. Cynthia retired from the museum in 1956 but continued to be active, publishing on dragonflies until 1964.

My studies on territorial behaviour and dispersal led to me being concerned about dragonfly conservation throughout the world, and that led to me organising dragonfly conservation on a world basis. But there was still no odonatological journal in a European language which could facilitate contacts between odonatologists in the British Isles and other European nations.

The break through came in 1971 when odonatologists from a number of European countries met in October in Ghent, Belgium for the first European Symposium of Odonatology. At the meeting it was decided to form an International Society, to be called Societas Internationalis Odonatologica (or SIO) "with the aim of perpetuating contacts among workers all over the World and promoting research by rapid diffusion of information" and to launch a journal (Odonatologica). Henri Dumont of Belgium was the first Secretary of SIO. In 1972 the first issue of Odonatologica appeared, under the editorship of Bastiaan Kiauta and Janny Van Brink of The Netherlands.

In its first number there were seven papers written by odonatologists from Belgium, France, Germany, The Netherlands, Poland, the United Kingdom and the USA; all but two of the papers were written in English. There was also

a section on Odonatological Abstracts which covered publications from the whole world. An international journal confined to articles on Odonata helped to bring odonatologists together from all parts the world, and this enabled new international acquaintances and friendships to develop, based on the study of dragonflies. The second symposium was held in Karlsruhe, Germany in September 1973 and the third in Lancaster, England in July 1975. These were now truly international meetings and Cynthia Longfield came over from Ireland to attend the one at Lancaster.

The SIO meetings were a real breakthrough for British odonatologists and paved the way to bring dragonflies into the public domain. In those days dragonflies were practically never used as decorations, illustrations, earrings or broaches. The public was scarcely aware of dragonflies. It was the formation of the BDS in 1983 which led to them becoming appreciated by the British public as a whole. The BDS held its first meeting at the Institute for Terrestrial Research, Monks Wood in May 1984 and the Dragonfly Conservation Group of the BDS was formed in 1986.

The formation of the BDS in 1983 coincided with the production of detailed procedures for selecting SSSI. These now included a special section on selecting SSSI entirely on odonatological criteria. What a change from the situation in previous decades!

References

Corbet, P.S. & Brooks, S.J. 2008. *Dragonflies*. Collins, London. 454pp.

Corbet, P.S. 1999. *Dragonflies: Behaviour and Ecology of Odonata*. Harley Books, Colchester. 829pp.

Longfield, C. 1937. *The Dragonflies of the British Isles*. Frederick Warne, London & New York. 220pp.

Lucas, W. J. 1900. *British Dragonflies (Odonata)*. L. Upcott Gill, London. 356pp.

Tillyard, R. J. 1917. The Biology of Dragonflies (Odonata or Paraneuroptera). Cambridge University Press, Cambridge. 396pp.

Folding wing behaviour in the Golden-ringed Dragonfly *Cordulegaster boltonii*

DEREK K. JENKINS

7 Lakewood Road, Ashurst, Southampton, Hants SO40 7DH

Summary

An unusual observation is reported of a specimen of the Golden-ringed Dragonfly *Cordulegaster boltonii* raising its wings over its back while at rest during a period of light rain.

Introduction

A key feature often quoted to differentiate Anisoptera from Zygoptera is that, when at rest, the former hold their wings horizontally at $90°$ to the line of the body while the latter fold them together vertically over the abdomen (e.g. Hammond, 1977; Brooks & Lewington, 1997; Smallshire & Swash, 2004). There are some obvious exceptions, notably the wings of *Lestes* species which are typically held back and away from the abdomen at around $45°$. Some calopterygid zygopterans, such as *Calopteryx* spp. may adopt the spread-wing position during pre-flight basking or throughout the night in cold weather (Zahner, 1960; I.Thompson in Paine, 1994; G. Barker in Paine, 1995); under poor weather conditions this may persist during the day (Heymer, 1972). Male *Calopteryx* spp. also spread their wings when displaying. Amongst anisopterans the wings of libellulids are pushed forward for rapid take-off when alarmed.

Observations

While carrying out transects in connection with a study of *Coenagrion mercuriale* at Acres Down in the New Forest, I came across two Golden-ringed Dragonflies *Cordulegaster boltonii* about 5m apart, hanging below Bog Myrtle *Myrica gale* leaves. Since two had emerged a few days earlier from the only nearby stream and one, or sometimes two, had been seen regularly in the intervening period, it seems likely that both insects were the same age. The weather was overcast and conditions such that few insects of any kind were visible (the normally abundant Keeled Skimmer *Orthetrum coerulescens* were few in number, low in the vegetation or on the ground, and dormant). During four transects of the site at 30-40 minute intervals, the two *C. boltonii* remained in exactly the same position, at the same height, with roughly the same overhead shelter, wings spread at $90°$ and the dorsal side facing south towards open ground. At this

juncture a light drizzle set in and the wings of one of the *C. boltonii* appeared to be set back at slightly less than a right angle. I started to watch both insects closely and the one already showing wing movement continued to move them backwards and upwards over a period of 20-25 seconds until they were in the position adopted by most resting Zygoptera, although the wings did not meet each other completely but remained parallel and approximately 5mm apart.

The drizzle continued for some 45 minutes, occasionally becoming heavier, but finally relented. Although the weather remained dull, the *C. boltonii* with closed wings very slowly spread them again until both insects were in their normal resting configuration. Anisoptera are physiologically capable of folding their wings above their back, but I have never seen this before under natural conditions, nor have I seen it recorded. It seems even stranger that only one of the two insects should do so under apparently identical conditions.

References

Brooks, S. & Lewington, R. 1997. *Field Guide to the Dragonflies and Damselflies of Great Britain and Ireland*. British Wildlife Publishing, Hampshire. 160pp.

Hammond, C. O. 1977. *The Dragonflies of Great Britain and Ireland*. Curwen, London. 115pp.

Heymer, A. 1972. *Verhaltensstudien an Prachtlibellen. Beiträge zur Ethologie und Evolutiuon der Calopterygidae Sélys, 1850 (Odonata: Zygoptera)*. Fortschritte Verhaltensf. 11. Parey, Berlin. 100pp.

Smallshire, D and Swash, A. 2004. *Britain's Dragonflies: A guide to the identification of the damselflies and dragonflies of Great Britain and Ireland*. WILDGuides. Old Basing, Hampshire. 168pp.

Paine, A. 1994. Notes and observations. *Journal of the British Dragonfly Society* **10:** 45-46.

Paine 1995. Notes and observations. *Journal of the British Dragonfly Society* **11:** 22-246.

Zahner, R. 1960. *Über die Bindung der mitteleuropäischen Calopteryx-Arten (Odonata, Zygoptera) an den Lebensraum des strömenden Wassers. II. Der Anteil der Imagines an der Biotopbindung.* International Revue of Hydrobiology **45:** 101-123.

Species Review 3:

The Large Red Damselfly *Pyrrhosoma nymphula* (Sulzer) with notes on its close relative the Greek Red Damselfly *Pyrrhosoma elisabethae* Schmidt

PETER J. MILL

School of Biological Sciences, University of Leeds, Leeds, LS2 9JT

Summary

Only four species belonging to the coenagrionid genus *Pyrrhosoma* are known to date, two in Europe and two in China. Our knowledge of *P. nymphula* is described in detail along with brief notes on the little known *P. elisabethae*. Some areas where further study would be useful are given in the conclusions.

Introduction

Pyrrhosoma is a genus within the Coenagrionidae and comprises only four species, the Large Red Damselfly *P. nymphula* (Sulzer, 1776) and the Greek Red Damselfly *P. elisabethae* Schmidt, 1948 in Europe and *P. tinctipennis* McLachlan, 1894 and *P. latiloba* Yu, Yang & Bu, 2008 in China. *P. elisabethae* was earlier thought to be a subspecies of *P. nymphula* (Davis & Tobin, 1984; Askew, 1988) and indeed some authors have found specimens in Austria and Greece that appeared to be intermediate in character (Buchholz, 1954; Stark, 1979). However, clear differences have now been described that separate these two species (Kalkman & Lopau, 2006). A subspecies of *P. nymphula*, *P. n. interposita* Varga, 1968 is found in Hungary (Davies & Tobin, 1984). Recently a molecular study on odonate phylogeny has indicated that *Pyrrhosoma* along with *Ceriagrion* and *Nehallenia* form a clade separate from the other coenagrionids (Dumont *et al.*, 2010).

> *Pyrrhosoma nymphula* (The Large Red Damselfly). The type locality is Switzerland but the location of the type is unknown. The species is widespread throughout most of Europe as well as in north Morocco. However, it is local in southern Spain and is absent from part of central Spain and much of northern Scandinavia (Askew, 1988; Dijkstra & Lewington, 2006). It occurs as far east as Siberia. In Britain and Ireland it is one of the most common and widespread of the damselfly species

present. It is the larger of our two red species and is considerably more robust than the Small Red Damselfly *Ceriagrion tenellum* (de Villers).

Pyrrhosoma nymphula interposita. The type locality is in Hungary and the type male is in Varga's collection.

Pyrrhosoma elisabethae (The Greek Red Damselfly). The type locality is in Greece and the type male is in Lund museum. It is endemic to Europe (Sahlén *et al.*, 2004). It has been recorded from only eight localities: four in northern Peloponnisos, three on the island of Kérkira (Corfu) and one in southern Albania (Kalkman & Lopau, 2006).

Pyrrhosoma tinctipennis. The type locality is in Szechuen, western China and the type is in the British Museum (Natural History). As far as is known it is confined to China.

Pyrrhosoma latiloba. The type locality is Zhongdian, Yunnan, China and the types are in the Institute of Entomology, College of Life Sciences, Nankai University, Tianjin, China (Yu *et al.*, 2008).

The Large Red Damselfly *Pyrrhosoma nymphula*

Description

Eggs

The eggs measure about 0.95 mm x 0.25 mm. They are cylindrical with a rounded base and a pointed anterior pole capped by a tanned pedicel. When they are first laid they are semi-transparent but become pale brown after a few days (Gardner & MacNeill, 1950) (Plate 1).

Plate 1. *P. nymphula* eggs in a stem of *Potamogeton natans*, magnified on the right to show the shape of the eggs (arrow) (Bennett & Mill unpublished).

Larvae

The larva is normally 19 – 22.5 mm long (15 mm – 17 mm excluding the lamellae). It is slightly squat in appearance and often sits with its caudal lamellae upturned (Gardner & MacNeill, 1950) (Plate 2). The lamellae are broad and taper abruptly at the tip and bear fine marginal setae in their apical half. Dark markings occur in the apical half and these may form a distinctive 'X-shaped' mark but they are very variable (Gardner & MacNeill, 1950; Cham, 2009). Two dark bands are present on the femora (Cham, 2009).

Plate 2. Larva of *P. nymphula*. Photograph by Peter Evennett.

Adults

Both sexes have red eyes and a broad red (yellow in young individuals and in one of the female morphs) ante-humeral stripe together with a broad lateral yellow stripe on each side of the thorax. The male has a largely red abdomen with clear black bands on segments 7-9 with red behind each black band (Plates 3, 4,). There are three colour forms of female, all of which have narrow yellow rings at the anterior end of abdominal segments 2-7. The most common one, f. *fulvipes*, is similar in colouration to the male but also has black bands at the posterior end of abdominal segments 5 and 6 and the black on segments 7 and 8 is more extensive than in the male (Plates 4-6). In f. *intermedia* (f. *typica*) the black band on abdominal segment 6 extends the length of the segment and there are black bands at the posterior end of the first five abdominal segments (Plates 7, 8). In f. *melanotum* the ante-humeral stripes are yellow and most of the dorsal surface of the abdomen is black; also the eyes are a duller red. In some specimens of this form the red on the abdomen is replaced by yellow (Plate 9, 10), although such individuals may not have achieved their final

Plate 3. Male *P. nymphula*. Photograph by Steve Cham.

colouration. The overall adult length is normally 33-36 mm with an abdomen of between 25 and 29 mm; the hind wing measures 19-24 mm in length (Sulzer, 1776; Brooks & Lewington, 2004; Dijkstra & Lewington, 2006).

Habitat

P. nymphula mostly breeds in still water – ponds, lakes, ditches and canals – but is also found in slow-flowing regions of streams and rivers. It is particularly

Plate 4. *P. nymphula* in tandem. The female is the *fulvipes* colour morph. Photograph by Peter Neal Taylor.

Plate 5. Young female *P.nymphula*. f. *fulvipes*. Photograph by Adolfo Cordero Rivera.

Plate 6. Mature female *P. nymphula* f. *fulvipes*. Photograph by David Kitching.

Plate 7. Young female *P.nymphula* f. *typica*. Photograph by David Kitching.

Plate 8. Mature female *P.nymphula* f. *typica*. Photograph by Adolfo Cordero Rivera.

Plate 9. Dorsal view of female *P. nymphula* f. *melanotum*. Photograph by Dave Smallshire.

Plate 10. Side view of female *P. nymphula* f. *melanotum*. Photograph by Dave Smallshire.

common in lowland areas but does extend to upland wetlands and has been recorded in swift moorland streams (Corbet, 1957). Indeed Corbet (1957) suggested that it probably has the widest ecological tolerance of any dragonfly in Britain. It seems to be tolerant of a wide range of pH and is less sensitive to eutrophication than are some species. The larvae tend to live at or near the bottom amongst weeds or debris.

Life Cycle

Eggs

The eggs are normally laid in the petioles of the Broad-leaved Pondweed *Potamogeton natans* (see 'Reproduction'). Gardner & MacNeill (1950) found that the eggs of individuals kept in captivity hatched after 18 days, whereas Corbet (1957) found that eggs kept in the shade at about 15°C began hatching after 32 days. However, Bennett & Mill (1995b), who took the stems of *P. natans* in which females had laid their eggs back to the laboratory, found that the batches of eggs varied in both the success rate of hatching and in the time they took to hatch, with an overall percentage hatching success of 75.10%±1.13% and with over 60% of the eggs hatching within 24-26 days after laying. Taking the figure of 1447 eggs laid by a female during her lifetime (see 'Reproduction') this gives an estimate of 1087.6 surviving to the second instar larval stage (Fig. 1).

Since oviposition occurs from the end of May through June (see 'Reproduction') and given the above hatching time of 24-26 days, hatching in the field should occur between about mid-June and the end of July. Indeed, Corbet (1957) found that hatching had started by mid-June but Lawton (1970b) first detected newly hatched larvae in his samples in the first half of July and Macan (1964) not until August.

Larvae

P. nymphula is normally a semivoltine species (taking two years to complete one generation) in those populations that have been studied in Britain, which range from 51° 25' N to 56° 44'N (Macan, 1964, 1974; Corbet, 1952, 1957; Lawton, 1970b; Corbet & Harvey, 1989, Bennett & Mill, 1993).

Macan (1974) found that passive dispersal by water currents of some of the newly hatched larvae away from the oviposition site (*Potamogeton natans*) occurred but that there was little movement of the older larvae, although he had noted earlier (Macan, 1964) that there was some movement into deeper water in the second summer. Conversely, Lawton (1970b) observed that the newly hatched larvae tended to remain close to the oviposition sites (*Potamogeton*)

throughout July and August at his site but showed movement away during September into a region of *Juncus* spp., where they overwintered. However, he confirmed that they did tend to remain in the same place throughout their second year. Thus, in this latter study there was almost complete spatial separation of the year classes, which may be important in preventing predation of smaller individuals by larger ones (Lawton, 1970b). A number of studies have found that the number of larvae caught by netting decreases in the winter (the so-called 'Winter Disappearance') before increasing again in the spring (Corbet, 1957; Lawton, 1970b; Bennett & Mill, 1993).

The larvae eat a variety of prey, their main food being chironomids and entomostracans but the larvae of the mayfly *Leptophlebia* spp. and planarians are also taken as well as possibly other *P. nymphula* larvae (Macan (1964, 1975, 1977). In an analysis of faeces from larvae in the 4th to last (12th) instars Lawton (1970a) found that chironomid larvae contributed 60-75% of the food energy consumed. In a laboratory experiment using *Daphnia* as prey, he found that assimilation efficiency decreased with increasing larval size from about 95% in instar 2 to about 86% in the final instar (Lawton, 1970a). The larvae do not demonstrate any metabolic acclimatisation, their respiratory rate increasing with increase in temperature (Q_{10} = 2.20 between 5°C and 10°C and 3.12 between 10°C and 16°C). Lawton (1971) calculated that 42-43% of larval energy consumption is used for growth and respiration. The respiratory rate decreases slightly as oxygen tension falls until the latter reaches 50%, below which it decreases markedly (Lawton, 1971).

Laboratory experiments have demonstrated that the larvae are territorial, defending feeding sites; also that larval size in the final instar is positively correlated with the amount of food provided during the last three or four larval instars (Harvey & Corbet, 1985). Dumont (1971) suggested that, in his study area in Eastern Flanders, Belgium, larvae of *P. nymphula* are out-competed by *Coenagrion pulchellum*, *Enallagma cyathigerum* and perhaps *Platycnemis pennipes* but that it co-occurs with both *Coenagrion puella* and *Ischnura elegans*. Conversely, Macan (1964) found that larvae of *P. nymphula* and *E. cyathigerum* can co-exist but, in his study, there was ecological separation of the larvae, with *P. nymphula* found in *Carex* and *E. cyathigerum* in *Myriophyllum*.

The major predators of the larvae are probably fish (see Macan, 1966, 1977). In the laboratory the larvae of the caddis *Phryganea* have been observed to eat *P. nymphula* larvae (Macan, 1975).

Including the brief prolarval stage there are 12 larval instars in *P. nymphula* (Gardner & MacNeill, 1950). In their first year the larvae reach the fifth or sixth instar before overwintering (Corbet, 1957). They generally reach the penultimate

(F-1) larval instar during their second summer and remain in that instar until late August, normally entering the final instar (F-0) between late September and early December (Corbet, 1957). Based on laboratory experiments, Corbet *et al.* (1989) suggested that larvae that reach F-1 before August enter into a 'long-day arrest', the long daylength at this time preventing progress to the final instar. Some larvae in F-1 may undergo a supernumary moult, remaining in F-1 but with larger wing-sheaths. The shortened day length in mid to late August allows a synchronised entry into F-0, the larvae then entering a period of diapause over the winter. Metamorphosis begins in most larvae before the end of March and they emerge in early summer (May – early July), i.e. a two year life cycle (Corbet, 1952, 1954, 1957; Macan, 1964; Lawton, 1970b; Corbet & Harvey, 1989). Because of the summer arrest in F-1 and the winter diapause in F-0 there is a fairly well-defined period of emergence the following spring, leading to the species being referred to as a 'Spring' species (Corbet, 1954).

In some years all larvae may follow the above pattern, entering their second winter in the final instar stage, but in others some may only reach F-1, although it is fairly unusual to have less than 90% in F-0. However, higher percentages of larvae only reaching the F-1 stage have been recorded by Corbet & Harvey (1989) and by Bennett & Mill (1993). Indeed, Corbet & Harvey (1989) found almost 100% overwintered as F-1 at their site in 1982/83, which they put down to the extremely cold winter the previous year delaying and retarding growth in the Spring of 1982. Those larvae that do enter their second winter in F-1 reach F-0 the following May and emerge somewhat later than those that overwintered as F-0 (Corbet & Harvey, 1989); such individuals are smaller both as F-0 larvae and as adults than those overwintering as F-0.

However, Macan (1964, 1974) noted that, when there are exceptionally large numbers of young larvae, some take three years to complete development, not having reached the F-1 instar by the start of their second winter, possibly because of intra-specific competition for food. Furthermore, Macan (1977) has suggested that such larvae are probably present in most years. Macan (1977) noted that the numbers emerging are only slightly affected by predation and has proposed how this may come about (Macan. 1966, 1974, 1977). Thus there may be insufficient good feeding territories for all larvae, particularly in years of high larval abundance. Those larvae that occupy such sites where food frequently comes within reach will grow rapidly but larvae in sub-optimal sites, where food is scarce, will grow more slowly; indeed the latter may well die unless better feeding sites become available. Availability of good sites is much more likely when fish such as the Brown Trout *Salmo trutta* are present and predate the larger larvae. The smaller larvae can then move into good feeding territories and thus act as a reservoir from which the loss of the large larvae can be made good. Thus there may be a self-regulating mechanism at work that

allows for a high predation level of large larvae without a major reduction in the number of those reaching maturity and emerging (Macan, 1977).

Univoltinism (one year life cycle) in the north of England is unlikely to occur. Hatching needs to be fairly early in the year for the larvae to have sufficient time to reach at least the F-1 instar by the onset of their first winter. It is possible that it may occur further south in their range and indeed Corbet (1957), working at a site in southern England, reported a hatching date of mid-June or earlier and considered it a possibility for some individuals at this site. Also Macan (1974) noted that some individuals may complete their development in one year at his site in the English Lake District.

Lawton (1970b) calculated the number of larvae per square metre, from which he deduced that mortality rates were constant for a given year class, although differing markedly between different year classes, with annual mortality being 99.5% in his 1965 year class, 78% in the 1966 year class and probably somewhat lower still in the 1967 one; the mortality rate being higher when the initial larval density was higher. However, his calculations were based on early October 1966 samples for the first two year classes and hence he had to extrapolate back to estimate hatching numbers. Only the 1966 year class included data from two years and, using his calculated figure for that year class, i.e. 340 larvae m^{-2}

Table 1. First and last observations of emergence in *Pyrrhosoma nymphula*. * end dates of studies rather than the end of emergence.

Year	First observed	Last observed	Grid Reference	Latitude (N)	Author(s)
1951	20 May	28 May*	SU651661	51° 25.0'	Corbet (1952;1957a)
1956	18 May	20 June	SD369982	54° 22.6'	Macan (1964)
1957	9 May	3 July	SD369982	54° 22.6'	Macan (1964)
1967	26 May	14 June	NZ291451	54° 43.5'	Lawton (1970b)
1968	16 May	16 June	NZ291451	54° 43.5'	Lawton (1970b)
1981	13 May	-	NO375606	56° 44.0'	Corbet & Harvey (1989)
1982	18 May	-	NO375606	56° 44.0'	Corbet & Harvey (1989)
1983	7 June	27 June	NO375606	56° 44.0'	Corbet & Harvey (1989)
1984	14 May	24 June	SE655373	53° 49.5'	Bennett & Mill (1993)
1985	16 May	3 June	SE655373	53° 49.5'	Bennett & Mill (1993)
1986	18 May	17 June	SE655373	53° 49.5'	Bennett & Mill (1993)
1987	7 May	1 June*	SE655373	53° 49.5'	McLoughlin (in Bennett & Mill (1993)
1987	13 May	27 June	SJ665915	53° 21.0'	Gribbin & Thompson (1991b)

shortly after hatching in 1966, and the number he found emerging (14.5 m^{-2}) in 1968, gives an overall survival rate of 4.26%, compared with 4.84% derived from the annual mortality rate of 78%.

Bennett & Mill (1993) suggested that early instars have a higher mortality rate than later ones; this seems more logical as their small size would make them vulnerable to a wider range of predators, including larger individuals of the same species. They (Bennett & Mill, unpublished observations) estimated that the density of second instar larvae at their study site in 1985 was 251.5 m^{-2} (see Reproduction). This year class would largely emerge as adults in 1987 and, in a study in that year at the same site, McLoughlin (pers. comm.) estimated that 335 larvae emerged or attempted to emerge, i.e. a density of 5.58 m^{-2}, giving the overall larval survival rate over the normal two years of larval life as 2.22% (a mortality rate of 97.78%) (Fig. 1).

Emergence

Larvae entering the final instar in their second winter show a synchronised emergence the following spring (above) and the main emergence period of this 'Spring' species is from mid-May to mid-June (Table 1), with some individuals emerging both before and after this period. The start of emergence varies from year to year with the earlier the water temperature reaches 10° – 12°C, the earlier the start of emergence (Macan & Maudsley, 1966; Macan 1974). In their study (from 1958 to 1964) this temperature rise always occurred in April. The peak of emergence tends to be towards the end of May (Macan, 1964; Bennett & Mill, 1993). Corbet (1952) noted that emergence at his site started at about 07.30 GMT, with the peak usually occurring between 08.00 and 09.00 GMT. However, if the weather is unfavourable at the peak emergence time, emergence is postponed to the next day (Corbet, 1952). Larvae that only reach the F-1 stage for overwintering show a later, small peak in emergence (Corbet, 1952; Bennett & Mill, 1993).

Records of the height at which emergence occurs vary considerably. Thus Corbet (1952) noted that most emergences took place about 1.25 cm above water level. Bennett & Mill (1993) found that 85-90% of emergences took place on their artificial emergence sites (fine netting), generally several centimetres above the water level but, in 1984 when the larval population density was quite high, several individuals were found to have emerged considerably higher – on tree trunks up to about 1.5 m above the water level (unpub. observations). It takes one or two hours for an individual to complete its emergence after the thoracic cuticle splits (Corbet, 1952).

Emergence is a relatively vulnerable time for any odonate. However, Bennett

& Mill (1993) and McLoughlin (pers. comm.) found that, over a four-year period (1984-1987) at Skipwith (North Yorkshire), the average mortality rate was only 3.75% with a minimum of 3.0% in 1984 and a maximum of 5.2% in 1986. The major causes were incomplete ecdysis or incomplete wing expansion, little predation being observed. In contrast, the site studied by Gribbin & Thompson (1990a) exhibited a loss of 27.9% at this stage, with 21.8% being accounted for by predators (ants, spiders and birds) and 6.2% by climatic factors, with mortality due to the latter being directly related to rainfall. In this last study at least 9.7% of the mortality was attributed to birds and ants, neither of which were

Table 2. Proportion of males at emergence in *Pyrrhosoma nymphula*. NS, not significant; *, based on only 9 days during peak of emergence; **, calculated from Lawton (1972).

%males	n	Significance	Author(s)
54.6	1014	P<0.01	Gribbin & Thompson (1991)
53.1	1099	P<0.05	Gribbin & Thompson (1991)
51.6	1426	NS	Bennett & Mill (1973)
50.9	283	NS	Bennett & Mill (1973)
49.6	272	NS	Bennett & Mill (1973)
51.9	549	NS	Mclaughlin (pers. comm.)
63.0*		P<0.02	Corbet (1952)
50.3**	149	NS	Lawton (1972)
50.7**	138	NS	Lawton (1972)
51.5**	383	NS	Lawton (1972)

noted to take emerging larvae at Skipwith (Bennett & Mill, 1993). Corbet (1952) recorded an incident in which a larva that had emerged from the water flicked its lamellae forwards, causing a spider to retreat. Larvae that have reached a possible emergence site have been observed to move their abdomen from side to side, possibly testing their grip on the support and/or making sure there is sufficient space for them to expand their wings (Corbet, 1952. However, over a short period (5-8 May) in 1995, Treacher (1996) noted that of 23 larvae that used leaves of the Yellow Flag *Iris pseudacorus* as emergence supports, 19 fell off and died at various stages of emergence, i.e. a mortality rate of 84%. This appeared to be due to the inability of the larvae to obtain a secure grip. Of the four that survived, two emerged on narrow leaves where a better grip could be obtained.   No evidence has been found for density-dependent mortality at emergence (Gribbin & Thompson, 1990a; Bennett & Mill. 1993). Daily percentage mortality is negatively correlated with the number emerging (Gribbin

& Thompson, 1990a) and the numbers emerging are directly correlated with atmospheric pressure (Gribbin & Thompson, 1990a).

Gribbin & Thompson (1991b) studied two ponds and found that emergence was earlier in one of them. In this pond the larval density was higher, the emerging adults were larger, the pond was somewhat deeper and the maximum daily temperature 10cm below the surface was usually higher.

Corbet (1952) and Gribbin & Thompson (1991b) found that significantly more males emerged than females, whereas Bennett & Mill (1993) did not observe any significant difference. Lawton (1972) mentioned a small but just significantly higher number of male larvae and exuviae (52%). However, separation of his data into larvae and exuviae revealed no significant difference in either group (Bennett & Mill, 1993) (Table 2). The value of 63% males recorded by Corbet (1952) may be an overestimate as the recording period was only nine days and Gribbin & Thompson (1991b) had shown that, in the two ponds they were studying, males emerged before females; significantly so at one pond.

Adults

Corbet & Harvey (1989) found that the size of newly emerged adults in the smaller, second period of emergence was smaller than those in the first, while Gribbin & Thompson (1991b) found a decrease in adult size over the emergence period. The size of one day old adults is correlated with larval size, which presumably means that larger adults result from larvae that are effective in defending their feeding sites (Harvey & Corbet, 1985).

Figures for survival of adults during the pre-maturation period are difficult to obtain as the adults leave water at this stage and hence are less easy to monitor. However, the indication is that the survival rate during this period is at least as good as that of mature individuals (Bennett & Mill, 1995a). Corbet (1952) estimated that individuals returned to water about 15 days after emerging, during which time they were maturing. Females have been shown to take longer (mean 18.6 days) than males (mean 12.6 days) to mature (Bennett & Mill, 1995a). However, these figures are based on the first recorded visit back to water. Since some individuals may not have been seen on their first visit, these figures are almost certainly overestimates and this would apply particularly to females because they spend longer away from water between visits (Bennett & Mill, 1995a), hence a figure of 15 days for females may be more accurate. Furthermore, individuals are rarely seen flying when the sun is not shining (Macan, 1964).

An average daily survival rate of 0.85 based on the whole flying season was

estimated by Corbet (1952), falling from more than 0.9 at the start of the season to below 0.85 at the end.   However, Bennett & Mill (1995a) found survival to be independent of age, with a daily survival rate of 0.886 for males and 0.894 for females, a difference that was not significant (P>0.05).   The mean lifespan of mature individuals, i.e. for those that survive the maturation period, was found by Bennett & Mill (1995a) to be 6.8 days for males and 6.6 days for females which agrees with the overall estimate of 6.67 days estimated by Corbet (1952). These figures give overall adult lifespans of 19.4 days (12.6 pre-reproductive + 6.8 reproductive) for males and 21.6 days (15 pre-reproductive + 6.6 reproductive) for females (Bennett & Mill, 1995a), again in close agreement with Corbet's estimate of 21.7 days. Corbet (1952) recorded a maximum adult lifespan of 46 days.

Reproduction

The main flying season for mature adults is in June, although individuals are still around in July (Corbet, 1952). Adults are territorial, particularly in areas where the population density is low. The male defends a perch from where he approaches potential mates as well as tandem pairs and patrolling males (Gribbin & Thompson, 1991a). Gribbin & Thompson (1991a) recorded that resident males won 97.5% (117 out of 120) disputes in spite of the resident male being the smaller in 56 of the encounters, size thus apparently having no effect on mating success. Sperm transfer by the male to its accessory genitalia takes place during the tandem phase (Williamson & Calvert, 1906).   When undisturbed, copulation has been observed to last up to 15 minutes (Robert, 1958).

Table 3. Oviposition details for *Pyrrhosoma nymphula*.

Average egg deposition rate (eggs/min)	Duration of oviposition		Clutch size	Clutches/lifetime	Reference
	At a single site (min)	To lay one clutch (min)			
			350.6		Gribbin & Thompson (1990b)
5.56	9.90±6.56				Martens (1993)
10.76		22.81±1.77	245	5.91	Bennett & Mill (1995)

In a number of studies the main oviposition sites were noted as being in Broad-leaved Pondweed *Potamogeton natans* (Macan, 1964, 1974; Lawton, 1970b; Martens, 1993; Bennett & Mill, 1995b) but oviposition has also been observed in other aquatic plants such as Bog Pondweed *P. polygonifolius* (Gardner & MacNeill, 1950), Bogbean *Menyanthes trifoliata* (Starmore, 2008), *Sphagnum* (T. Beynon, pers. comm.), Brooklime *Veroniuca beccabunga* (T. Taylor pers. comm.) and occasionally into rush *Juncus* sp. stems that have been bent over into the water (T. Beynon, pers. comm.) or even floating rush and reed debris (K. Heath, pers. comm.). Typical of coenagrionids in general, the male mate-guards the female during oviposition. The male assumes a vertical posture (the sentinel position) and retains his hold on the female while she lowers her abdomen into the water and inserts eggs into a stem of *P. natans* or *M. trifoliata*. In *P. natans* the majority of eggs are laid in the petiole or leaf base but some are laid in the underside of the leaf (Martens, 1993). The female steadily submerges her abdomen but usually no further than the point where her wings touch the water surface (Macan, 1964). However, cases of complete submergence by the female have been reported (Starmore, 2008; Cham, in Starmore, 2008) and of complete submergence by the male also (Sherwin, 2009).

At a site in northern Germany, Martens (1993) calculated that females of *P. nymphula* oviposit at a rate of 5.56±1.74(s.d.) eggs/minute, whereas, at a site in Yorkshire (Skipwith Common), Bennett & Mill (1995b) found that they laid eggs at a mean rate of 10.76±0.40 eggs/minute (Table 3). In both cases the females were ovipositing in species of *Potamogeton* and, although Martens (1993) found that there was some increase in the rate of egg laying with increase in water temperature, the two studies were conducted at comparable water temperatures. The difference could possibly be due to behavioural differences between the two populations.

Martens (1993) recorded that contact of the female's abdomen with a leaf of *P. natans* lasted between 3s and 26.22 min for any one visit and that it was unusual for any eggs to be laid during visits lasting under 1 min. He found that the average duration of an undisturbed single bout of oviposition lasted 9.90±6.56(s.d.) minutes with the female laying an average of 57.7±43.4 (s.d.) eggs. However, more than one bout normally occurs for a female to lay her whole clutch and Bennett & Mill (1995b) recorded that females spent on average 22.81±1.77 minutes overall ovipositing with an average clutch size of 245 eggs (based on an oviposition rate of 10.76 eggs/minute), and estimated that the average number of clutches laid by a female was 5.91. This gives a total of 1447 eggs laid during her lifetime. In this study, the weather was good and oviposition was observed on all days. However, in breeding seasons with poor weather, overall egg production may be much lower (Bennett & Mill, 1975b). A higher mean clutch size of 350.6±14.5(s.e.) eggs was reported by Gribbin
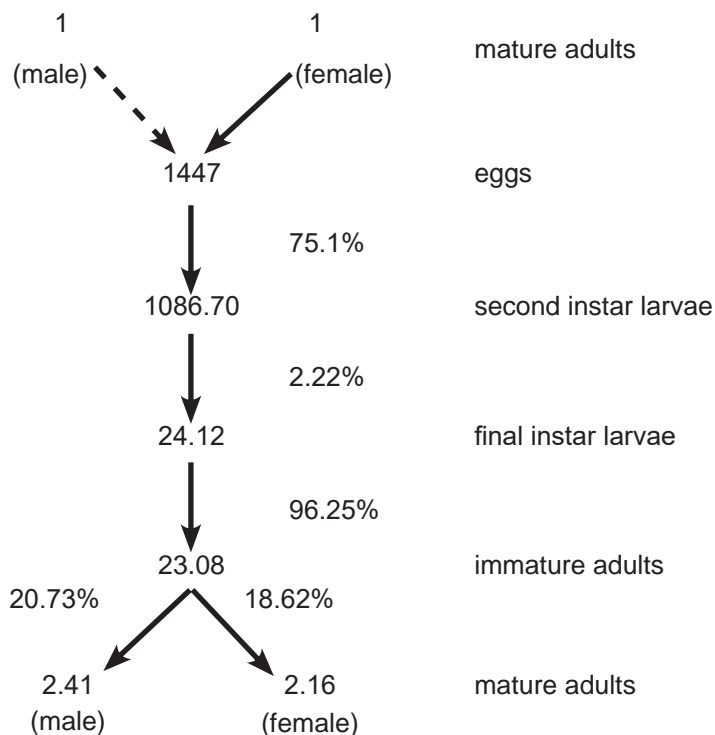
Figure 1. Life cycle of *Pyrrhosoma nymphula*. Percentages indicate estimated survival rate at each stage. Based on the data of Bennett & Mill (1993; 1995a,b; unpublished observations) and McLoughlin (pers. comm.)

& Thompson (1990b), based on dissection of females, who noted that clutch size decreased over the season. The two different mean clutch sizes recorded may have been because all eggs are not laid during a single visit to water. However, it could also result from a difference in inter-clutch intervals resulting from weather conditions (Bennett & Mill, 1995b). Females ovipositing early in the year lay larger clutches of larger eggs than those that oviposit later in the season, irrespective of body size (Gribbin & Thompson, 1990b)

When frog predators are absent, the number of tandem pairs ovipositing increases with both the size of the site and with the number of tandem pairs that are already there (Rehfeldt, 1990) and indeed Martens (1993) demonstrated that conspecific pairs are attracted to a motionless male fixed in the sentinel position to a *P. natans* leaf and then start to oviposit. Pairs often oviposit in groups (T. Beynon, pers. comm.) and it has been shown that they prefer to

oviposit close to already ovipositing pairs but do not stay as long as those pairs that are ovipositing on their own (Rehfeldt, 1990). In the presence of frogs, fewer tandem pairs land to oviposit. Groups of ovipositing pairs do not affect the predation success of the frogs (Rehfeldt, 1990).

Bennett & Mill (unpublished observations) estimated that 82 clutches of eggs were laid in 1985 in their site of 60 m^{-2}. Since each clutch is on average 245 eggs, this gives 334.8 eggs m^{-2}. At 75.1% hatching success this leads to 251.5 second instar larvae m^{-2} (Fig. 1).

Summary

Using the figures determined by Bennett & Mill (1993; 1995a,b) and by McLoughlin (pers comm.), from one female laying 1447 eggs 2.16 females survive to maturity, thereby rather more than doubling the size of the population in one generation (116% increase) (Fig. 1). However, cataclysmic events may drastically reduce population size, such as the drought in the summer of 1984 at Skipwith Common, where Bennett & Mill (1993) carried out their study. Also, predation at emergence, for example, will vary from site to site. Thus, taking the emergence mortality rate of 27.9% given in the study by Gribbin & Thompson (1990a) and applying it to the other survival rates shown in Fig. 1, results in only 1.62 females surviving to maturity (but still a 62% increase in population size).

Dispersal

Little is known about the ability of *P. nymphula* to disperse. In a linear habitat (a ditch) Bennett & Mill (1995a) recorded that females were significantly more mobile than males (P<005) with a higher proportion of males returning to approximately the same part of the ditch on consecutive days (54.7% of males and 38.0% of females returning to within 19 m), even though the maximum distance moved by the sexes (207 m for a male and 192 m for a female) on consecutive days was similar.

Parasites

Individuals of *P. nymphula* have few larval mites present during their maiden flights but become more infested when they return to the water for reproduction (Åbro, 1982), the load increasing during the damselfly's reproductive phase (Åbro, 1990). In contrast, Corbet recorded mature adults with the larval stage of the mite *A. cuspidifer* attached and noted that the mites drop off within two days of the mature adult damselfly returning to water (in Corbet & Harvey, 1989).

Åbro (1990) noted two different colours of mites, olive-green and bright red, the

latter being attached to the soft cuticle in the deep pleural folds of the abdomen. The mites *Arrenurus bruzelli* and *A. bicuspidator* have been found on the thorax of adult *P. nymphula* from sites near Szczecin, Poland (Baker *et al.*, 2007).

Conservation

Pyrrhosoma nymphula is not an endangered species and indeed is common throughout most/all of its range.

The Greek Red Damselfly *Pyrrhosoma elisabethae*

Description

Adult

The adults are very similar to those of *P. nymphula* (Plates 11, 12). Although there is a tendency for the thorax to be fairly uniformly dark in *P. elisabethae*, colour is not reliable for separating the species. The overlap of colour markings between *P. elisabethae* and *P. nymphula* probably explains why the former was thought for some time to be a subspecies of *P. nymphula* (Buchholz, 1954; Stark, 1979; Ottolenghi, 1991). However, Kalkman & Lopau (2006) have described morphological differences.   Thus, in the male of *P. elisabethae* the inferior (lower) appendages are slightly longer than the superior appendages, whereas in *P. nymphula* these appendages are of similar length. Furthermore, the hook-shaped ventral branch of the superior (upper) appendages of *P. elisabethae* is only about one third the length of the appendages compared to two thirds the length in *P. nymphula* (Fig. 2). In females there is a deep, raised fold on each side of the posterior margin of the pronotum in *P. elisabethae*; in *P. nymphula* they are only slight pleats (Fig. 3) (Kalkman & Lopau, 2006). The overall length of the adult is 36-38 mm with an abdomen of between 28 and 30 mm and a hind

Plate 11. Male *P. elizabethae*. Photograph by Jean-Pierre Boudot.

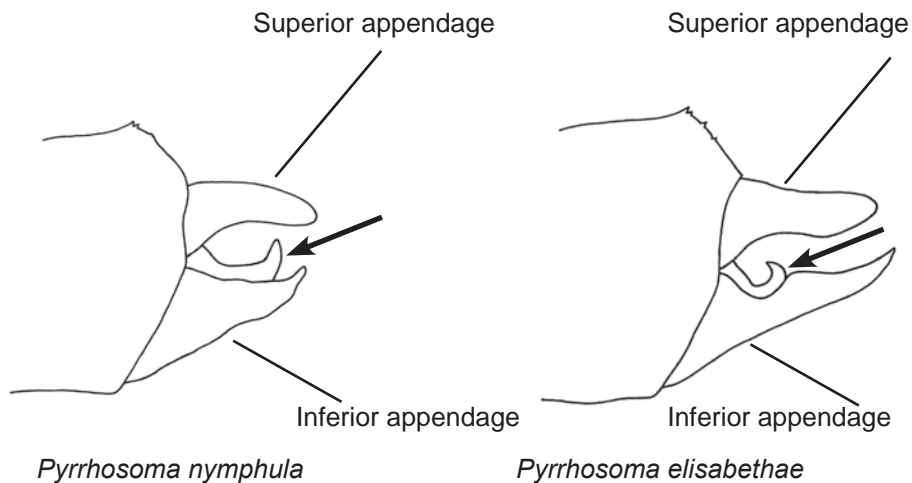**Plate 12**. *P. elisabethae* in tandem. Photograph by Jean-Pierre Boudot.

Superior appendage

Superior appendage

Inferior appendage

Inferior appendage

Pyrrhosoma nymphula

Pyrrhosoma elisabethae

Figure 2. Male appendages. ➤ ventral branch of superior appendage. From Kalkman & Lopau (2004).

Pronotum

Pronotum

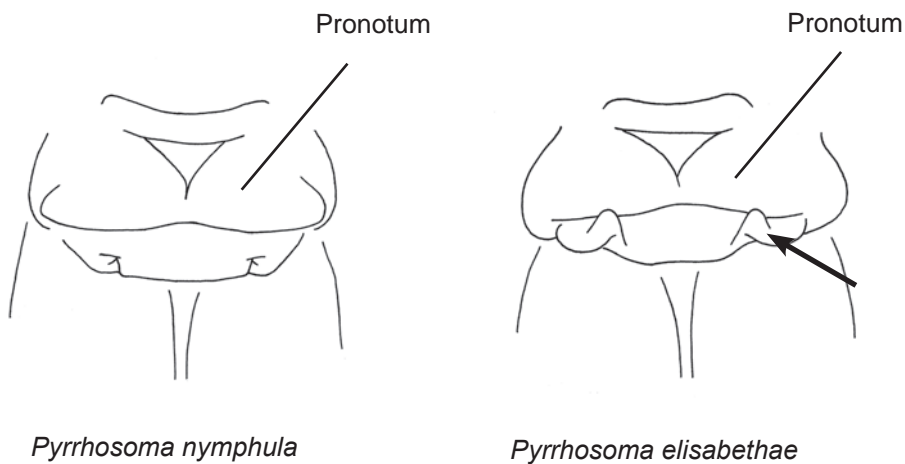*Pyrrhosoma nymphula*

Pyrrhosoma elisabethae

Figure 3. Female pronotum. ➤ fold at rear of pronotum in *P. elisabethae*. From Kalkman & Lopau (2004).

wing length of 20-24 mm (Dijkstra & Lewington, 2006).

Apart from the typical female form, only a black form, f. *melanotum*, has been found so far (Dijkstra & Lewington, 2006).

Behaviour

Oviposition has been observed in grasses, sedges and plantain, either just above or below the water surface (Kalkman & Lopau, 2006). It has been suggested that its flying season is similar to that of *P. nymphula* (Kalkman & Lopau, 2006).

Habitat

It has only been found so far in running water including ditches, brooklets and a slow-flowing river (Kalkman & Lopau, 2006).

Conservation

The populations appear to be declining in numbers. In northern Greece (Peloponnisos) it is reliant on small brooks for breeding and these are under threat: indeed W. Lopau visited one of the sites in Peloponnis in 1998, where the species had been seen the previous year, only to find that the brook had been cleared of vegetation and the species was not seen. In 2004, although the brook now had vegetation, a further visit by W. Lopau still failed to reveal the species (Kalkman & Lopau, 2006). More detailed surveys of its distribution and the habitat quality are needed. If none of the populations are in protected areas, it is important to redress this or at least obtain legal protection for the species. The species is listed as 'vulnerable' (IUCN, 2009) and a conservation action plan for the brook habitats of the Peloponnisos has been recommended (Arkive, 2006).

Conclusions

It is clear that, even for one of our commoner species of dragonfly (*P. nymphula*), there is still much to learn. Many of the details are based on only one or two studies and often there are differences in the details resulting from different studies. Furthermore, there is a marked lack of information on *P. elisabethae*. Below are just a few of the areas where further study would be helpful:

P. nymphula
- How prevalent is the colour polymorphism? Are all three female colour varieties present throughout the range or are there perhaps differences

between north and south? At what stage do the antehumeral stripes change from yellow to red?

- What is the range of plants in which the female oviposits?
- Does the rate of egg- laying vary in different parts of its range?
- At what height does the final moult take place and what influences the height?
- How good is *P. nymphula* at dispersing?

P. elisabethae

- How widespread is it? Anyone visiting Albania or Greece could provide useful information on this.
- What is the preferred habitat?
- How many female colour morphs are there?
- What is the larva like and how does it differ from the larva of *P. nymphula*?
- Any information on its life cycle and behaviour would be useful

Acknowledgement

References

Åbro, A.1982. The effects of parasitic water mite larvae (*Arrenurus* spp.) on zygopteran imagoes (Odonata). *Journal of Invertebrate Pathology* **39:** 373-381.

Åbro, A. 1990.The impact of parasites in adult populations of Zygoptera. *Odonatologica* **19:** 223-233.

Askew, R. R. 1988. *The Dragonflies of Europe*. Harley Books, Colchester. 291pp.

Baker, R.A., Mill, P.J. & Zawal, A. 2007. Mites on Zygoptera, with particular reference to *Arrenhurus* species, selection sites and host preferences. *Odonatologica* **36:** 339-347.

Bennett, S. & Mill, P. J. 1993. Larval development and emergence in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica* **22:** 133-145.

Bennett, S. & Mill, P. J. 1995a. Pre- and post-maturation survival in adults of the damselfly *Pyrrhosoma nymphula* (Zygoptera: Coenagrionidae). *Journal of Zoology* **235:** 559-575.

Bennett, S. & Mill, P. J. 1995b. Lifetime egg production and egg mortality in the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Hydrobiologia* **310:** 71-78.

Buchholtz, K. F. 1954. Zur Kenntnis der Odonaten Griechenlands. *Bonner Zoologische Beiträge* **Sonderband 1954:** 51-71.

Brooks, S. & Lewington, R. 2004. *Field Guide to the Dragonflies and Damselflies of Great Britain and Ireland.* 4th ed. British Wildlife Publishing, Hook, Hampshire. 160 pp.

Cham, S. 2009. *Field Guide to the Larvae and Exuviae of British Dragonflies. Volume 2: Damselflies (Zygoptera).* The British Dragonfly Society, Peterborough. 75pp.

Corbet, P. S. 1952. An adult population study of *Pyrrhosoma nymphula* (Sulzer) (Odonata: Coenagrioniidae). *Journal of Animal Ecology* **21:** 206-222.

Corbet, P. S. 1954. Seasonal regulation in British dragonflies. *Nature, London* **174:** 655 [erratum 777].

Corbet, P. S. 1957. The life-histories of two spring species of dragonfly (Odonata: Zygoptera). *Entomologist's Gazette* **8:** 79-89.

Corbet, P. S. & Harvey, I. F. 1989. Seasonal regulation in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). 1. Seasonal development in nature. *Odonatologica* **18:** 133-145.

Corbet, P. S., Harvey, I. F., Abisgold, J. & Morris, F. 1989. Seasonal regulation in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). 2. Effect of photoperiod on larval development in spring and summer. *Odonatologica* **18:** 333-348.

Davis, D. A. L. & Tobin, P. 1984. The Dragonflies of the World: A systematic list of the extant species of Odonata. Vol. 1 Zygoptera, Anisozygoptera. *Societas Internationalis Odonatologica Rapid Communications (Supplements)* No. 3. 127pp.

Dijkstra, K-D, B. & Lewington, R. 2006. *Field Guide to the Dragonflies of Britain and Europe.* British Wildlife Publishing, Gillingham, Dorset. 320 pp.

Dumont, H. J. 1971. A contribution to the ecology of some Odonata. The Odonata of a "trap" area around Denderleeuw (eastern Flanders: Belgium). Bulletin et Annales de la Société Royale Entomologique de Belgique **107:** 211-235.

Dumont, H. J., Vierstraete, A. & Vanfleteren, J. R. 2010. A molecular phylogeny of the Odonata (Insecta). *Systematic Entomology* **35:** 6-18.

Gardner, A. E. & MacNeill, N. 1950. The life history of *Pyrrhosoma nymphula* (Sulzer) (Odonata). Part I Life History (Gardner); Part II Final instar nymph and ecological notes (MacNeill). *Entomologists Gazette* **1:** 163-182.

Gribbin, S. D. & Thompson, D. J. 1990a. A quantitative study of mortality at emergence in the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Freshwater Biology* **24:** 295-302.

Gribbin, S. D. & Thompson, D. J. 1990b. Egg size and clutch size in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica* **19:** 347-357.

Gribbin, S. D. & Thompson, D. J. 1991a. The effects of size and residency on territorial disputes and short-term mating success in the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Animal Behaviour* **41:** 689-695.

Gribbin, S. D. & Thompson, D. J. 1991b. Emergence of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae) from two adjacent ponds in northern England. *Hydrobiologia* **209:** 123-131.

Harvey, I. F. & Corbet, P. S. 1985. Territorial behaviour of larvae enhances mating success of male dragonflies. *Animal Behaviour* **33:** 561-565.

Kalkman, V. J. & Lopau, W. 2006. Identification of *Pyrrhosoma elizabethae* with notes on its distribution and habitat (Odonata: Coenagrionidae). *International Journal of Odonatology* **9:** 175-184.

Lawton, J. H. 1970a. Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata: Zygoptera). *Journal of Animal Ecology* **39:** 669-689.

Lawton, J. H. 1970b. A population study on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). *Hydrobiologia* **36:** 33-52.

Lawton, J. H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). *Journal of Animal Ecology* **40:** 385-423.

Lawton, J. H. 1972. Sex ratios in Odonata larvae, with particular reference to the Zygoptera. *Odonatologica* **1:** 209-219.

Macan, T. T. 1964. The Odonata of a moorland fishpond. *Internationale Revue der gesamten Hydrobiologie* **49:** 325-360.

Macan, T. T. 1966. Predation by *Salmo trutta* in a moorland fishpond. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **16:** 1081-1087.

Macan, T. T. 1974. Twenty generations of *Pyrrhosoma nymphula* (Sulzer) and *Enallagma cyathigerum* (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica* **3:** 107-119.

Macan, T. T. 1975. VIII. Fishponds: Structure of the community in the vegetation of a moorland fishpond. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **19:** 2298-2304

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. *Biological Reviews of the Cambridge Philosophical Society* **52:** 45-70.

Macan, T.T. & Maudsley, R. 1966. The temperature of a moorland fishpond. *Hydrobiologia* **27:** 1-22.

Martens, A. 1993. Influence of conspecifics and plant structures on oviposition site selection in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica* **22:** 487-494.

McLachlan, R. 1894. XLVI. - On two small collections of Neuroptera from Tachienlu,in the province of Szechuen, western China, on the frontier of Thibet. Annals and Magazine of Natural History series 6 **13:** 421-436.

Ottolenghi, C. 1991. Contriubuto alla conoscenza degli odonati di Grecia. *Bollettino del Museo Civico di Storia Naturale Verona* **15 (1998):** 231-242.

Rehfeldt, G. E. 1990. Anti-predator strategies in oviposition site selection of *Pyrrhosoma nymphula* (Zygoptera: Odonata) *Oecologia* **85:** 233-237

Robert, P.-A. 1958. Les Libellules (Odonates) Neuchâtel, Delachaux et Niestle. 364pp.

Sahlén, G., Bernard, R., Rivera, A. C., Ketelaar, R. & Suhling, F. 2004. Critical species of Odonata in Europe. In: *Guardians of the watershed. Global status of dragonflies: critical species, threat and conservation*. (Eds Clausnitzer, V. & Jödicke, R.) *International Journal of Odonatology* **7:** 385-398.

Schmidt, E. 1948. *Pyrrhosoma elisabethae* n. sp. eine neue Odonatenart aus Griechenland. *Opuscula Entomologica Lund* **13:** 69-74.

Sherwin, G. 2009. Submergence of both sexes during oviposition in the Large Red Damselfly *Pyrrhosoma nymphula* (Sulzer) in Norfolk. *Journal of the British Dragonfly*

Society **25:** 62-67.

Stark, W. 1979. Mischformen von *Pyrrhosoma n. nymphula* (Sullzer, 1776) und *P. n. elisabethae* Schmidt, 1948 aus der Steiermark, Oesterreich (Zygoptera: Coenagrionidae). *Notulae Odonatologicae* **1:** 61-62.

Starmore, A. 2008. Submerged oviposition behaviour in the Large Red Damselfly *Pyrrhosoma nymphula* (Sulzer) on the Isle of Lewis. *Journal of the British Dragonfly Society* **24:** 45-50.

Sulzer, J. H. 1776. *Abgekiirze Geschichte der Insekten nach dem Linneischen System* 24

Treacher, P. 1996. Mortality of emerging *Pyrrhosoma nymphula* (Sulzer) at a garden pond. *Journal of the British Dragonfly Society* **12:** 61-62.

Varga, Z. 1968. Eine neue Unterart von *Pyrrhosoma nymphula* Sulz. aus Südost-Europa. *Acta Biologica Debrecina* **6:** 187-204. [In Hungarian; German summary].

Williamson, E. B. & Calvert, P. P. 1906. Copulation of Odonata. Part I. *Entomological News* **17:** 143-148.

Yu, X., Yang, G.-H. & Bu, W.-J. 2008. A study of the genus *Pyrrhosoma* from China with description of a new species (Odonata, Coenagrionidae). [In Chinese with English summary] *Acta Zootaxonomica Sinica* **33:** 358-362

Web Sites

Arkive 2006. Information validated by Boudot, J-P.
http://www.arkive.org/greek-red-damsel/pyrrhosoma-elisabethae/

IUCN 2009 *IUCN Red List of Threatened Species. Version 2009.2.* Assessed 2006 by V.J. Kalkman; evaluated by V. Clausnitzer & F. Suhling (Odonata Red List Authority). http://www.iucnredlist.org